M. IRFAQ [1], MIR AJAB [2],
MA HONGXIANG [3], GSS KHATTAK [1]

[1] Crop Breeding Division, Nuclear Institute for Food and Agriculture (NIFA), Peshawar, N.W.F.P., Pakistan
[2] Faculty of Plant Science, Department of Biological Sciences, Quaid-i-Azam University, Islamabad, Pakistan
[3] Institute of Biotechnology, Jiangsu Academy of Agricultural Sciences, Nanjing, Jiangsu, P.R. China

ASSESSMENT OF GENES CONTROLLING AREA UNDER DISEASE PROGRESS CURVE (AUDPC) FOR STRIPE RUST (*P. STRIIFORMIS* F. SP. *TRITICI*) IN TWO WHEAT (*TRITICUM AESTIVUM* L.) CROSSES

Genetic effects on controlling stripe rust resistance were determined in two wheat crosses, Bakhtawar-92 × Frontana (cross 1) and Inqilab-91 × Fakhre Sarhad (cross 2) using Area under Disease Progress Curve (AUDPC) as a measure of stripe rust resistance. The resistant and susceptible genotypes for crosses were identified by initial assessment of 45 wheat accessions for stripe rust resistance. Mixed inheritance model was applied to the data analysis of six basic populations P_1, F_1, P_2, B_1, B_2, and F_2 in the crosses. The results indicated that AUDPC in cross 1 was controlled by two major genes with additive-dominance epistatic effect plus polygenes with additive-dominance epistatic effects (model E). Whereas in case of cross 2, it was under the control of two major genes with additive-dominance epistatic effect plus additive-dominant polygenes (model E-1). Additive effect was predominant then all other types of genetic effects suggesting the delay in selection for resistance till maximum positive genes are accumulated in the individuals of subsequent generations. Occurrence of transgressive segregants for susceptibility and resistance indicated the presence of resistance as well as some negative genes for resistance in the parents. The major gene heritability was higher than the polygene heritability in B_1, B_2 and F_2 for the crosses. The major gene as well as the polygene heritability was ranging from 48.99 to 87.12 % and 2.26 and 36.80 % for the two crosses respectively. The highest phenotypic variations in AUDPC (2504.10 to 5833.14) for segregating progenies (BC_1, BC_2 and F_2) represent that the character was highly influenced by the environment.

Introduction. Stripe (yellow) rust caused by a fungus *Puccinia striiformis* f. sp. *tritici,* is a major disease of wheat word wide especially in moist and cool environments [1]. The disease appeared in epidemic form in Pakistan during the year 2004–2005 because of the environmental conditions made highly conducive through tsunami effect. Grain yield losses from 20 to 60 % in susceptible wheat cultivars have been reported in case of severe out break of the disease during ear emergence [2]. Cultivation of genetically resistant cultivars is the effective measure to control the disease. Race specific or vertical resistance has remained no longer effective because of the evolution and population diversity of new virulent pathotypes [3]. Durable resistance controlled by the combined effect of both major and minor genes is desired to control the disease for longer time in an environment conducive for the disease development. This requires the availability of well known resistant genetic resources, a better understanding of the host-pathogen interaction and suitable techniques to utilize the desired genes. Adult plant resistance is most often desired by wheat breeders in order to avoid/reduce yield losses caused by the disease at adult plant stage [4]. Identification of genetically variable lines with respect to stripe rust resistance is of great help to select the parents for cross combination so as to pyramid genes from different resistant resources in to a single genotype with durable resistance. The aim of the present study was to identify genotypes with high level of resistance to stripe rust, transferring of resistant genes from resistant to suitable genotype through successful cross combination and to study the genetic basis of resistance in wheat by using Area under Disease Progress Curve (AUDPC) as a measure of stripe rust resistance.

Materials and methods. *Field evaluation of germplasm for AUDPC at adult plant stage***.** Seeds of 45 bread wheat genotypes differing in their genetic make up and origin were collected from different sources viz Pakistan, India, CIMMYT and Brazil. Twenty of these genotypes were belonging from Pakistan, fifteen from CIMMYT, Mexico, nine from India and 1 from Brazil. The accessions were planted as stripe rust screening nursery in two replications in two-meter-long rows per entry with 20 seeds per row in randomized complete block design at experimental farm of Nuclear Institute for Food and Agriculture (NIFA), Peshawar, Pakistan during rabi, 2003–2004. The plot size per entry in each set was kept 1.2 m^2.

Creation of artificial epiphytotic condition in the nursery. Each entry of the nursery was bordered with a susceptible check of 'Morocco' as a spreader of stripe rust. Artificial stripe rust epiphytotic conditions was created in the field as referred by [5], inoculated the nursery material at tillering stages in late afternoon with uniform spray of spore suspension containing mixture of urediospores of different stripe rust (*Puccinia striiformis*) races prevalent in Pakistan, through turbo air sprayer at the end of February, 2004. Urediospore mixture was obtained from National Wheat Diseases Research Program (NWDRP) at National Agriculture Research Center (NARC) Islamabad, probably consisting of 67E0, CYR32, 78S84, 110E143A, 230E150, 230E134, Pst 106, E139A and 110E143A pathotypes. These races has virulence formula against the stripe rust resistant genes as Yr1,2,3,4, 5, 6, 7, 8, 9, 10, 15, 17, YrA, and Yr27 [1, 6]. Tween 20 was added in fresh tap water by dissolving urediospores at a rate of 1 gram/litter with approximate concentration of 30000/ml in the suspension as determined by haemocytometer. The nursery material was covered with plastic sheets to keep the moisture for making conditions conducive to spore germination and to avoid washing of spores by dew drops. For spore multiplication and disease development, plane water in the late afternoon was sprayed on to the nursery material with the intervals of two days (for a period of fortnight) until the disease symptoms appeared in the field.

Methodology for disease scoring and determining AUDPC. After successful disease development, data for rust severity (percentage of leaf area with symptoms) was recorded on the top three leaves of five randomly selected plants from each accession on 0–9 points rating scale with little modification to those of [7], as suggested by [8] (Table 1). Second reading of all selected plants was recorded after seven days of the first reading. Observations on response and severity of stripe rust were recorded according to [9]. Rust severity was determined by visual observation and recorded from 0 to 100 % of rust infection on 5 selected plants with in each population according to the modified Cobb scale [10]. For recording correct readings of severity up to interval 2 on individual plants, the term trace (T) was used below 5 % severity. A five percent interval was used from 5 to 20 percent severity and 10 percent intervals for higher readings. The response of individual plants within each population to the type of stripe rust infection was recorded in Table 2. Severity and reaction were recorded together with severity first. The Coefficient of infection (CI) for the rust was calculated in the manner used in CIMMYT and IRN (USDA) i.e., by multiplying the response value with the intensity of infection in percent. Average coefficient of infection (ACI) was derived from the sum of CI values of each entry divided by the number of replications. Based on scale by [11] for selecting wheat varieties to powdery mildew, little modifications were made and a rating scale for disease resistance as adapted by PARC Islamabad, Pakistan for measuring cereal rusts severity [12], and later adopted by ARC (Agricultural Research Council) of Great Britain for the farmers was followed in this study. Using the following formula, Area under disease progress curve (AUDPC) was calculated for individual plants from the calculated C.I. values of the original rust severity data

$$\text{AUDCP} = \Sigma[(X_i + X_{i+1})/2]t_i,$$

where X_i and X_{i+1} are severity on date i and date $i + 1$, respectively and t_i is the number of days between date i and date $i + 1$.

Genotypes/accessions selected for genetic studies. After performing cluster analysis, for AUDPC, seven bread wheat genotypes with wide range of genetic variability Viz. Bakhtawar-92, Frontana, Saleem-2000, Tatara, Inqilab-91, Fakhre-Sarhad, and Karwan were used as parent material for hybridization. The accession Inqilab-91 was formerly described to have resistance to stripe rust based on Yr9 and Yr27 [13]. Pedigrees and Salient features of the parent varieties are detailed as under. In the present paper, only four genotypes Viz. Bakhtawar-92, Frontana, Inqilab-91and Fakhre-Sarhad were used in two crosses. Crosses between other genotypes are to be left for further papers to avoid complication.

Evaluation of six populations against stripe rust. After making successful crosses between the selected genotypes Viz. Bakhtawar-92 × Frontana and Inqilab × Fakhre-Sarhad, six multi-generations (P_1, F_1, P_2, B_1, B_2, F_2) of each cross were planted in the experimental field of Nuclear Institute for Food and Agriculture (NIFA), Peshawar, Pakistan during rabi 2006–2007 in three replications with Randomized Complete Block Design (RCBD). The row length of 5 meters was kept for each pop-

ulation but number of rows were varied i.e. two rows for parents and F_1, four rows for BC_1 and BC_2 and 8 rows for F_2 populations of all the two crosses in each replication. The plant to plant and row to row spacing was maintained 10 and 30 cm respectively. Seeds were sown at 2.5 cm depth at the rate of 2 seed per hil which were later on thinned to single healthy seedling per hil after germination. Same methodology was used for creating artificial epiphytotic conditions, recording disease severity and working out AUDPC as mentioned for the germplasm. Starting from March 24, 2007 when the wheat plants were at growth stages from booting to milk [14], rust severity was recorded at four intervals (24th March, 31st March, 7th April and 14th April 2007 with in elapse of one week interval between to consecutive readings) on the same randomly selected plants (60 plants from each of the parental, 90 from F_1s, 150 plant from each of B_1s and B_2s while 210 plants from each of the F_2s populations). Data collection was completed with in 12 hours on each recording date.

Statistical Analysis. Mean values regarding AUDPC and standard deviations for all the accessions were worked out by using MS excel programme. For performing cluster analysis with respect to classification of germplasm, Euclidean distance was estimated for all pairs of accessions. The resulting Euclidean dissimilarity coefficient matrices were used to established the relationship between the accessions using wardrs method (Statistica version 7.0)

Joint Segregation Analysis (JSA). The data regarding AUDPC were analyzed according to five

Table 1

Assessment and evaluating of stripe rust reaction and measurement of coefficient of infection

O – No visible infection
R – Resistant. Necrotic areas with or without minute uredia
MR – Moderately resistant. Small uredia present surrounded by necrotic areas
MS – Moderately susceptible. Medium uredia with no necrosis but possibly some distinct chlorosis
S – Susceptible Large uredia and little or no chlorosis present
TR – Trace severity of resistant type infection
10MR – 10 percent severity of a moderately resistant type infection
50S – 50 percent severity of a susceptible type infection

Reaction	Observation	Response value
No disease	O	0.0
Resistant	R	0.2
Resistant to Moderately Resistant	R-MR	0.3
Moderately Resistant	MR	0.4
Moderately Resistant to Moderately Susceptible	MR-MS	0.6
Moderately Susceptible	MS	0.8
Moderately Susceptible to Susceptible	MS-S	0.9
Susceptible	S	1.0

Table 2

The response of individual plants within each population to the type of stripe rust infection

Genotype	Pedigree	Origin/Source	AUDPC
Bakhtawar-92	KAUZ 'S'	Pakistan (CIMMYT based)	143.40
Frontana	Fronteira/Mentana	Brazil	35.10
Saleem-2000	CHAM-6//KITE/PGO	Pakistan (CIMMYT based)	103.20
Tatara	JUP/ALD "S"//RLT 'S'/3VEE'S')	NIFA, Peshawar	45.67
Inqilab-91	WL 711/CROW 'S'	Pakistan (CIMMYT based)	244.80
Fakhre-Sarhad	PFAU 'S'/SERI/BOW 'S'	Pakistan (CIMMYT based)	60.29
Karwan	C182.2/C166.3/3/CNO/7C2*//CC//TOB/SWM6828	Pakistan (CIMMYT based)	70.50

Table 3

Grouping based on different clusters for 45 Bread wheat accessions evaluated during 2003

Cluster	Frequency	% age	Mean/SD	Accessions with Euclidean Distances							
				Group A							
1	9	20	104.49 ± 14.31	Saleem-2K (6.63)	CT-02248 (4.34)	CT-01183 (6.65)	CB-61 (8.43)	CB-185 (8.62	AS-2002 (7.84)	CB-145 (10.61)	BANA-4 (16.16)
				CB-171 (4.83)							
2	11	24.44	133.88 ± 13.66	B-92 (7.51)	CT-02306 (5.89)	CT-01084 (4.19)	Metal Tail (5.90)	CB-82 (6.21)	CB-148 (4.64)	CB-195 (9.77)	UQAB (6.40)
				DRRM 03 (7.14)	CM-03-04 (5.44)	V-2156 (6.65)					
3	13	28.88	73.57 ± 18.84	Frontana (13.68)	Tatara (7.34)	F-Sarhad (7.76)	CT-02009 (5.54)	CT-02019 (6.48)	CT-02081 (6.48)	CT-02266 (2.44)	CT-02267 (3.45)
				CT-02204 (3.38)	CT-02390 (5.54)	Karwan (2.81)	CT-99022 (4.98)	V-03007 (8.46)			
				Group B							
4	9	20	178.65 ± 12.94	CT-02192 (5.18)	V-84051 (7.10)	Soleman (4.37)	CB-179 (6.92)	CB-196 (6.50)	CB-325 (4.44)	E-41 (4.24)	Mango (6.28)
				E-29 (5.91)							
5	3	6.67	244.40 ± 6.61	Inqilab-91 (6.46)	CB-197 (9.79)	CB-289 (5.80)					

Note. In Parentheses is the Euclidian distance representing the repartition/closeness among the lines including in the same cluster.

different groups of genetic models as outlined by Gai [15, 16]. 1. One major-gene inheritance (A-1, A-2, A-3 and A-4). 2. Two major-gene inheritance (B-1, B-2, B-3, B-4, B-5 and B-6). 3. Polygene and polygene inheritance (D, D-1, D-2, D-3 and D-4). 5. Two Major gene and polygene inheritance (E, E-1, E-2, E-3, E-4, E-5 and E-6).

The observations were recorded on individual plants from each of the six populations i.e. the two homozygous parents (P_1 and P_2), the first filial generation (F_1), the two backcrosses (B_1 and B_2)), and the second filial generation (F_2). Based on the assumptions [13, 14], the data was subjected to 24 types of genetic models of five groups. The most suitable genetic models in each cross were chosen by using maximum log of likely hood values [13, 17, 18] and Akaikers information criterion (AIC). Further selection of the best fit genetic model was made on the basis of least number of significant values of χ^2 statistics, Smirnov statistics and Kolmogorov statistics [14]. The data were analyzed by using statistical software Sin. Exe, the major gene-polygene mixed inheritance model to a joint analysis of multi-generations [16] specially designed for six generations i.e. P_1, P_2, F_1, BC_1, BC_2, and F_2. In case of the best fit model the values of second order genetic parameters as well as and for B_1, B_2 and F_2 were worked out by using excel program of windows.

Results. *Genetic diversity for stripe rust and selection of genotypes for crosses***.** Based on Area Under Disease Progress Curve (AUDPC), Euclidean dissimilarity coefficient matrix (not shown) was constructed for 45 wheat accessions and phenogram

Table 4

Frequency distribution of plants population under AUDPC level in P_1, F_1, BC_1, BC_2 and F_2 generation of two bread wheat (*Triticum aestivum* L.) crosses

Genera-tion	Range of Area Under Disease Progress Curve (AUDPC)														Sample Size	Mean	Phenotypic Variance/SD
	0-	25-	50-	75-	100-	125-	150-	175-	200-	225-	250-	275-	300-	325-			
Cross 1 (Bakhtawar-92 × Frontana)																	
P_1								3	20	19	14	4			60	233.28	545.16 ± 23.35
F_1		8	17	25	21	14	5								90	155.00	144.91 ± 12.04
P_2	8	20	20	11	1		24								60	65.98	565.72 ± 65.98
BC_1				5	29	25	9 18	21	19	13	7	7			150	3699.50	3699.50 ± 60.82
BC_2	11	27	29	24	18	14		8	6	4					150	2504.10	2504.08 ± 50.04
F_2	7	20	20	20	21	19		22	21	20	15	7			210	5769.50	5769.53 ± 75.96
Cross 2 (Inqilab-91 × Fakhre-Sarhad)																	
P_1										2	5	17	21	15	60	233.28	545.16 ± 23.35
F_1						6	12	49	23						90	155.00	144.91 ± 12.04
P_2		5	22	22	7	4									60	65.98	565.72 ± 65.98
BC_1			5	8	23	15	15	14	15	15	12	12	7	9	150	3699.50	3699.50 ± 60.82
BC_2		10	8	12	21	23	24	23	18	11					150	2504.10	2504.08 ± 50.04
F_2		6	12	15	20	18	19	19	18	19	21	21	14	8	210	5769.50	5769.53 ± 75.96

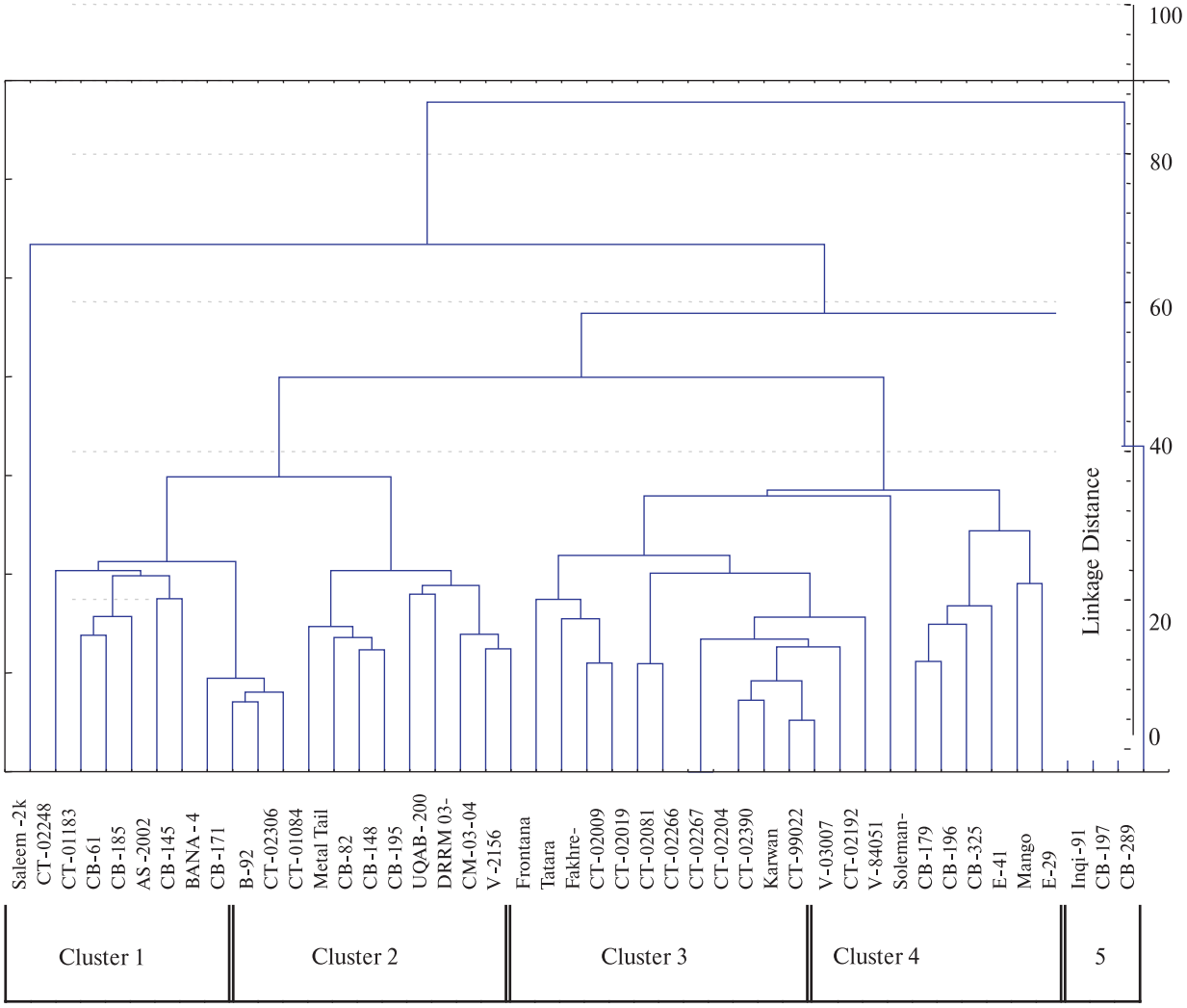
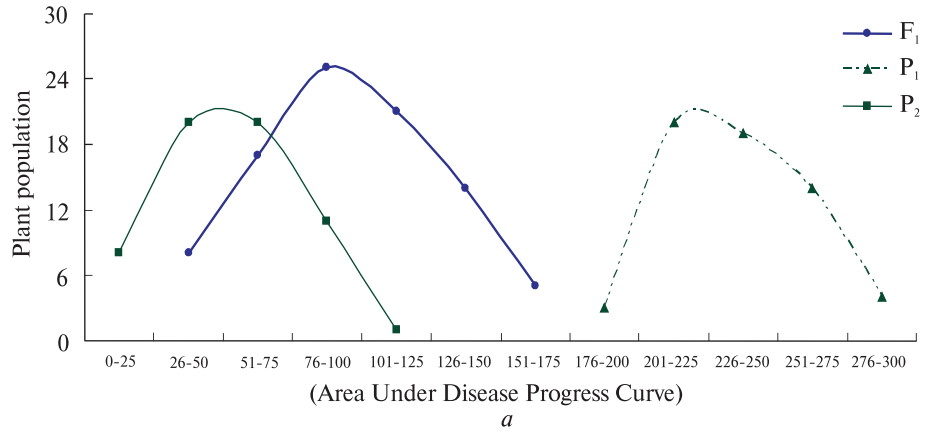


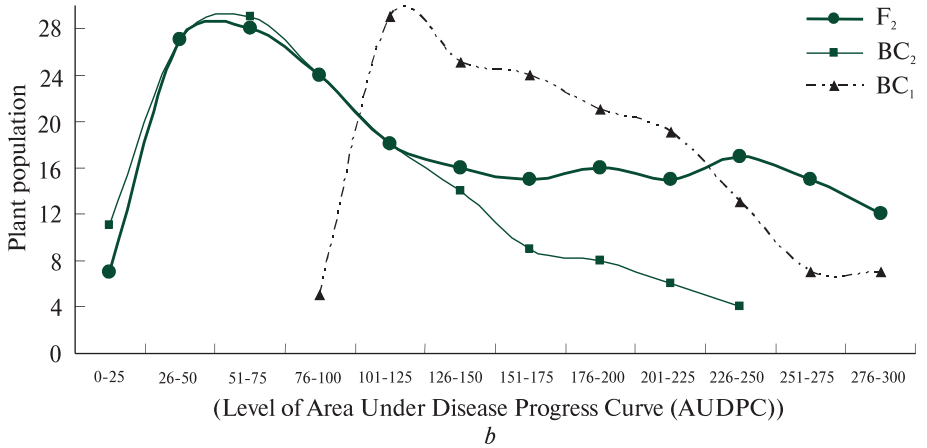
Fig. 1. Phonogram based on eleven quantitative traits in 45 wheat genotypes used as germplasm

constructed is presented in Fig. 1. The dissimilarity range was from 2.44 to 16.16 among all the accessions. The dendrogram showed two groups and five clusters. Group A consisted on three clusters and B on two ones. Since the cluster analysis is based on AUDPC therefore, the clusters were obtained on the basis of linkage distance and related traits. Grouping based on different clusters along with Euclidean distances, means and standard deviation is presented in Table 3. In group A, nine genotypes i.e. Saleem-2k, CT-02248, CT-01183, CB-61, CB-185, AS-2002, CB-145 and BANA-4 were in cluster 1 which presents 20 percent of the total material (Table 4). The accessions in cluster 1 (9 % of the total material) showed AUDPC in acceptable range (104.49 ± 14.31) < (182). Cluster 2 (Table 3) accounts for 24.44 percent of the total material and consists of eleven accessions (Bakhtawar-92, CT-02306, CT-01084, Metal Tail, CB-82, CB-148, DRRM-03–04, CM-03–04, V-2156).

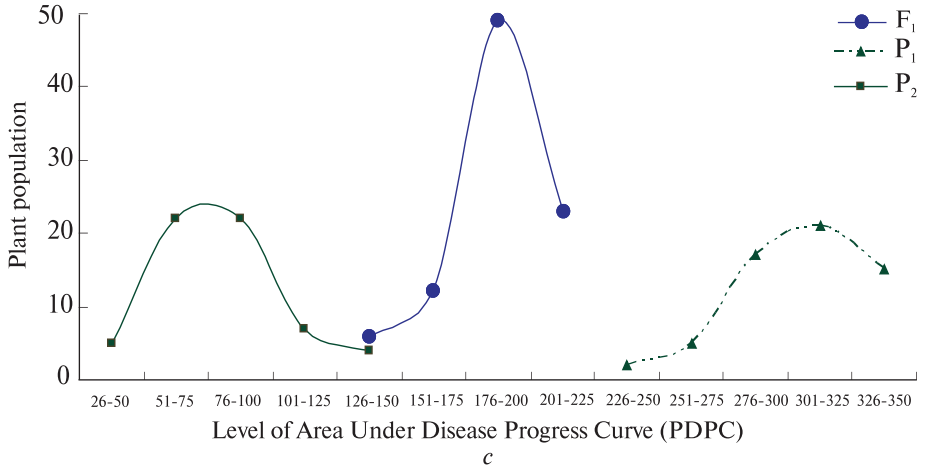
Cluster 3 is consisted of 28.88 % of the total population and comprised of thirteen accessions (Frontana, Tatara, Fakhre-Sarhad, CT-02009, CT-02019, CT-02081, CT-02266, CT-02267, CT-02204, CT-02390, Karwan, CT-99022 and V-03007). Having very low AUDPC (73.57 ± 18.8), the accessions included in this cluster showed high level of resistance to the disease and can be utilized as source of resistance for stripe rust. Clusters 4 and 5 representing 20 and 7 % of the total materi-



a

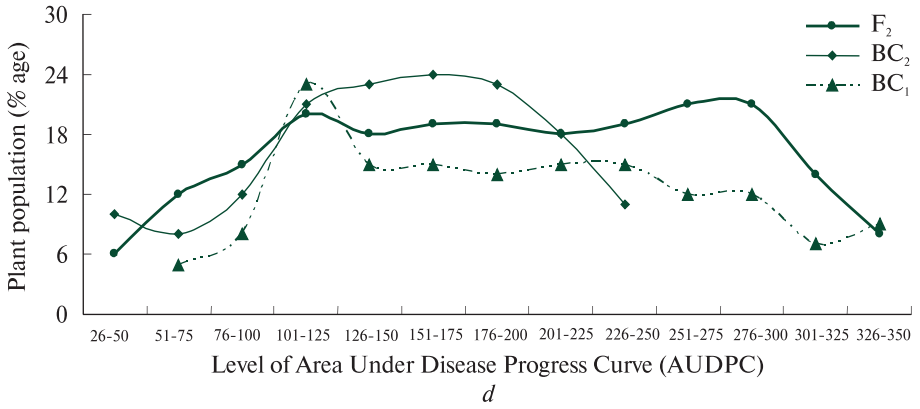


b



c

Fig. 2. Frequency distribution of plant population: *a* – under AUDPC level of F_2, P_1 and P_2 in cross 1; *b* – under AUDPC level in F_2, BC_1 and BC_2 for cross 1; *c* – under AUDPC level in F_1, P_1 and P_2 for cross 3; *d* – under AUDPC F_2, BC_1, and BC_2 for cross 3



d

Fig. 2. Finish

Table 5

Maximum likelihood estimates and *AIC* values for AUDPC under various genetic models estimated through the IECM* algorithm

Model	Maximum log of likelihood	*AIC*	Model	Maximum log of likelihood	*AIC*
Cross 1: Bakhtawar-92 × Frontana			Cross 2: Inqilab-91 × Fakhre-Sarhad		
A-1	−3862.55	7733.10	A-1	−3900.42	7808.83
A-2	−3874.50	7755.00	A-2	−3913.78	7833.56
A-3	−3992.06	7990.12	A-3	−4086.09	8178.18
A-4	−3922.90	7851.80	A-4	−4038.12	8082.24
B-1	−3727.13	7474.26	B-1	−3769.34	7558.69
B-2	−3807.06	7626.12	B-2	−3852.96	7717.92
B-3	−3858.87	7725.74	B-3	−3945.91	7899.82
B-4	−3911.65	7829.32	B-4	−3929.03	7864.05
B-5	−3991.57	7991.15	B-5	−4074.69	8157.38
B-6	−3991.57	7989.15	B-6	−4074.69	8155.38
C	−3771.80	7563.60	C	−3788.73	7597.46
C-1	−3813.54	7641.08	C-1	−3828.23	7670.46
D	−3737.84	7499.68	D	−3768.41	7560.83
D-1	−3759.35	7536.71	D-1	−3778.32	7574.65
D-2	−3759.35	7534.71	D-2	−3778.32	7572.65
D-3	−3807.42	7630.84	D-3	−3813.94	7643.88
D-4	−3785.38	7586.77	D-4	−3793.32	7602.65
E	−3701.76	7439.53	E	−3756.51	7549.02
E-1	−3722.78	7475.57	E-1	−3760.58	7551.16
E-2	−3765.82	7553.64	E-2	−3790.63	7603.26
E-3	−3729.67	7477.34	E-3	−3778.03	7574.06
E-4	−3781.47	7578.94	E-4	−3796.56	7609.13
E-5	−3800.74	7619.48	E-5	−3816.85	7651.71
E-6	−3771.56	7559.12	E-6	−3781.50	7579.00

*IECM: Iterated Expectation and Conditional Maximization (Gai and Wang, 1998)

al and with AUDPC of 178.65 and 244.0 respectively were lying in susceptible and highly susceptible range. On the basis of susceptibility and high level of resistance to stripe rust, the crosses were performed between highly susceptible and highly resistant parents so as to determine the gene action on the control of the disease.

Genetic control of stripe rust resistance (AUDPC). The frequency distribution and the mean values (Table 3), show the tendency of F_1 and BC_2 towards the resistant parents (Frontana, and Fakhre-Sarhad) which were used as the pollen donor parents in the crosses. Normal distribution of F_2 and occurrence of transgressive segregants of resistant as well as susceptible types indicate the quantitatively controlled nature of AUDPC. Transgressive segregation for resistant plants refers to the presence of resistant genes in the parents for controlling stripe rust. The susceptible transgressive segregants refer to the fact that some negative genes were also dispersed in the parents which affected the resistance when came in accumulation in individual of F_2 or those of subsequent generations. The frequency distribution represented as linear bar chart for six generations (Fig. 2) clarify the behaviour and tendency of each generation in the crosses. Highest phenotypic variances ranged between 2504.08 and 6658.02 for the segregating progenies (Table 4) indicate that the trait was highly influenced by the environmental conditions.

Genes pattern and selection of suitable genetic models for controlling AUDPC. Using the criterion of the maximum log of likelihood estimates and smaller *AIC* values (Table 5), Model E, E-1 and B-1 were most suitable for controlling AUDPC in

cross 1 while models E-1, D-2 and B-1 were suitable for cross-2. Further selection of the best fit model for each cross was made on the basis of least number of significant values of the five statistics presented in Table 6, clearly showing that E and E-1 were the best fit models for cross 1 and cross 2 respectively. Using the component parameters given in Table 7 the first and second order genetic parameters for corresponding best fit genetic model for the two crosses were calcu lated (Table 8).

Table 6

Tests for goodness-of-fit regarding AUDPC of model B-1, E and E-1 for crosses Bakhtawar-92 × Frontana and Inqilab-91 × Fakhre-Sarhad

Model	Generation	U_1^2	U_2^2	U_2^3	${}_nW^2$	D_n
			Cross 1: Bakhtawar 92 × Frontana			
E	P_1	0.08(0.77)	0.33 (0.57)	11.59 ***	0.28 (>0.05)	0.13 *
	F_1	0.01 (0.92)	1.42 (0.23)	19.00 ***	0.43 (>0.05)	0.13 *
	P_2	0.67 (0.41)	2.52 (0.11)	10.08 ***	0.10 (>0.05)	0.13 *
	B_1	0.82(0.36)	0.06(0.80)	6.37 **	0.25(>0.05)	0.07 *
	B_2	0.02(0.89)	0.15(0.70)	0.96(0.32)	0.05 *	0.05*
	F_2	0.60 (0.43)	0.69(0.40)	0.11(0.73)	0.11 (>0.05)	0.05 *
B-1	P_1	0.51 (0.47)	1.58 (0.21)	5.10 **	0.18*	0.11 *
	F_1	12.59 ***	19.51 ***	15.42 ***	1.85 (>0.05)	0.23 (>0.05)
	P_2	0.17(0.68)	0.82 (0.36)	4.12 **	0.22 (>0.05)	0.12**
	B_1	0.00 (0.95)	0.03 (0.86)	0.24 (0.62)	0.04 **	0.04 **
	B_2	0.01(0.92)	0.00 (0.96)	0.03 (0.86)	0.04***	0.05***
	F_2	35.21 ***	46.81 ***	19.23 (0.15)	3.77 (>0.05)	0.21 (>0.05)
E-1	P_1	0.07 (0.79)	0.28 (0.59)	9.77***	0.24 (>0.05)	0.11**
	F_1	0.00(0.94)	1.18(0.28)	21.15 ***	0.49 (>0.05)	0.14*
	P_2	0.84(0.36)	2.66 (0.10)	8.87 ***	0.39 (>0.05)	0.13**
	B_1	0.75 (0.38)	0.80 (0.37)	0.06(0.81)	0.19 (>0.05)	0.08 **
	B_2	0.67 (0.41)	0.59 (0.44)	0.10(0.90)	0.09 **	0.06*
	F_2	6.86**	8.11***	1.56 (0.21)	0.69 (>0.05)	0.09**
			Cross 2: Inqilab-91 × Fakhre-Sarhad			
E	P_1	0.00(0.99)	0.57(0.45)	9.15***	0.23 (>0.05)	0.09**
	F_1	0.00 (1.0)	0.54(0.46)	8.65 ***	0.19 (>0.05)	0.11***
	P_2	0.00 (1.0)	0.79 (0.37)	12.62***	0.24 (>0.05)	0.11 ***
	B_1	2.75 *	2.16(0.14)	0.30(0.58)	0.34 (>0.05)	0.08**
	B_2	0.01(0.93)	0.00(0.98)	0.20(0.65)	0.03 **	0.04**
	F_2	1.22(0.27)	2.07(0.15)	2.16(0.14)	0.23 (>0.05)	0.07**
E-1	P_1	0.12(0.73)	0.18(0.67)	9.11***	0.24 (>0.05)	0.11**
	F_1	0.00(0.98)	0.52 (0.43)	8.71 ***	0.19 (>0.05)	0.11**
	P_2	0.12(0.73)	1.49(0.22)	12.57 ***	0.31 (>0.05)	0.12**
	B_1	3.57(0.59)	3.63(0.06)	0.09(0.76)	0.38 (>0.05)	0.09**
	B_2	3.02(0.08)	2.83(0. 09)	0.00(0.99)	0.28 (>0.05)	0.07*
	F_2	1.20(0.27)	2.77(0.09)	5.83**	0.28 (>0.05)	0.07*
B-1	P_1	0.12(0.73)	0.03(0.84)	0.38 (0.54	0.07 *	0.07**
	F_1	0.12(0.73)	0.85(0.35)	25.52***	0.60 (>0.05)	0.17(>0.05)
	P_2	0.14(0.70)	0.00(0.94)	1.28(0.26)	0.09 **	0.07**
	B_1	6.77 **	6.15 **	0.03 (0.87)	0.77 (>0.05)	0.12(>0.05)
	B_2	0.40(0.52)	1.75(0.19)	8.00***	0.33 (>0.05)	0.10***
	F_2	2.25(0.13)	4.23*	5.82**	0.36 (>0.05)	0.09**

Note. In parenthesis is the probability value. *, **, *** represents the 0.05, 0.01, 0.001 significance levels respectively U_1^2, U_2^2, U_2^3: χ^2 statistics with 1 degree of freedom; ${}_nW^2$: Smirnov's statistics; D_n: Kolmogorov's statistics.

Table 7

Maximum likelihood estimates of component parameters regarding AUDPC for four Bread wheat crosses in their respective best fit models

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
Cross 1: Bakhtawar 92 × Frontana (Model E)							
μ_1	233.28	μ_{44}	130.23	μ_{62}	240.96	μ_{68}	44.31
μ_2	155.00	μ_{51}	154.00	μ_{63}	208.67	μ_{69}	39.67
μ_3	65.98	μ_{52}	101.33	μ_{64}	182.91	σ^2	355.65
μ_{41}	249.10	μ_{53}	60.55	μ_{65}	137.76	σ_4^2	931.67
μ_{42}	233.42	μ_{54}	55.91	μ_{66}	85.10	σ_5^2	759.40
μ_{43}	175.38	μ_{61}	256.63	μ_{67}	91.03	σ_6^2	355.65
Cross 2: Inqilab 91 × Fakhre-Sarahad (Model E-1)							
μ_1	309.53	μ_{44}	207.04	μ_{62}	95.29	μ_{68}	205.12
μ_2	185.32	μ_{51}	148.04	μ_{63}	299.87	μ_{69}	145.02
μ_3	78.23	μ_{52}	228.41	μ_{64}	95.04	σ^2	276.12
μ_{41}	287.82	μ_{53}	175.61	μ_{65}	177.54	σ_4^2	1083.18
μ_{42}	124.80	μ_{54}	115.52	μ_{66}	257.91	σ_5^2	1560.68
μ_{43}	124.54	μ_{61}	258.32	μ_{67}	299.87	σ_6^2	963.41

Genetic model E for cross 1 determines mixed additive-dominant-epistatic effect of major genes plus additive – dominant-epistasis of polygenes. The additive (d_a, d_b) and dominant (h_a, h_b) effects contributed by two major genes (A & B) to the control of AUDPC were estimated to be 83.65, 24.83 and –25.19, –6.37 respectively. The positive signs of the additive effect with respect to major genes in the cross indicated that AUDPC was controlled by the positive additive action of the major genes where as the negative signs of the dominant components of the major genes indicate that resistance to stripe rust was adversely affected by the dominant action of the major genes. The dominant ratios (h_a/d_a and h_b/d_b) of the gene A and B was –0.30 and –0.26 respectively, representing the predominance of the additive gene action due to major genes rather then the dominant effect. The negative signs of non allelic dominant interaction of the two major genes as well as of additive × additive effect (*i*) in the cross indicate the dispersion of some negative genes in parents (Bakhtawar-92 and Frontana), which adversely affected resistance to stripe rust. Therefore, selection for resistance should be delayed to subsequent generations till maximum resistant polygenes are accumulated in the individual plants. The additive × dominant effect of gene A over gene B (J_{ab}) and that of B over A (J_{ba}) was 14.67 and 24.08 respectively. The dominant × dominant type of non allelic interaction (*l*) was recorded as 10.

Genetic control of AUDPC in cross 2. Model E-1(best fit for cross 2), representing mixed action of two major additive-dominance epistatic genes plus additive-dominant polygenes. The population mean (242.98) (Table 8) refers to the average AUDPC equal to the mean of F_2 generation. The negative signs of the dominant effect (–74.29& –100.56) due to first and second major genes (A & B) in these crosses represent that resistance to stripe rust is controlled by negative dominant effect of the major genes. Additive effect due to the two major genes (A & B) was conspicuous in controlling AUDPC in cross Inqilab-91 × Fakhre Sarhad with higher effect due to gene A (28.32) then that of gene B (4.34). The negative sign under mixed additive × additive (*i*) type of genetic effect represents the dispersion of some negative polygenes between the parents (Inqilab and Fakhre Sarhad) which adversely affect the AUDPC when come in combination in the segregating progenies. However, the over all additive effect due to polygene was higher and positive (91.29) representing the conspicuous favourable effect of polygene on AUDPC. The dominant × dominant (*l*) type effect was the highest (101.63) representing the favurability of

Table 8

Estimates of first and second order genetic parameters for Stripe rust resistance (AUDPC) in four bread wheat crosses

1st order parameter	Estimate	1st order parameter	Estimate	2nd order parameter	Estimate		
					BC_1	BC_2	F_2
Cross 1: Bakhtawar-92 × Frontana (Model E)							
m_1	125.65	h_a	−25.19	σ_p^2	3699.50	2504.1	5769.5
m_2	166.24	h_b	−6.37	σ_{mg}^2	2718.6	1226.82	5026.59
m_3	175.31	h_a/d_a	−0.30	σ_e^2	355.65	355.65	355.65
m_4	141.47	h_b/d_b	−0.26	σ_{pg}^2	625.26	921.63	387.29
m_5	165.24	i	−0.85	h_{mg}^2 (%)	73.49	48.99	87.12
m_6	145.98	j_{ab}	14.67	h_{pg}^2 (%)	16.90	36.80	6.71
d_a	83.65	j_{ba}	24.08				
d_b	24.83	l	10.12				
Cross 2: Inqilab-91 × Fakhre-Sarhad (Model E-1)							
m	242.98	i	−49.10	σ_p^2	5833.14	3138.64	6658.02
d_a	28.32	j_{ab}	−83.24	σ_{mg}^2	4244.2	1979.20	5742.29
d_b	4.34	j_{ba}	−109.76	σ_e^2	276.12	276.12	276.12
h_a	−74.29	l	101.63	σ_{pg}^2	1312.80	883.32	639.62
h_b	−100.56	[d]	91.29	h_{mg}^2 (%)	72.76	63.06	86.25
h_a/d_a	−2.62	[h]	15.57	h_{pg}^2 (%)	22.51	28.14	9.61
h_b/d_b	−23.17						

mixed epistasis due to major genes and polygenes in controlling AUDPC in Inqilab-91 × Fakhre-Sarhad. Dominance due to polygenes though smaller (15.57) but was favourable because of its positive sign value for controlling the trait (Table 8).

Under the second order genetic parameters (Table 7), the phenotypic variation (σ_p^2) is partitioned into genetic and environmental variation (σ_e^2) for the two crosses. The genetic component of variation in turn is subdivided into variation due to major genes (σ_{mg}^2) and polygenes (σ_{pg}^2). Since resistance to stripe rust is controlled by two major genes plus polygenes therefore, the phenotypic variance (σ_p^2) in BC_1, BC_2 and F_2 was higher in both the crosses. The major-gene heritability (h_{mg}^2) which is the most important second order parameter was 73.49, 48.99 and 87.12 in BC_1, BC_2 and F_2 respectively for cross 1. The polygene heritability (h_{pg}^2) which is less important component was estimated as 16.90, 36.80 and 6.71 for BC_1, BC_2 and F_2 respectively in cross Bakhtawar-92 × Frontana. For cross 2, the major gene heritability was 72.76, 63.06 and 86.25 where as the polygene heritability was 22.51, 28.14 and 9.61 for BC_1, BC_2 and F_2 respectively.

Discussion and conclusions. Using AUDPC as the measure of stripe rust resistance in wheat, the data analysis of the present paper was made under the procedures outlined by [15, 19] with the advantage over the method suggested by [20] as the former has the power to determine the number of major genes, individual effects due to the major genes as well as collective effect of the polygenes involved in the controlling of the trait. Moreover, the data is subjected to twenty-four different genetic models as suggested by [16]. According to the procedure, individual effects of the major genes were also determined under the second order genetic parameters (Table 8). In contrast the later procedure measures the trait only as the polygenic system without measuring the effect of individual genes [19].

The crosses were between resistant and susceptible parents using the resistant one as the pollen donor parent in F_1. Frequency distribution of plant population for AUDPC revealed transgressive segregation with respect to susceptibility and resistance in the segregating generations (F_2) of all the crosses. Susceptible transgressive segregants have

also been reported by Bjarko and Line [21] for leaf rust and Ma et al. [22] for stripe rust in wheat. Transgressive segregants in half diallel wheat crosses have also been mentioned in case of *Septoria tritici* blotch resistant [23]. Both susceptible and resistant type of transgressive segregants for stripe rust were reported by [8] in F_2 and F_3 generations of some wheat crosses.

The fitness of the two different models (model E for cross1 and model E-1 for cross 2) in the two crosses is because of the difference in the genetic background of the parents involved in the two crosses. However, AUDPC in both the crosses was under the control of two major genes plus polygenes. The ratios of dominance to additive effect (h/d) for both the major genes in the two crosses have negative sign valves, referring to the recessively controlled nature of AUDPC in both the crosses. The positive sign and higher values of the additive effects due to the major genes show pre dominance of the additive effect on AUDPC in both the crosses. The estimated additive effects due to major gene A and B in the crosses were ranging from 28.32 to 83.65 and 4.34 to 24.83 respectively (Table 8). The negative and positive signs of the additive as well as dominant effect due to the major genes and polygenes in different crosses may occur due to the difference in the genetic background of the parents involved in the crosses [19]. Generally, the dominant and additive effects exerted by polygenes were less than those of the major genes. It is because the polygenes contributed very low fraction to the phenotypic variation (σ_p^2) with very low values of polygene heritability (16.90, 36.80, 6.71 % in cross 1 and 22.51, 28.14, 9.61 % in cross 2 for BC_1, BC_2 and F_2 respectively). The present results are in accordance to those found by [19] regarding resistance to bean fly in soybean with respect to heritability values due to major genes as well as polygenes. Under the mix epistasis effect of both major as well as polygenes for cross 1, negative genes for controlling AUDPC were present among the two parents which means that selection for resistance should be delayed to subsequent generations till maximum resistant polygenes are accumulated in more or less homozygous form in the individual plants. Additive effect with respect to stripe rust resistance has also been reported by some recent investigators in some wheat crosses [17]. The additive × dominant effect (J) due to the second major gene and dominant × dominant effect (*l*) under epistasis was positive for cross 1. Additive × dominant as well as dominant × dominant epistasis for leaf rust in some wheat crosses has also been reported by [21] which coincides with the present results in case of cross 1. An additive/modifying action of two genes for stripe rust in a segregating generation resulted from a cross between susceptible and resistant cultivars of wheat have also been suggested [4]. In another study [8], segregation ratio of 1: 2: 5, has been reported suggesting the involvement of three genes with epistasis for resistance to stripe rust at seedling stage. In a cross between highly resistant and susceptible parents, two genes were suggested with additive effect to be responsible for stripe rust resistance in wheat [22].

Based on a joint scaling test, while conducting studies on gene action regarding durable, high-temperature, adult-plant (HTAP) resistance for stripe rust in parental, F_1, F_2 and backcross populations for some crosses in wheat, [24] reported the involvement of epistasis in controlling AUDPC with significant additive × additive component. Using generation mean analysis, [25] has reported additive-dominance model (absence of epistasis) digenic epistasis with predominant additive gene effect, significant «*i*» type and «*l*» type of epistatic interaction for powdery mildew in different crosses of wheat. The previous results are more or less in correspondence with the two crosses of the present study.

However, the contradictions between the present and the previous results might because all these previous investigators used either diallel or generation mean analysis as the statistical approach which measure the genetic effect as the polygenic system and have no power to determine the effect of the individual major genes and aggregate effect of the polygene.

The first author acknowledges the award of scholarship by Higher Education Commission of Pakistan (HEC) as a visiting Scientist to Institute of Biotechnology, Jiangsu Academy of Agricultural Science, Nanjing, China. The statistical procedures adapted in the present study were suggested by Prof. Dr. Hongxiang Ma, Head, Institute of Biotechnology, Jiangsu Academy of Agricultural Science, Nanjing, China for which the author acknowledges his efforts.

M. Irfag, Mir Ajab, Ma Hongxiang, GSS Khattak

ASSESSMENT OF GENES CONTROLLING AREA UNDER DISEASE PROGREESS CURVE (AUDPC) FOR STRIPE RUST

Генетические эффекты контроля устойчивости к желтой ржавчине злаков были определены в двух скрещиваниях пшеницы Bakhtawar-92 × Frontana (скрещивание 1) и Inquilab-91 × Fakhre-Sarhad (скрещивание 2) с использованием Area Under Disease Progress Curve (AUDPC) для измерения устойчивости. Устойчивые и чувствительные генотипы в этих скрещиваниях были определены с помощью начальной оценки на устойчивость к желтой ржавчине 45 образцов пшеницы. Модель смешанного наследования была применена к анализу данных шести основных популяций P_1, F_1, P_2, B_1, B_2 и F_2 в скрещиваниях. Результаты показали, что AUDPC в скрещивании 1 контролируется двумя основными генами с аддитивно-доминантным эпистатическим эффектом и полигенами с аддитивно-доминантными эпистатическими эффектами (модель Е). В случае скрещивания 2 – под контролем двух основных генов с аддитивно-доминантным эпистатическим эффектом плюс аддитивно-доминантных полигенов (модель Е-1). Аддитивный эффект был преобладающим над всеми остальными типами генетических эффектов, что позволяет предположить задержку селекции на устойчивость до тех пор, пока максимальное количество позитивных генов накапливается у особей последующих поколений. Наличие трансгрессивных сегрегантов на чувствительность и устойчивость показало наличие как генов устойчивости, так и неких негативных генов у родителей. Наследуемость основного гена было выше, чем наследуемость полигенов для B_1, B_2 и F_2 в скрещиваниях. Наследуемость основного гена так же, как и полигенов, была в пределах от 48,99 до 87,12 % и от 2,26 до 36,80 % для двух скрещиваний соответственно. Наибольшая фенотипическая вариабельность в AUDPC (от 2504.10 до 5833,14) в сегрегирующих поколениях (BC_1, BC_2 и F_2) показывает, что на проявление признака влияют факторы окружающей среды.

M. Irfag, Mir Ajab, Ma Hongxiang, GSS Khattak

ASSESSMENT OF GENES CONTROLLING AREA UNDER DISEASE PROGREESS CURVE (AUDPC) FOR STRIPE RUST

Генетичні ефекти контролю стійкості до жовтої іржі злаків були визначені в двох схрещуваннях пшениці Bakhtawar-92 × Frontana (схрещування 1) и Inquilab-91 × Fakhre-Sarhad (схрещування 2) з використанням Area Under Disease Progress Curve (AUDPC) для вимірювання стійкості. Стійкі та чутливі генотипи в цих схрещуваннях були визначені за допомогою початкової оцінки на стійкість до жовтої іржі 45 зразків пшениці. Модель змішуваного спадкування була застосована до аналізу даних шести основних популяцій P_1, F_1, P_2, B_1, B_2 та F_2 в схрещуваннях. Результати показали, що AUDPC у схрещуванні 1 контролюється двома основними генами з адитивно-домінантним епістатичним ефектом і полігенами з аддитивно-домінантними епістатичним ефектами (модель Е). У випадку схрещування 2 – під контролем двох основних генів з адитивно-домінантним епістатичним ефектом плюс адитивно-домінантних полігенів (модель Е-1). Адитивний ефект був переважаючим над всіма іншими типами генетичних ефектів, що дозволяє припустити затримку селекції на стійкість до того часу, поки максимальна кількість позитивних генів накопичується у особин наступних поколінь. Наявність трансгресивних сегрегантів на чутливість та стійкість показала наявність як генів стійкості, так і деяких негативних генів у батьків. Успадковування основного гена було вище, ніж успадкування полігенів B_1, B_2 та F_2 в схрещуваннях. Успадковування основного гена, також як і полігенів була в межах від 48,99 до 87,12 % та від 2,26 до 36,80 % для двох схрещувань, відповідно. Найбільша фенотипічна варіабельність в AUDPC (від 2504.10 до 5833.14) в сегрегуючих поколіннях (BC_1, BC_2 та F_2) показує, що на виявлення ознаки впливають фактори оточуючого середовища.

REFERENCES

1. *Jing Feng, Zhongjun Zhang, Guohui Li, Yu Zhou1, Haihong Wang, Qinggang Guo and Jian Sun.* 2007. Inheritance of resistance to stripe rust in winter wheat cultivars Aquileja and Xian Nong 4. J Appl Genet. 48(1):43–46.
2. *Imtiaz M., Cromey M.G., Hampton J.G., Ogbonnaya F.C.* 2005. Genetics of stripe rust resistance in `Karamur wheat. Australian Journal of Agricultural research, Vol. 56:619–624.
3. *Hojjatollah Ghaledozdani*. 2005. Variability of *Puccinia striiformis* in Iran. Procedings of the Second Asian Conference on Plant Pathology, Faculty of Science, National University of Singapore (25–28 June 2005) Singapore P. 64.
4. *Imtiaz M., Cromey M.G., Hampton J.G., Ahmad M.* 2003. Inheritance of durable adult plant resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*) in 'Otane' wheat (*Triticum aestivum*). New Zealand Journal of Crop and Horticultural Science, Vol. 31:23–31.
5. *Zadoks J.C., Chang T.T., Konzak C.F.* 1974. A decimal code for the growth stages of cereals. Weed Res. 14: 415–421.
6. *McDonald D.B., McIntosh R.A., Wellings C.R., Singh R.P., Nelson J.C.* 2004. Cytogenetical studies in wheat XIX. Location and linkage studies on gene Yr27 for resistance to stripe (yellow) rust. Euphytica 136: 239–248.
7. *Line R.F., Konzak C.F., Alan R.E.* 1974. Evaluating

resistance to *Puccinia striiformis* in wheat. Induced mutation for disease resistance in crop plants. Proceedings of a research Co-ordination meeting, IAEA Austria. P. 125–132.

8. *Imtiaz M., Cromey M.G., Hampton J.G., Hill M.J.* 2003. Inheritance of seedling resistance to stripe rust (*Puccinia striifomis* f. sp. tritici) in 'Otan' and 'Tritea' wheat (*Triticum aestivum*). New Zealand Journal of Crop and Horticultural Science, 2003, Vol. 31: 15–22.
9. *Loegering W.Q.* 1959. Methods for recording cereal rust data U.S.D.A. international spring wheat nursery.
10. *Peterson R.F., Campbell A.B., Hannah A.E.* 1948. A diagnostic scale for estimating rust intensity on leaves and stems of cereals. Canadian J. Res., 26: 496–500.
11. *Doling D.A.* 1965. A method for the transformation of field data for comparing the mildew resistance of cereal varieties and the systemic deviation of the values in NIAB farmerrs leaflets. J. Nat. Inst. Agric. Bot. 10: 169–179.
12. *Aslam M.* 1982. Uniform procedure for development and release of improved wheat varieties. Mimeograph, PARC, Islamabad.
13. *McLachlan G.J.* 1988. Mixture models: inference and applications to clustering. Marcel Dekker, Inc., New York.
14. *Yuan-Ming Zhang, Jun-Yi Gai, Yong-Hua Yang.* 2003. The EIM algorithm in the joint segregation analysis of quantitative traits. Genet. Res., Camb, 81, P. 157–163. Cambridge University Press 157. DOI: 10.1017/S0016672303006141 Printed in the United Kingdom.22.
15. *Gai J.Y., Wang J.K.* 1998. Genetic system of quantitative traits in plants. Theor. Appl. Genet. 97: 1162–1168.
16. *Gai J.Yi., Yuan Z., Wang J.* 2003. Mixed genetic model for two major genes plus multi-genes. Genetic System of Quantitative Traits in Plants. 1st Ed. P. 277–285. Science Press, Beijing.
17. *Dempster A.P., Laird N.M., Robin D.B.* 1977. Maximum likelihood from incomplete data via the EM algorithm. Journal of Royal Statistical Society B 39:1–38.
18. *Wang J.K., Gai J.Y.* 1997 Identification of major gene and polygene mixed inheritance and estimation of genetic parameters in F_2 progeny. Chinese J Genet 24: 181–190.
19. *Wang J., Junyi Gai,* 2001. Mixed inheritance model for resistance to agromyzid beanfly (*Melanagromyza sojae* Zehntner) in soybean. Euphytica, 122: 9–18.
20. *Kearsey M.J., Pooni H.S.* 1996. The genetic analysis of quantitative traits. Champan and Hall, London.
21. *Bjarko M.E., Line R.F.* 1988. Heritability and number of genes controlling leaf rust resistance in four cultivars of wheat. Phytopathology, 78(4): 458–461.
22. *Ma H., Singh R.P., Abdalla O.*1997. Resistance to stripe rust in five durum wheat cultivars. Plant Dis. 81:27–30.
23. *Arama P.F., Parlevliet J.E., Van Silfhout C.H.* 2000. Trangressive segregation for resistance in wheat to septoria tritici blotch. African Crop Science Journal, 8(3): 213–222.
24. *Xianming Chen, Marcelo A. Soria, Guiping Yan, Jun Sun, Jorge Dubcovsky.* 2003. Development of sequence tagged site and cleaved amplified polymorphic sequence markers for wheat stripe rust resistance gene Yr5. Crop Sci. 43:2058–2064.
25. *Das M.K., Rajaram S., Mundt C.C., Kronstad W.E.* 2004. Number of genes controlling slow rusting resistance to leaf rust in five spring wheat cultivars. Annals of Applied Biology, 145(1): 91–94.

Received 26.06.08