

Comparison of two crossing and four selection schemes for yield, yield traits, and slow rusting resistance to leaf rust in wheat

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Summary

The most important breeding objectives in crop improvement are improving grain yield, grain quality, and resistances to various biotic and abiotic stresses. The objectives of our study were to compare two crossing and four selection schemes for grain yield, yield traits, and slow rusting resistance to leaf rust (*Puccinia recondita*) based on additive genes in wheat (*Triticum aestivum*), and to identify the most efficient crossing and selection methodologies in terms of genetic gains and cost efficiency. Segregating populations were derived from 18 simple crosses and the same number of top (three-way) crosses. Half of the crosses were derived from Yecora 70 and the other half from Veery #10 as the common leaf rust susceptible parents. The four selection schemes were: pedigree, modified bulk (F_2 and F_1 -top as pedigree, selected lines in F_3 , F_4 , F_2 -top, F_3 -top as bulk; and pedigree in F_5 and F_4 -top populations), selected bulk (selected plants in F_2 , F_3 , F_4 , F_1 -top, F_2 -top and F_3 -top as bulk; and pedigree in F_5 and F_4 -top populations), and nonselected bulk (bulk in F_2 , F_3 , F_4 , F_1 -top, F_2 -top and F_3 -top; and pedigree in F_5 and F_4 -top populations). A total of 320 progeny lines, parents and checks were tested for grain yield, other agronomic traits and leaf rust resistance during the 1992/93 and 1993/94 seasons in Ciudad Obregon (Sonora State, Mexico) which represents a typical high yielding irrigated site. The influence of the type of cross and the selection scheme on the mean grain yield and other traits of the progenies was minimal. The selection of parents was the most important feature in imparting yield potential and other favourable agronomic traits. Moreover, the highest yielding lines were distributed equally. Progeny lines derived from Veery #10 crosses had significantly higher mean grain yield compared to those derived from the Yecora 70 crosses. Furthermore, a large proportion of the highest yielding lines also originated from Veery #10 crosses. Mean leaf rust severity of the top cross progenies was lower than that of the simple cross progenies possibly because two parents contributed resistance to top cross progenies. Mean leaf rust severity of the nonselected bulk derivatives was twice that of lines derived from the other three schemes. Selected bulk appears to be the most attractive selection scheme in terms of genetic gains and cost efficiency.

Introduction

Improved grain yield, grain quality and resistances to various biotic and abiotic stresses are the most important breeding objectives in most crop improvement programs. Leaf rust, caused by *Pucci-*

nia recondita tritici, is an important biotic constraint for the sustainable production of wheat (*Triticum aestivum* L.) in most environments. Among several possible approaches currently known to reduce losses due to leaf rust, CIMMYT's chosen strategy is to search for resistance,

understand its genetic basis, and incorporate durable sources of resistance into high yielding germplasm. Durable resistance to leaf rust in wheat usually results from the additive interactions of a few (two to four) minor genes of partial (slow rusting) nature (Bjarko & Line, 1988; Broers & Jacobs, 1989; Kuhn et al., 1980; Singh & Rajaram, 1992). When these partial genes are present alone, resistance is not complete. However, resistance based on the interactions of three to four such genes is highly effective and stable across environments (Singh & Rajaram, 1995). Singh & Rajaram (1995) discuss the steps being followed at CIMMYT to generate different combinations of such genes. These steps include: limiting the use of currently effective hypersensitive genes; crossing parents that carry different sets of additive genes; exposing segregating generations to high disease pressure generated by epidemics artificially created with selected pathotypes; selecting plants or lines with low terminal disease severity; conducting multilocational testing to evaluate the effectiveness and stability of resistance across environments; and genetically analysing the resistance in selected wheats to confirm the presence of additive genes.

In wheat breeding, simple, top (three-way) and double (four way) crosses are used most often to combine desirable traits from two, three or four parents, respectively. Pedigree and bulk methods of selection are classic, textbook methods (Allard, 1960). Both methods have their advantages and disadvantages in terms of genetic gains and cost efficiency. CIMMYT's bread wheat breeding program in the mid 1980s shifted from the pedigree method to a modified bulk selection scheme to improve cost efficiency without sacrificing progress in genetic gains. In theory, selecting for traits controlled by single major genes is easily achieved using any crossing and selection scheme. However, which selection scheme is most suitable for traits under polygenic or quantitative genetic control remains debatable. Modifying selection schemes that further reduce operational costs without affecting the efficiency of genetic gains are warranted.

The objectives of our study were to compare two crossing and four selection schemes for grain yield, yield traits, and slow rusting resistance to leaf rust in

wheat and to identify the most efficient methodology in terms of genetic gains and costs.

Materials and methods

Two leaf rust susceptible parents Yecora 70 and Veery #10 were crossed during the 1988-89 winter season at Ciudad Obregon, Sonora State, Mexico, with the same nine leaf rust resistant parents. Our previous studies had indicated that the adult plant resistance of the seedling susceptible parents involved additive interactions of two to four slow rusting genes. The F_1 hybrids were planted during the 1989 summer season at CIMMYT's research station at El Batán, Mexico State. Each of the nine F_1 s involving Yecora 70 and Veery #10 were top crossed with a third leaf rust resistant parent. The second and third leaf rust resistant parents were, therefore, common to all crosses involving Yecora 70 and Veery #10. A total of 13 leaf rust resistant parents were involved in the simple and top crosses.

The F_1 hybrids from the simple crosses were bulk harvested, and approximately 1500 F_2 plants were space sown (10 cm between plants) on 90-cm wide raised beds with two rows, 20 cm apart, on top of the beds during the winter 1989/90 season. Eight beds 11-m long were used for each F_2 population. Approximately 200 hybrid seeds of each top cross were also space sown on one 11 m long bed. The leaf rust epidemic was created by inoculating spreader rows with an equal mixture of pathotypes TCB/TD and TBD/TM of *P. recondita tritici* (Singh, 1991). These pathotypes were chosen because the parents were susceptible as seedlings to at least one of them. Plants with acceptable levels of leaf rust resistance and good agronomic traits were tagged in both the F_2 and F_1 -top populations. The four selection schemes diverged at this point and are described below. Segregating generations were grown alternately at El Batán and Cd. Obregon locations. Leaf rust epidemics were artificially created at both locations using the same pathotypes.

Nonselected bulk

These populations were synthesised by bulk har-

vesting and threshing of one spike from each of the F_2 or F_1 -top plants. The subsequent F_3 , F_4 and F_5 generations from the simple crosses, and the F_2 -top, F_3 -top and F_4 -top generations from the top crosses were grown on two 11-m long raised beds. Approximately 800 seeds of each population were space sown 5 cm apart in the F_3 , F_4 , F_2 -top and F_3 -top generations. One spike from each plant was bulk harvested and threshed. Approximately 400 seeds of each F_5 and F_4 -top population were space sown 10 cm apart. Plants showing good leaf rust resistance and acceptable agronomic features were selected and harvested individually. Plants with good grain characteristics were retained to obtain advanced lines.

Selected bulk

These populations were synthesised by bulk harvesting and threshing of one spike from each of the selected F_2 and F_1 -top plants. Subsequent generations were grown in a manner similar to that described for the nonselected bulk population. One spike from only those plants which had acceptable leaf rust resistance and good agronomic features were bulk harvested in the F_3 , F_4 , F_2 -top and F_3 -top generations. The selection procedures in the F_5 and

F_4 -top were same as those described for the nonselected bulk schemes.

Pedigree

Plants selected in the F_2 and F_1 -top generations were harvested individually. Those with good seed characteristics were advanced to subsequent generations. Approximately 40 seeds of each line in the F_3 , F_4 , F_5 , F_2 -top, F_3 -top and F_4 -top generations were space sown 10 cm apart in two rows, 2 m in length, on the 90-cm wide raised beds. A maximum of three plants from lines producing plants with desirable agronomic features and acceptable leaf rust resistance was selected and harvested individually. Plants with poor seed characteristics were discarded in each generation.

Modified bulk

Approximately 80 seeds of the selected F_2 or F_1 -top plants retained in the pedigree method were also grown on 2-m long beds. The F_3 and F_2 -top lines were evaluated visually, and those with enough plants showing acceptable leaf rust resistance and good agronomic features were retained for harvest. Between 20 to 30 spikes of each retained line were bulk harvested and graded for seed characteristics.

Table 1. Grain yield and other traits of top performing parents and progenies

Trait	Top performing		% gain over the top parent
	Parent	Progeny	
Grain yield ($t\ ha^{-1}$)	6.7 b ¹	7.1 a	5.6
Biomass ($t\ ha^{-1}$)	16.4 b	17.1 a	4.0
Harvest index (%)	50.2 a	49.8 a	-0.8
Kernel wt (mg)	43.6 b	49.6 a	13.8
Spikes m^{-2}	411.0 b	454.0 a	10.5
Kernels m^{-2}	20825.0 a	21037.0 a	1.0
Kernels/spike	43.5 b	49.9 a	14.7
Test wt ($kg\ hl^{-1}$)	82.4 a	83.2 a	1.0
Earliest heading (d)	72.0 a	63.0 b	12.5
Latest heading (d)	84.0 b	95.0 a	13.1
Earliest maturity (d)	124.0 a	119.0 b	4.0
Latest maturity (d)	133.0 b	138.0 a	3.8
Leaf rust (%)	1.0 a	1.0 a	0.0

¹ Means followed by different letters denote significant differences at $P = 0.05$.

Table 2. Mean grain yield and other traits of 160 lines obtained from 18 crosses involving Yecora 70 or Veery #10 as a parent

Trait	Common parent in the crosses		LSD (P = 0.05)
	Yecora 70	Veery #10	
Grain yield (t ha ⁻¹)	5.80 b ¹	6.16 a	0.06
Biomass (t ha ⁻¹)	13.46 b	14.36 a	0.17
Harvest index (%)	43.34 a	43.11 a	0.40
Kernel wt (mg)	39.18 a	39.34 a	0.39
Spikes m ⁻²	322.71 a	302.28 b	6.43
Kernels m ⁻²	14939.50 b	15796.00 a	223.76
Kernels/spike	35.30 b	39.28 a	0.61
Test wt (kg hl ⁻¹)	80.74 b	80.90 a	0.15
Heading (d)	74.19 b	76.83 a	0.59
Maturity (d)	125.37 b	126.40 a	0.46
Height (cm)	89.60 a	88.25 b	0.71
Leaf rust (%)	4.88 a	5.83 a	1.14

¹ Means followed by different letters denote significant differences at P = 0.05.

Similar selection pressure was applied in the F₄ and F₃-top generations. Approximately 40 plants were space sown 10 cm apart in the F₅ and F₄-top generations for selection of individual plants.

Advanced lines from each selection method were grown on 2-m long plots on raised beds and evaluated for homogeneity of leaf rust resistance and agronomic features. Selected lines were retained for yield trials.

Comparisons of grain yield and other agronomic traits were conducted on 80 progeny lines derived from each of the four selection schemes. Of these 80 lines, 40 were derived from simple crosses and 40 from top crosses. Of the 40 lines in each of the two crossing methodologies, 20 were derived from Yecora 70 and 20 from Veery #10. In other words, a total of 160 lines included in the yield trial were derived from each of the simple and top crosses, or from

crosses where Yecora 70 and Veery #10 were common parents. A total of 320 lines, parents and checks were planted during the 1992-93 and 1993-94 seasons at the experiment station in Cd. Obregon following the alpha-lattice design with two replicates in each year. Field plots consisted of eight 5-m rows; 4 m of the six centre rows were combine harvested (harvested area = 5 m²). Yield traits were estimated by a sampling procedure described in Ma & Singh (1996). A factorial ANOVA was used for the combined statistical analysis of the two-year experiment. Because there was no gain in the efficiency using alpha-lattice, the experiment was analysed following the randomised block design; actual means are presented in the results. Grain yield, biomass and kernel weight are adjusted to 0% moisture.

Leaf rust resistance was evaluated in separate ex-

Table 3. Origin of the highest yielding 10, 20 and 30 lines from 18 crosses involving Yecora 70 or Veery #10 as a parent

No. of highest yielding lines	Highest yielding lines derived from parent		χ^2 _{1:1}
	Yecora 70	Veery #10	
10	2	8	3.6 ¹
20	3	17	9.8 ²
30	3	27	19.2 ²

¹ Non significant χ^2 values at P = 0.05.

² Significant χ^2 values at P = 0.01.

Table 4. Comparison of mean grain yield and other traits of all 160 lines obtained from each of two types of crosses

Trait	Type of Cross		LSD (P = 0.05)
	Simple	Top	
Grain yield, (t ha ⁻¹)	6.01 a ¹	5.94 b	0.06
Biomass (t ha ⁻¹)	13.88 a	13.94 a	0.17
Harvest index (%)	43.54 a	42.91 b	0.40
Kernel wt (mg)	40.03 a	38.49 b	0.39
Spikes m ⁻²	304.30 b	320.69 a	6.43
Kernels m ⁻²	15127.00 b	15608.40 a	223.76
Kernels/spike	37.92 a	36.65 b	0.61
Test wt (kg hl ⁻¹)	80.75 a	80.88 a	0.15
Heading (d)	75.54 a	75.48 a	0.59
Maturity (d)	125.72 b	126.05 a	0.46
Height (cm)	89.09 a	88.77 a	0.71
Leaf rust (%)	6.12 a	4.60 b	1.14

¹ Means followed by different letters denote significant differences at P = 0.05.

periments where two 1-m rows were artificially inoculated with *P. recondita* pathotypes TCB/TD and TBD/TM. These two pathotypes were chosen because the selected lines included in the yield trials were susceptible as seedlings to one or both pathotypes. Leaf rust severity estimates for adult plants were based on the modified Cobb scale (Peterson et al., 1948).

Results

The mean grain yield (over the two years) of the highest yielding progeny was significantly higher (5.6%) than the highest yielding parent (Table 1). Yield traits also showing significant progress were biomass, kernel weight, spikes m⁻² and kernels/spike, whereas the harvest index, kernels m⁻² and test weight remained unchanged (Table 1). Trans-

gressive segregation for both earlier and later heading and maturing phenotypes was also evident (Table 1). Leaf rust severities of the best parent and the progeny were same (Table 1). These results, thus, indicate advances in grain yield and several other traits in response to selection.

The mean grain yield of Veery #10 derived progeny lines was significantly higher than those of Yecora 70 (Table 2). Lines with Veery #10 also had significantly higher biomass, kernels m⁻², kernels/spike, test weight, days to heading and maturity. Yecora 70 derivatives were slightly taller and significantly better for spikes m⁻². Differences were non-significant for harvest index, kernel weight, and leaf rust severity (Table 2). Although 8 of the 10 highest yielding lines were derived from Veery #10, the distribution was in accordance to a 1:1 ratio (Table 3). Seventeen of the top 20, and 27 of the top 30 highest yielding lines were again derived from Veery #10

Table 5. Origin of the highest yielding 10, 20 and 30 lines from two types of crosses

No. of highest yielding lines	Highest yielding lines derived from			$\chi^2_{1:1}$
		Simple crosses	Top crosses	
10	3		7	1.6 ¹
20	8		12	0.8 ¹
30	16		14	0.1 ¹

¹ Non significant χ^2 values at P = 0.05.

Table 6. Comparison of mean grain yield and other traits of 80 lines obtained from four selection schemes

Trait	Selection scheme				LSD (P=0.05)
	Pedigree	Modified bulk	Nonselected bulk	Selected bulk	
Grain yield (t ha ⁻¹)	6.09(1)a ¹	5.98(3)b	5.87(4)c	5.99(2)b	0.09
Biomass (t ha ⁻¹)	13.97(1)a	13.95(3)a	13.76(4)a	13.96(2)a	0.24
Harvest index (%)	43.85(1)a	43.07(3)b	42.87(4)b	43.11(2)b	0.56
Kernel wt (mg)	38.72(4)b	39.44(2)a	39.47(1)a	39.40(3)a	0.55
Spikes m ⁻²	318.40(1)a	314.90(2)ab	308.20(4)b	308.50(3)b	9.09
Kernels m ⁻²	15904.00(1)a	15272.00(3)b	15002.00(4)b	15293.00(2)b	316.00
Kernels/spike	37.96(1)a	36.76(4)b	37.06(3)b	37.38(2)ab	0.86
Test wt (kg hl ⁻¹)	75.50(3)a	74.50(4)b	76.00(2)a	76.10(1)a	0.84
Heading (d)	125.80(3)ab	125.50(4)b	126.10(2)ab	126.20(1)a	0.65
Maturity (d)	85.91(4)c	89.52(2)b	91.02(1)a	89.27(3)b	1.00
Height (cm)	80.86(2)a	80.70(4)a	80.87(1)a	80.84(3)a	0.21
Leaf rust (%)	3.37(4)b	4.32(2)b	9.91(1)a	3.83(3)b	1.61

¹ Numbers in parentheses indicate the ranking; different letters denote significant differences at P = 0.05.

(Table 3), which clearly indicated that Veery #10 was a better combiner than Yecora 70. The results, therefore, clearly indicate that the choice of parent did affect grain yield performance.

Mean grain yield of lines derived from simple crosses was slightly, but significantly, higher than those from top crosses (Table 4). Harvest index, kernel weight and kernels/spike were significantly higher for simple cross derivatives, whereas spikes m⁻², kernels m⁻² and maturity were higher for top

cross derivatives. Other traits did not show any significant differences. Average leaf rust severity was significantly lower for top cross derivatives (Table 4), which was to be expected because the F₁s were always crossed with a resistant top cross parent. The highest yielding 10, 20 and 30 lines originated equally from simple and top crosses (Table 5). These results, therefore, indicated that although the mean grain yield was higher for the simple cross derivatives, the origin of the highest ranking lines was un-

Table 7. Comparison of mean grain yield and other traits of the 10 highest yielding lines obtained from each of four selection schemes

Trait	Selection scheme				LSD (P=0.05)
	Pedigree	Modified bulk	Nonselected bulk	Selected bulk	
Grain yield (t ha ⁻¹)	6.65(3)a ¹	6.79(1)a	6.71(2)a	6.79(1)a	0.16
Biomass (t ha ⁻¹)	14.99(3)a	14.98(4)a	15.20(2)a	15.46(1)a	0.68
Harvest index (%)	44.60(2)a	45.44(1)a	44.47(3)a	44.10(4)a	2.00
Kernel wt (mg)	38.10(3)a	39.25(1)a	38.89(2)a	39.25(1)a	2.64
Spikes m ⁻²	317.46(4)a	322.46(3)a	331.16(2)a	334.11(1)a	38.06
Kernels m ⁻²	17583.00(1)a	17365.00(4)a	17402.00(2)a	17400.00(3)a	1353.00
Kernels/spike	41.17(2)a	41.61(1)a	40.92(3)a	38.48(4)a	3.39
Test wt (kg hl ⁻¹)	80.78(4)a	81.50(1)a	81.43(2)a	81.07(3)a	1.01
Heading (d)	76.63(2)a	75.88(3)a	75.85(4)a	79.50(1)a	3.69
Maturity (d)	126.45(2)ab	125.88(3)b	125.05(4)b	128.70(1)a	2.51
Height (cm)	85.25(4)a	90.00(1)a	88.50(2)a	87.38(3)a	5.75

¹ Numbers in parentheses indicate the ranking and different letters denote significant differences at P = 0.05.

Table 8. Origin of the highest yielding 10, 20 and 30 lines from four selection schemes

No. of highest yielding lines	Highest yielding lines derived from					χ^2 1:1:1:1
	Pedigree	Modified bulk	Nonselected bulk	Selected bulk		
10	1	4	2	3		1.9 ¹
20	4	4	5	7		1.2 ¹
30	5	9	5	11		4.1 ¹

¹ Non-significant χ^2 values at $P = 0.05$.

affected by the type of cross. Moreover, using two resistant parents in the cross was more beneficial than using only one.

The mean grain yield performance of progeny lines derived from the pedigree selection scheme was slightly but significantly higher than with the other three selection schemes (Table 6). It was followed by the selected bulk and the modified bulk schemes, which were slightly but significantly superior to bulk selection. The differences for other traits were also minimal (Table 6). For example, the ranking of selection schemes for biomass followed the same order as grain yield; however, the differences were nonsignificant (Table 6). The ranking was the same for harvest index and kernels m^{-2} , but the pedigree selection was significantly superior. Mean leaf rust severities for pedigree, modified bulk and selected bulk schemes were similar, however the mean leaf rust severity for bulk selection was almost twice as high. This indicated that the nonselected bulk method was the least desirable

method for selecting for leaf rust resistance when such resistance is based on the additive interactions of slow rusting genes.

Comparison of grain yield and other traits of the 10 highest yielding lines obtained from each of the four selection schemes did not reveal any statistical differences for all traits, except for days to maturity (Table 7). Although the highest yielding 10, 20 and 30 lines statistically were distributed equally in the four selection schemes, a bias was evident in favour of the selected bulk and modified bulk schemes (Table 8). These results, therefore, indicate that the distribution of the highest yielding lines in the four selection schemes was independent of their population mean.

Phenotypic correlation coefficients between grain yield and other traits are given in Table 9. Biomass and kernels m^{-2} had the highest influence on grain yield, followed by spikes m^{-2} , kernels/spike, harvest index, test weight, etc. Kernel weight and

Table 9. Phenotypic correlations between grain yield and other traits

Trait	Biomass	Harvest index	Kernel weight	Spikes m^{-2}	Kernels m^{-2}	Kernels/spike	Test weight	Heading	Maturity	Height
Grain yield	0.68***	0.31***	-0.05	0.47***	0.69**	0.37***	0.23***	0.12*	0.08	-0.19***
Biomass		-0.48***	-0.26**	0.14*	0.63**	0.21**	0.03	0.32**	0.31**	0.06
Harvest index			0.26***	0.40***	0.02	0.13*	0.25***	-0.29***	-0.32***	-0.33***
Kernel weight				-0.22***	-0.75***	-0.34***	0.24***	-0.37***	-0.41***	0.09
Spikes m^{-2}					0.48***	-0.41***	0.22***	0.02	-0.01	-0.42***
Kernels m^{-2}						0.46***	-0.01	0.34***	0.33***	-0.20***
Kernels/spike							-0.12*	0.15**	0.17**	0.08
Test weight								-0.34***	-0.42***	0.03
Heading									0.85***	0.04
Maturity										-0.02

*, **, and *** denote significant r values at $P = 0.05$, 0.01, and 0.001, respectively.

Table 10. Comparison of four selection schemes for land use efficiency from the growing of F_1 generation to the obtaining of advanced lines

Selection method	Total area (m ²)	Total advanced lines obtained	Land/line obtained (m ²)
Pedigree	8143.1	553	17.7
Modified bulk	5094.8	170	30.0
Nonselected bulk	4112.0	149	27.6
Selected bulk	4112.0	407	10.1

maturity did not influence grain yield performance of the progenies.

Discussion

The results indicate that selecting the parents was much more important than choosing the type of cross or selection schemes to be followed in breeding for increased yield potential. The selection criteria in segregating generations used by most wheat breeders include: desirable plant height, plant architecture, tillering ability, spike morphology, high spike fertility, leaf hygiene, disease resistances, desirable days to heading and maturity. Selection for grain characteristics such as grain colour, size, plumpness, etc., is also practised. Only a few plants with all the desirable traits possess high grain yield potential. Therefore, obtaining a progeny with higher grain yield potential than the parents cannot be predicted before the cross is made and the yield trial carried out. Selecting for plant and grain characteristics only enhances the probability of identifying outstanding progenies. Thus, any selection scheme that shifts the population towards desirable phenotypes should result in higher frequencies of the desired genotypes.

Pedigree selection is a very time consuming and costly method of crop improvement. In contrast, bulk selection appears to be the cheapest alternative. In our study we were able to compare the land used by each advanced line produced at the end of the selection (Table 10). Selected bulk was the most efficient selection scheme according to this criterion, followed by pedigree selection, which used almost twice the land area. Modified bulk and nonselected bulk were the least efficient methodologies and used three times the area when compared to the

selected bulk scheme. The cost of both scientific and technical labour in terms of selecting, harvesting, threshing, planting, etc., is expected to be several times higher for the pedigree method. Moreover, any number of desirable plants can be maintained as a population in the selected bulk segregating generations with only a slight increase in the operational cost compared to the nonselected bulk scheme. Selected bulk, therefore, appears to be the most attractive selection scheme in terms of genetic gains and cost efficiency. This method showed a definite superiority over bulk selection and was similar to the pedigree and modified bulk schemes for improving leaf rust resistance based on additive genes. The selected bulk scheme is now being practised on a larger scale by CIMMYT's bread wheat improvement program.

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