INHERITANCE OF RESISTANCE TO STRIPE AND LEAF RUSTS IN SPRING WHEAT.

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Abstract

This study aimed to estimate the relative magnitude of genetic components and combining ability for resistance to stripe and leaf rust diseases. Seven bread wheat (*Triticum aestivum* L) cultivars namely, Sakha 61, Sakha 93, Giza 163, Giza 164, Giza 168, Gemmeiza 9 and Sids 1 were crossed in a half diallel set. Parents and F_1 's were grown in space – planted experiment in 2001/2002 season at Sakha Agric. Res. Stn. Significant genotypic variation for stripe and leaf rust resistance was observed. General combining ability (GCA) for the two traits was larger than specific combining ability (SCA), with 2 GCA / (2GCA + SCA) values of 0.97 and 0.96 for leaf and stripe rust, respectively. Combining ability analysis and estimates of the genetic components from the diallel, indicated that primary part of the genetic variability for the rust traits was associated with additive gene action. However, dominance effects also appeared to be involved in the inheritance of the two traits.

The additive gene action was larger in its magnitude than dominance, resulting in average degree of dominance (H_1/D) ^{1/2} less than one for both traits, indicating partial dominance. The F value was positive and significant for stripe rust, indicating an excess of dominant alleles compared with recessive alleles, while the opposite was shown for leaf rust. The direction of dominance was towards resistance for stripe rust and susceptibility for leaf rust. Broad and narrow senses heritability values were high for the two studied traits. Results suggested that early generation selection for both characters would be effective for improving these characters within the studied material.

INTRODUCTION

Stripe and leaf rusts, caused by *Puccinia striiformis* and *Puccinia recondita* respectively, are the two most serious diseases of bread wheat (*Triticum aestivum*) in Egypt. The most effective way of controlling these diseases is to develop resistant cultivars. Therefore, developing new resistant cultivars is a main target of the National Wheat Research Program in Egypt. Understanding the genetic behavior of wheat

resistance to these diseases is essential for deciding the breeding method that maximizes the genetic improvement of these characters (Shehab El-Din *et al.*, 1991). Recently, there is much interest in the type of resistance that is expressed under natural field conditions as opposed to seedling resistance (Broers *et al.* 1996 and Yadav *et al.* 1998). Field resistance is usually long lasting and quantitatively inherited (Yadav *et al.* 1998). However, for sustainable wheat production, emphasis is given to develop cultivars with durable resistance to diseases and tolerant to environmental stress (Charan and Bahadur 1997).

Wheat resistance to rusts has been documented to be a simply inherited traits governed by one, two or a few number of major gene pairs (Millus and Line, 1986; Ezzahiri and Roelfs, 1989 and Shehab El-Din *et al.* 1996). However, other studies indicated that resistance may be quantitatively controlled (polygenic), and sensitive to environmental conditions (Walkins *et al.* 1995, Shehab El-Din and Abdel-Latif 1996 and Mohgoub, Hayam 2001). Rust resistance was found to be dominant over susceptibility in most cases (Kolmer and Dyck 1994 and Shehab El-Din *et al.* 1996); while recessive or partially recessive inheritance was found in others (Ali *et al.* 1994, Singh *et al.* 1998 and Ageez and Boulot 1999). Additive gene action was more important in some studies while, dominance and / or epistasis were more pronounced in others (Shehab El-Din and Abdel-Latif 1996 and Mahgoub, Hayam 2001). Reported estimates of broad and narrow sense heritabilities of resistance were generally high (Boulot and El-Sayed 2001and Zhang *et al.* 2001)

Information regarding different types of gene action involved in inheritance of stripe and leaf rust resistance traits, the magnitude of genetic components of variance as well as estimates of combining ability are essential. Such information will help wheat breeders in their identification of good parents and selection procedures. This study was undertaken to determine the mode of inheritance, combining ability and heritability estimates for stripe and leaf rust resistance in some selected spring wheat cultivars.

MATERIALS AND METHODS

A seven parents diallel cross of spring wheat cultivars, excluding reciprocals, was used in this study at Sakha Agricultural Research Station, Agricultural Research Center, during the two wheat – growing seasons 2000-2001 and 2001-2002. The parental genotypes differed in resistance to stripe and leaf rust as indicated in Table 1.

Table 1. Name, pedigree and reactions to stripe and leaf rusts of the studied parental bread wheat cultivars.

Parent #	Name	Cross Name & Pedigree	YR*	LR
1	Sakha 61	Inia / RL 4220 // 7c / Yr "S"	R**	S
		CM154302S-5S-0S-0S		
2	Sakha 93	Sakha 92/ TR 810328	R	5
		S 8871-1S-2S-15-0S		
3	Giza 163	T. Aestivun / Bon // Cno / 7c	S	\$
		CM33009 -F-15M-4Y-2M-1M-1M-1Y-0M		
4	Giza 164	KVZ / Buha "S" // Kal / Bb	S	S
		CM33027-F-15M-500Y-0M		
5	Giza 168	Mrl / Buc // Seri	R	R
		CM 93046-8M-0Y-0M-2Y-0B		
6	Gemmeiza 9	Ald "S" / Huac // Cmh 74A. 630 / Sx	R	R
		CGM 4583-5GM-1GM-0GM		
7	Sids 1	HD 2172 / Pavon "S" // 1158.57/ Maya 74 "S"	R	S
		Sd 46-4Sd-2Sd-1Sd-0Sd		

^{*}YR and LR= yellow (stripe) and leaf rust, respectively.

In 2000/2001, parents were crossed in all possible combinations (excluding reciprocals). In 2001/2002, the parents and F_1 's were evaluated in a randomized complete block design with three replications. Each genotype was grown in a single row; 2m long and 30 cm apart, with plants spaced 20 cm apart within rows. The experiment was surrounded by wheat cultivars highly susceptible to stripe and leaf rusts as spreader. Artificial inoculation was not carried out for stripe rust since the Sakha location is considered a hot spot for this disease. Meanwhile, plants were artificially inoculated by leaf rust by spraying a mixture of fresh uredeniospores of leaf rust isolates, mixed with talcum powder at a rate of 1:20 at the booting stage .The recommended package of cultural practices was followed. The infection types and severity for stripe and leaf rusts were recorded and expressed in terms of Average

^{**}R= Resistant and S= Susceptible.

Coefficient of Infection (ACI) to be easy for statistical analyses, following the method adopted by Saari and Wilcoxson (1974) and adjusted by Shehab El-Din and Abdel-Latif (1996). Data were recorded on five randomly selected plants per row in each of the three replications.

ACI data of stripe and leaf rust reactions were transformed using square root scale. Data obtained were statistically analyzed on plot mean basis. Analysis of variance used to partition the genotypes sum of squares to general combining ability (GCA) and specific combining ability (SCA) according to Method 2, Model 1 of the diallel cross analysis provided by Griffing (1956), using parents and F_1 's and assuming a fixed model. Data of the diallel were also subjected to genetic analysis according to model suggested by Hayman (1954). This analysis provides estimates of the following components of genetic variation: Variation due to additive gene effects (D), covariance of additive and dominance effects (F), variation due to dominant gene effects (H₁), dominance effect adjusted by gene frequency (H₂), dominance variation over all heterozygous loci (h2), variation due to environmental effect (E). Hayman's analysis also provides estimates of following proportions: The mean degree of dominance at each locus $(H_1/D)^{1/2}$, the ratio of genes with positive and negative effects in the parents (H₂/4H₁), the ratio of dominance and recessive genes in the parents (KD/KR), an estimator of number of gene groups exhibiting dominance involved in the inheritance of the trait (K), the coefficient of correlation between the parental order of dominance and parental measurement (r), value of most dominant and recessive parent (YD&YR) and heritability.

RESULTS AND DISCUSSION

The analyses of variance for stripe and leaf rust resistance scores (ACI) indicated the significant of genetic variation for the two traits among tested genotypes (Table 2). These results suggesting wide genetic diversity among parents in allelic constitution for resistance to both stripe and leaf rusts. Hence, these attributes would be improved by selecting the appropriate parent for each character. The parents vs. hybrids mean squares was highly significant (Table2) indicating that average heterosis due to nonadditive gene action plays an important role in the inheritance of resistance to both diseases.

Table 2. Mean squares from	analysis of variance of a	7-parents wheat	diallel cross for
resistance to stripe	and leaf rusts.		

Source of variation	df	Stripe rust	Leaf rust
Replicates	2	0.115	0.376
Genotypes	27	19.636**	23.583**
Parents	(6)	47.609**	29.963**
Hybrids	(20)	11.316**	22.643**
Parents vs. hybrids	(1)	17.914**	7.242**
General combining ability	(6)	22.874**	28.317**
Specific combining ability	(21)	1.880**	2.016**
Error	54	0.105	0.765

^{**} Significant at 0.01, probability level.

Because significant differences were detected among genotypes for resistance to the two rusts traits, a combining ability analysis was conducted (Table2). Mean square of both GCA and SCA were significant for the studied characters. For the two studied traits, GCA was more important than SCA. The ratio of mean squares, 2GCA / (2GCA + SCA), was higher for leaf rust (0.97) than for stripe rust (0.96). Because this ratio is close to unity, the importance of additive genetic effects is proved (Baker, 1978). Therefore, the stripe and leaf rust resistance are mainly influenced by additive gene action in these crosses. However, non-additive gene action may play an important role in certain crosses. Similar results were obtained by Shehab El-Din and Abdel-Latif (1996), Shehab El-Din et al. (1996), Ageez and Boulot (1999) and Boulot and El-Sayed (2001).

Giza 163 and Giza 164 (susceptible cultivars to stripe rust) displayed significant positive GCA effects for stripe rust, whereas the other cultivars (resistant parents) had significant negative GCA effects for this trait (Table 3). In contrast, the parents Sakha 61, Sakha 93 and Sids 1 (susceptible parents to leaf rust) showed significant positive GCA effects for leaf rust, while other parents reflected significant negative effects. GCA effects for both rusts (Table3) were high correlated with parental mean performance because the major part of genetic variability associated with rust traits was additive. Crossing the parents with highest and negative GCA effects would provide the greatest possibility of producing superior progeny for stripe and leaf rust resistance. Therefore, the two cultivars Giza 168 and Gemmeiza 9 were the good combiners for the both rusts, while, Sakha 93 and Sakha 61 were the best

combiners for stripe rust alone. On the other hand, Giza 163 followed by Giza 164 and Sids 1 followed by Sakha 61 had the poorest GCA effects for resistance to stripe and leaf rusts, respectively.

Table 3. Estimates of general combining ability effects for wheat stripe and leaf rust for seven parents

Parent	Stripe rust	Leaf rust
Sakha 61	-1.237**	2.008**
Sakha 93	-1.362**	0.922**
Giza 163	2.436**	-1.301**
Giza 164	2.114**	-0.410**
Giza 168	-0.334**	-1.860**
Gemmeiza 9	-0.667**	-1.738**
Sids 1	-0.951**	2.378**
LSD gi 0.05	0.116	0.306
0.01	0.156	0.412
LSD gi-gj 0.05	0.176	0.415
0.01	0.234	0.633

^{**} Significant at 0.01, probability level

Table 4, shows the estimates of SCA effects for the two studied characters in the 21 crosses. These effects were negative and significant for resistance to stripe and leaf rusts in seven and five crosses, respectively. However, the highest negative effects were detected in the crosses Sakha 93 / Giza 163, Sakha 61 / Giza 164 and Sakha 93 / Giza 164 for stripe rust. for leaf rust, the crosses Sakha 61 / Giza 163, Sakha 93 / Gemmeiza 9 and Giza 163 / Giza 168 showed the highest negative effects. These results suggest the presence of non-additive gene effects in these crosses. Similar results were obtained by Millus and Line (1986), Shehab El-Din and Abdel-Latif (1996) and Mahgoub, Hayam(2001).

Table 4. Estimates of specific combining ability effects for wheat stripe and leaf rusts of F_1 diallel crosses.

Hybrid	Stripe rust	Leaf rust
Sakha 61 / Sakha 93	1.067**	0.862*
Sakha 61 / Giza 163	-1.605**	-2.312**
Sakha 61 / Giza 164	-2.410**	-0.140
Sakha 61 / Giza 168	0.038	2.691**
Sakha 61 / Gemmeiza 9	0.371**	0.982*
Sakha 61 / Sids 1	0.655**	-0.968*
Sakha 93 / Giza 163	-2.606**	0.101
Sakha 93 / Giza 164	-2.284**	2.534**
Sakha 93 / Giza 168	0.163	0.024
Sakha 93 / Gemmeiza 9	0.497**	-2,065**
Sakha 93 / Sids 1	0.780**	0.119
Giza 163 / Giza 164	0.864**	0.029
Giza 163 / Giza 168	0.735**	-1.880**
Giza 163 / Gemmeiza 9	-0.241	0.937*
Giza 163 / Sids 1	-0.878**	2.158**
Giza 164 / Giza 168	0.857**	-1.014**
Giza 164 / Gemmeiza 9	-0.500**	0.566
Giza 164 / Sids 1	-1.133**	0.834*
Giza 168 / Gemmeiza 9	0.135	-0.310
Giza 168 / Sids 1	-0.248	0.171
Gemmeiza 9 / Sids 1	0.085	0.362
LSD ij 0.05	0.280	0.757
0.01	0.369	0.996
LSD sij-ski 0.05	0.459	1.235
0.01	0.604	1.625

^{*, **} Significant at 0.05 and 0.01, probability levels respectively.

Hayman analysis:

Unbiased estimates of additive and dominance genetic variances can be obtained from a diallel cross only in the absence of epistasis. The slopes of the regression of Wr vs. Vr for the two studied characters in the present diallel were 0.808 and 0.979, both of which differed significantly from zero but not from one (Table 5). Furthermore, the t² test for each trait was non-significant. Therefore, the validity of the genetic assumptions for the Hayman (1954) analysis was verified.

Table 5. Values of t^2 , regression coefficient of covariance (Wr) on variance (Vr) and t-values for b=0 and b=1 for wheat stripe and leaf rust resistance.

Characters	t² coefficient	Regression for	t value for	t value		
			b=0	b=1		
Stripe rust	0.235	0.979	6.603**	0.137		
Leaf rust	1.126	0.808	6.651**	1.582		

b=0 and b= 1 indicate difference of regression coefficient value from 0 and 1 (unit), respectively.

Table 6 shows the components of variation and their standard errors for the rust traits. The additive (D) and dominance (H_1 and H_2) effects were highly significant in both traits. The additive effects were also higher in magnitude than the dominance effects in both characters. Thus the additive genetic variance was a major factor contributing to the performance of the two studied characters; suggesting that, selection in early segregating generations would be effective in developing promising resistant lines to stripe and / or leaf rusts. These results are in agreement with Yadav et al. (1998) and Boulot and El-Sayed (2001). However, these result are in contrast to Shehab El-Din and Abdel-Latif (1996) and Mahgoub, Hayam (2001).

The sign of F indicates the relative frequencies of dominant and recessive alleles in the parents. The F value was positive and highly significant for stripe rust, indicating an excess of dominant over recessive alleles, while the opposite is shown for leaf rust (Table 6).

The estimates of h² values were significant for stripe rust indicating that unidirectional dominance and the existence of many positive genes controlling this character. Meanwhile, the overall dominance effects (h²) were not significant for leaf rust, indicating the absence of dominance over all loci in heterozygous phase. That could be ascribed to differences among parents in the direction of dominance effects.

^{**} Significant at 0.01, probability level

Table 6. Estimated genetic and environmental components of variance for wheat stripe and leaf rust resistance in F₁ diallel crosses. (Hayman 1954).

Components	Stripe rust		Leaf	Leaf rust		
of variation	MS	SE	MS	SE		
D	15.834**	±1.088	9.739**	±0.565		
F	8.896**	±2.610	-3.148*	±1.356		
H ₁	8.083**	±2.619	7.638**	±1.360		
H ₂	6.038**	±2.308	6.967**	±1.199		
h ²	3.327*	±1.550	1.230	±0.805		
E	0.035	±0.385	0.248	±0.200		

^{*, **} Significant at 0.05 and 0.01, probability levels, respectively.

The degree of dominance $(H_1/D)^{-1/2}$ was < one for both traits, indicating average partial dominance (Table 7). Additionally, the proportion of genes with positive and negative effects in the parents $(H_2/4H_1)$ confirmed the results obtained from H2 estimate and showed unequal frequencies of positive and negative genes among parents. The ratio of dominant to recessive alleles in the parents, (KD / KR) was greater than one for stripe rust reflecting greater frequency of dominant genes while, the opposite was true for leaf rust. These results confirmed deductions from the positive and negative values of the F component and the highly significant H_1 and H_2 estimate in the two studied characters.

The estimated number of effective factors (K), controlling each rust trait and exhibiting dominance to a certain degree, showed the presence of at least one effective factor for stripe or leaf rust resistance (Table7). The parents possessed most increasing or decreasing genes, might be detected by comparing Wri + Vri with Yr. If the correlation coefficient (r) between them is negative, then the parents having most of the increasing genes will have the lowest value of Wri + Vri and Vice versa (Singh and Choudhary 1977). Therefore, the data obtained indicated that dominance direction was towards resistance for stripe rust and towards susceptibility for leaf rust which was confirmed by estimates of the most dominant (YD) and most recessive (YR) parent (Table 7). A completely recessive parent was higher than completely

dominant one for stripe rust. Thus, resistance was dominant over susceptibility. In contrast, for leaf rust the completely dominant parent was higher than completely recessive one, indicating that susceptibility was dominant over resistance

Table 7. Estimates of genetic ratios and heritability for rust reaction in F₁ diallel crosses.

Parameters	Characters		Parameters	Char	acters
	Stripe rust	Leaf rust		Stripe rust	Leafrust
(H ₁ /D) ^{1/2}	0.714	0.886	YD	-0.381	11.135
H ₂ /4H ₁	0.187	0.228	YR	8.893	0.564
KD/KR	2.296	0.691	h(n)	0.744	0.772
h²/ H₂ (K)	0.551	0.176	h(₅)	0.994	0.971
r	0.887	-0.761			

As shown in Table 7, broad and narrow-sense heritability values were high, revealing that most of the phenotypic variability was due to genetic effects and indicating that the additive genetic component was the major contributing factor in the performance of these characters. Therefore, selection could be practiced in early segregating generations for stripe and / or leaf rust resistance. These conclusions are in harmony with Shehab El-Din and Abdel-Latif (1996), Boulot and El-Sayed (2001) and Zhang *et al.* (2001).

In conclusion wheat breeders could manipulate stripe and / or leaf rust resistance to develop cultivars resistant to these destructive diseases, via selection for these traits in early generations. Combining ability analyses can also help breeders in choosing those parental combination which when crossed will result in the highest proportion of desirable segregates.

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وراثة المقاومة لمرض الصدأ المخطط وصدأ الأوراق في القمح الربيعي

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* البرنامج القومي لبحوث القمح - معهد بحوث المحاصيل الحقلية - مركز البحوث الزراعية **معمل بحوث أمراض النبات-محطة بحوث سخا

يهدف البحث إلى دراسة الأهمية النسبية لمكونات التباين الوراثي والقدرة العامة والخاصة للتآلف بالنسبة لصفات المقاومة لمرض الصدأ المخطط (الأصفر) وصدأ الأوراق (البرتقالي) في قمح الخبز. وباستخدام سبعة أصناف من القمح متباينة المقاومة وهي سخا ٢١، سخا ٩٣، جيزة ١٦٣، جيزة ١٦٤، جيزة ١٦٤، جيزة ١٦٤، جيزة ١٦٤، جيزة ١٦٤، جيزة ١٦٤، جيزة ١٠٤/ بحميزة وسدس ١ .تم تهجينا دائريا مستبعداً الهجن العكسية . زرعت الأباء وهجسن الجيل الأول في تجربة حقلية كنباتات فردية في ثلاث مكررات في ٢٠٠٢/٢٠٠١ بمحطسة السبحوث الزراعية بسخا . أوضح التحليل وجود اختلافات وراثية بين التراكيب الوراثية لمقاومة مرض الصدأ المخطط وصدأ الأوراق .وأظهر تحليل القدرة على التالف زيادة القدرة العامة (GCA) على القدرة الخاصة (SCA) للصفتين، وكانت قيمة النسبة (+ 2GCA) (SCA) على التآلف بالنسبة لكل من الصفتين في حين كان الصنفان جميزة ٩ وجيزة ١٦٨ أفضل الأباء قدرة على التآلف اصفة المقاومة لمرض الصدأ المخطط . بينما كان الصنفان جيزة ١٦٣ أعلى الأصناف قدرة على التآلف بالنسبة للصدأ المخطط . بينما كان الصنفان جيزة ١٦٣ وجيزة ١٦٨ أوجيزة ١٦٤ أقل الأصناف قدرة على التآلف بالنسبة للصدأ المخطط . بينما كان الصنفان جيزة ١٦٣ أقل الأصناف قدرة على التآلف النسبة للصدأ المخطط .

أظهر تحليل كل من القدرة على التآلف والمكونات الوراثية بطريقة (1954) Hayman (1954) أن الجرزء الأساسي من الاختلافات الوراثية ناتج عن الفعل الجيني المضيف ، ولكن كان للتأثيرات السيادية دورا أقل أهمية في وراثة هذه الصفات . وكان ذلك واضحاً من انخفاض درجة السيادة عن الوحدة مما يعني سيادة جزئية في الصفتين و كانت قيمة F موجبة ومعنوية لصفة المقاومة لمرض الصدأ الأصفر مما يدل على زيادة جينات السيادة بالمقارنة مع الجينات المتنحية في حين كانت عكس ذلك بالنسبة لصدأ الأوراق . كما اتجهت المقاومة بالنسبة للصدأ المخطط إلى السيادة بينما كان العكس هو الصحيح في حالة المقاومة لصدأ الأوراق . كما أوضحت النتائج ارتفاع قيم درجة التوريث بمعناها الواسع والضيق لكلنا الصفتين، مما يشير إلى أن الانتخاب في الأجيال الانعزالية المبكرة ربما يكون فاعلا في الحصول على تراكيب وراثية تحمل صفة المقاومة .