

MASTER NEGATIVE NUMBER: 09295.58

Arunachalam, V. and Srivastava, P. S. L.
Assessment of Genetic Potential of Multiple
Crosses in Triticale.

Genetica Agraria, 34 (1980): 245-256.

Record no. D-39

ASSESSMENT OF GENETIC POTENTIAL OF MULTIPLE CROSSES
IN TRITICALE

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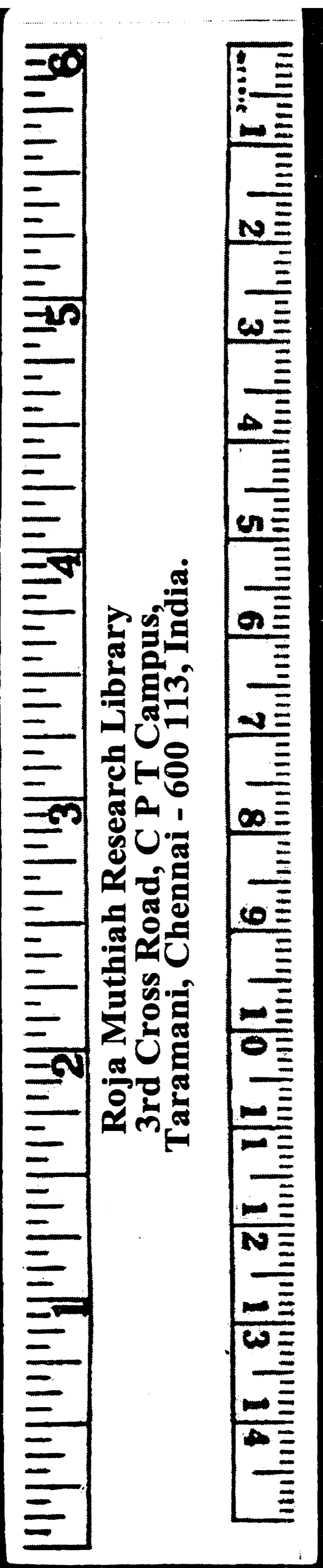
Received: January 27, 1979

INTRODUCTION

New concepts of breeding lay greater emphasis on improvement in physiological, biochemical and genetic components of yield to realise quantum jumps in yield itself. Plant breeders strive to record simultaneous improvement in many of these components but to succeed it is necessary to start with a population having a broad genetic base. Most of the yield components are known to be under polygenic control; so much so, a plant breeder would need as close a genetic characterisation as possible of parents yet through phenotypic measurements. The combining ability effects, general (gca) and specific (sca), are some realistic parameters to serve this purpose. Gca effect is proportional to the additive genetic effect and breeding value (FALCONER, 1964) and sca effect is a manifestation of all non-additive effects.

A criterion for genetic characterisation of parent or cross should include as many yield components as possible. It is then worthwhile to relate this criterion with the performance of single and multiple crosses as measured by their overall heterosis, and to

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discover the underlying genetic basis. If this is done, it is possible to identify certain repeatable steps to produce single or multiple crosses for the desired purpose. Obviously such a programme will produce the desired results with some probability. It will be our attempt to search for that particular programme which has this probability as high as possible.

Experiments on single and multiple crosses undertaken in triticale during 1972-1974 had the following major objectives:

a) Genetic characterisation of single and multiple crosses, their parents and grandparents,

b) Analysis of the improvement in multiple crosses in relation to the genetic status of their immediate and grandparents and

c) New approaches to breeding of triticale, and self-pollinated crops, in general.

MATERIALS AND METHODS

Ten triticale varieties, A147, B90, LST2, ST69-2, TCL1, TH2, T1, T15, M1019 and T5003, were chosen on the basis of intra- and inter-varietal genetic divergence (SRIVASTAVA and ARUNACHALAM, 1977). A full diallel set of crosses including reciprocals, grown in a randomised block design in plots of single rows each 300 cm in length, was evaluated during 1972-73 (F1A) and 1973-74 (F1B). Observations were recorded on random samples of five plants on X1: number of days to flower, X2: plant height (cm), X3: number of effective tillers, X4: number of grains in the main ear, X5: 100-grain weight (gm) and X6: grain yield per plant (gm). Single plant data were analysed on fixed effects model of GRIFFING (1956). When the value of the hybrid differed significantly in the desired direction from that of its better parent, heterosis was estimated as the percent increase of the hybrid over the better parent.

A new approach following BANDYOPADHYAY (1976) was adopted to classify a parent as high (H) or low (L), on the basis of its gca effects over the six yield components. A norm (m) which is the mean of only the statistically significant (from zero) gca effects, was obtained for each character. Parents whose gca effects fell above m were H and the rest L. Based on a score of + 1 for H, 0 for non-significant gca and - 1 for L, a total score over the six characters was computed for each parent. The mean of these scores provided the norm to classify finally the parents as H or L. Like-

wise sca was classified as H or L for each cross. Some crosses received an overall score zero (which corresponded to L status) due to *a*) mutual cancellation of H and L over the six characters denoted by LC and *b*) non-significant sca for every character denoted by LN. A cross was defined to be heterotic if it showed heterosis for at least two of the six characters (based on the criteria derived by BANDYOPADHYAY, 1976).

Six single crosses (in their F1) formed in a half-diallel design without parents and reciprocals, from T1, LST2, B90, TCL1, were chosen as the female parents of 3-way (TW) and 4-way (FW) crosses. They were: F1 = T1 X LST2; F2 = T1 X B90; F3 = T1 X TCL1; F4 = LST2 X B90; F5 = LST2 X TCL1 and F6 = B90 X TCL1. The male parents of TW were the varieties, TD1, 6TA204, B46 and T4989. Those of FW formed a similar half-diallel as for the female parents. They were: M1 = M1019 X T15; M2 = M1019 X TH2; M3 = M1019 X A147; M4 = T15 X TH2; M5 = T15 X A147 and M6 = TH2 X A147. TW and FW were made in a line \times tester design where the lines were the single crosses in half-diallel. The following model was of relevance for TW and FW:

$$X_{abcd} = \mu + G_a + G_b + S_{ab} + r_c + e_{abcd} \text{ where}$$

μ = general mean,

a = female parent that is itself a single cross of the type (*i* \times *j*), *i*, *j*, = 1 to 4, *j* > *i*,

b = male parent that is a single variety, say *m*, *m* = 1 to 4 for TW and is itself a single cross of the type (*k* \times 1), *k*, *l* = 1 to 4, *l* < *k* for FW,

G_a = gca effect of the female parent in TW or FW

$$= g_i + g_j + s_{ij} \text{ where}$$

g_i = gca effect of the grand female,

g_j = gca effect of the grand male,

s_{ij} = sca effect of grandparents on the female side,

G_b = gca effect of the male parent

$$= g_m \text{ in TW}$$

$$= g_k + g_l + s_{kl} \text{ in FW with similar meanings as in } G \text{ but on male side,}$$

S_{ab} = sca effect at the multiple cross level,

r_c = effect due to c^{th} replication,

e_{abcd} = environmental effect peculiar to the d^{th} plant of the cross, $a \times b$, in the c^{th} replication.

The combining ability ANOVA follows the usual line \times tester model. The analysis of marginal means of the parents (by method 4 of GRIFFING, 1956) provides the estimates of the gca and sca effects at grandparental level.

RESULTS

Besides the gca and sca mean squares, the estimates of the respective variances indicated both additive and non-additive gene action in single and multiple crosses. No relationship was apparent between the means and the gca effects of the parents.

Single crosses: Based on six yield components, A147, LST2, ST69-2, T15, M1019 and T5003 were high and the rest, B90, TCL1, TH2 and T1 low general combiners both in F1A and F1B. All high parents showed good gca effect for earliness (except T15), yield and in general, number of tillers and number of grains per ear. The situation was reverse, in general, for the low parents.

Of the 48 heterotic crosses, 23 were heterotic in HH, giving a proportion 23/48 of heterotic crosses in F1A. It was 22/48 and 3/48 for HL and LL respectively. HL was inferior to HH for X3 and superior for X5 in F1A while it was superior to HH for X3 and inferior for X6 in F1B (Table 1). By and large, HH and HL did not differ very greatly in the expression of heterosis.

TABLE 1

Frequency of heterotic single crosses in different groups defined by gca

Group n	HH 30		HL 48		LL 12		Total 90	
	F1A	F1B	F1A	F1B	F1A	F1B	F1A	F1B
X1	7	4	5	4	2	1	14	12
X3	15	4	8	9	0	3	23	16
X5	22	24	39	25	10	5	71	54
X6	21	16	19	12	2	0	42	28
Overall	23	16	22	11	3	3	48	30

n = number of crosses made in each group.

15 each of the heterotic crosses showed overall high sca effects in HH and HL in F1A (Table 6) in contrast to 11 in HH and only 6 in HL in F1B. Further, almost an equal percentage of heterotic crosses showed low sca effects both in HH and HL (this being true more of L and LC categories). Crosses showing LN grade of sca effects were to be found in F1A under HH category only. No heterosis was observed for X2 and X4. A majority of HH crosses showed heterosis in their reciprocals also.

Two hybrids, ST69-2 X LST2 and T5003 X ST69-2 were heterotic for all the four characters in F1A and the latter was so in F1B too. LST2 X TH2 and TH2 X ST69-2 were heterotic under HL in F1A and ST69-2 X TCL1, ST69-2 X TH2 and T1 X T15 in F1B. Heterotic hybrids were mostly produced by LST2, ST69-2, T5003 (of H status) and TH2 (of L status). All crosses heterotic for three or more characters showed invariably high sca effects, except A147 X LST2 in F1A and T15 X ST69-2 in F1B under HH and B90 X T15 in F1A and T1 X T15 in F1B under HL.

Multiple crosses: The gca status of the female parents remained the same in TW and FW except for the parent, B90 X TCL1. T1 X LST2, LST2 X B90 and LST2 X TCL1 were uniformly high general combiners while M1019 X T15, M1019 X TH2, M1019 X A147 and T15 X A147 were superior as male parents of FW (Table 2). Only TD1 was a high male parent in TW.

The gca effects, gf and gm, of grandparents and the sca effect, s at grandparental level were estimated for the first time (Table 3). The gca of a parent of the multiple cross, g, is the sum of gm, gf and s. The magnitude and direction of the combining ability effects of the grandparents could be related to the heterotic performance of a multiple cross. For instance, all the female H parents in TW had, in general, high grandparental sca effect except LST2 X B90 (Table 2). But the gca effects of grandparents were in opposing direction like L, H or H, L except for B90 X TCL1 where both were L. The trend was similar in FW except for the parents, LST2 X B90 and T1 X LST2 which had L grand parental sca. of the H male parents of FW, only M1019 X A147 had low grandparental sca.

The 8 parents, T1, LST2, B90, TCL1, M1019, T15, TH2 and A147, were remarkably stable in their gca in F1A, F1B, TW and FW. On an analysis of heterosis, it was observed that HL as a female produced higher frequency of heterotic crosses than LL

TABLE 2

Combining ability components of the grandparents and frequency of heterotic multiple crosses produced by them

Parents	gea status		Grandparental gea		grandparental sca		number of heterotic hybrids	
	a	b	Female	male	a	b	a	b
Female								
F1	H	H	L	H	H	L	3	4
F2	L	L	L	L	H	H	2	2
F3	L	L	L	L	L	L	1	1
F4	H	H	H	L	L	L	4	4
F5	H	H	H	L	H	H	3	4
F6	H	L	L	L	H	L	2	0
Male								
M1	—	H	H	H	—	H	—	4
M2	—	H	H	L	—	H	—	4
M3	—	H	H	H	—	L	—	2
M4	—	L	H	L	—	L	—	
M5	—	H	H	H	—	H	—	
M6	—	L	L	H	—	H	—	1

a = TW; b = FW; O = same status in TW, FW, F1A and F1B.

TABLE 3

Combining ability effects of parents of FW in terms of those of grandparents

Parents	X3				X6			
	g	gf	gm	s	g	gf	gm	s
Female								
F1	-0.34	-0.53*	0.75*	-0.56	-1.52*	-3.12*	2.68*	-1.08*
F2	-0.30	-0.53*	-0.19	0.52*	-0.55	-3.12*	1.13*	1.44*
F3	-0.44	-0.53*	-0.03	-0.112	-4.17*	-3.12*	-0.69	-0.36
F4	0.68*	0.75*	-0.19	0.12	3.46*	2.68*	1.13*	-0.35
F5	1.13*	0.75*	-0.03	0.41*	3.43*	2.68*	-0.69	1.44*
F6	-0.74*	-0.19	-0.03	-0.52*	-0.65	1.13*	-0.69	-1.09*
Male								
M1	0.16	0.36*	-0.31	0.11	2.45*	1.74*	-0.35	1.06*
M2	-0.02	0.36*	-0.37*	-0.01	0.58	1.74*	-1.45*	0.29
M3	0.55*	0.36*	0.32	-0.13	0.44	1.74*	0.06	-1.36*
M4	-0.82*	-0.31	-0.37*	-0.14	-3.15*	-0.35	-1.45*	-1.35*
M5	0.01	-0.31	0.32	—	-0.01	-0.35	0.06	0.28
M6	0.11	-0.37*	0.32	0.16	-0.32	-1.45*	0.06	1.07*

(*) Significant at P = 0.05.

TABLE 4

Distribution of heterotic crosses in various groups of TW and FW

Female Parent	Male Parent						
	3-way			4-way			
	H	L	Total	HH	HL	Total	
HL	n	3	9	12	9	9	18
	nh	3	7	10	7	5	12
LL	n	3	9	12	9	9	18
	nh	1	4	5	2	1	3
Total	n	6	18	24	18	18	36
	nh	4	11	15	9	6	15

n = number of crosses made; nh = number of heterotic crosses.

(Table 4) both in TW and FW. (HL) X (HH) and (HL) X (HL) ranked high in FW. The results were based on relative frequencies of heterotic crosses though the number of crosses made in each category could not be kept constant.

Judging the contribution of grandparents by the frequency of heterotic crosses produced by them for (a) any two characters, (b) tiller number and yield and (c) yield (Table 5), B90, LST2; T1, TCL1 were the two groups to be preferred in that order on the

TABLE 5

Contribution of grandparents to heterosis in TW and FW

	Grandparent	Female Side				Male Side				
		g	a	b	c	Grandparent	g	a	b	c
TW	T1	L	6	0	1	TD1	H	4	0	2
	LST2	H	10	3	5	6TA204	L	2	2	2
	B90	L	8	5	7	B46	L	4	1	3
	TCL1	L	6	2	7	T4989	L	5	2	3
FW	T1	L	7	2	4	M1019	H	10	5	8
	LST2	H	12	4	6	T15	H	8	3	5
	B90	L	6	6	6	TH2	L	6	2	2
	TCL1	L	5	0	2	A147	H	6	0	3

g = grandparental gca; a = heterotic for any two characters; b = heterotic for tiller number and yield; c = heterotic for yield only.

female side, T4989, B46; 6TA204, TD1 were those on the male side in TW and M1019, T15; TH2; A147 in FW.

An analysis of the role of sea and hence of epistatic interaction in producing heterosis (Table 6) showed that heterosis in HH and HL was mostly due to high sea in single crosses. HL was undoubtedly superior as female or male parent in TW and FW and produced heterosis with low or nonsignificant sea.

TABLE 6

Heterosis in single and multiple crosses and their relation to overall sea status

Group	sea	p		q	r	s
		F1A	F1B			
HH	n	30		—	—	18
	nh	23	16	—	—	9
	H	15	11	—	—	—
	L	3	2	—	—	0
	LC	3	3	—	—	2
	LN	2	0	—	—	2
HL	n	48		12	18	18
	nh	22	11	10	12	6
	H	15	6	3	6	3
	L	4	2	2	0	0
	LC	3	3	1	2	1
	LN	0	0	4	4	2
LL	n	12		12	18	—
	nh	3	3	5	3	—
	H	2	2	1	2	—
	L	1	1	1	0	—
	LC	0	0	2	1	—
	LN	0	0	1	0	—
Total	n	90		24	36	36
	nh	48	30	15	15	15
	H	32	19	4	8	8
	L	8	5	3	0	0
	LC	6	6	3	3	3
	LN	2	0	5	4	4

p = single crosses; q = as female parents of TW; r = as female parents of FW; s = as male parents of FW; n = number of crosses made; nh = number of heterotic crosses.

DISCUSSION

While literature is vast on diallel crosses in many crop plants, studies searching for repeatable breeding concepts in them are scarce. In addition to such studies, we have evaluated here multiple crosses made on known designs for the first time.

The methodology, utility and stability of designating a parent as high or low general combiner were substantiated by the performance of the single and multiple crosses. It was found that HL category was superior not only as single but as parents of 3- and 4-way crosses as well. HH though ranked equal to HL in some cases, as in single crosses and as male parents of FW, produced heterosis more through large sca effects in contrast to HL. Supporting evidence is provided by this study and those in other crop plants like pearl millet (REDDY, 1975) and *Brassica campestris* (BANDYOPADHYAY, 1976) for the feasible hypothesis advanced by LANGHAM (1961) for such a superiority of HL.

Promising crosses heterotic for several yield components and yield were between parents belonging to HL or HH groups. For example, (LST2 X B90) X (M1019 X TH2) and (LST2 X B90) X (T15 X A147) heterotic for four components without epistatic effects, belonged to (HL) X (HL) and (HL) X (HH) respectively. The genetic effects brought together from four divergent varieties without undesirable epistasis in TW and FW are worthy of canalisation into superior pure lines through biparental matings. The crosses, (T1 X LST2) X T4989, (T1 X LST2) X (T15 X A147), (LST2 X B90) X 6TA204, (LST2 X B90) X T4989, (LST2 X TCL1) X TD1, (LST2 X TCL1) X (M1019 X TH2) and (B90 X TCL1) X T4989 can also lend themselves to such a treatment.

The combined diallel-(line \times tester) design adopted for 3- and 4-way crosses permitted partitioning of gea effect of a single cross parent into the grandparental gea and sca effects. When the crosses from a 3-parent diallel (without parents and reciprocals) are used as parents of multiple crosses, the sca effects at grandparental level are zero and the relationships — $s_{12} = s_{34}$; $s_{13} = s_{24}$ and $s_{14} = s_{23}$, where 1 to 4 are the grandparents — hold when they are from a 4-parent diallel.

LST2 and B90 were the grandparents to produce high frequency of heterotic crosses (Table 5) on the female and M1019, T15 and T4989 on the male side. LST2 X B90, T1 X LST2 and LST2 and LST2 X TCL1 were such female and M1019 X T15,

M1019 X TH2 and T15 X A147 male parents of multiple crosses.

(HL) X H, (HL) X L, (HL) X (HH) and (HL) X (HL) would be the desirable groups of 3- and 4-way crosses for breeding new triticale varieties. Based on a single year of testing of single crosses in F_1 , appropriate parents for multiple crosses can be chosen and the required multiple crosses made. Pedigree breeding in further segregating generations would identify superior derivatives. Corroborative evidence of the productivity of a HL 3-way cross is available on maize (HANDOO, 1964). WEATHERSPOON (1970) reported broadly similar results on single, 3-way and double crosses of maize.

Some flexibilities can be introduced in the breeding programmes. For instance, hybridisation of a high and low multiple cross can be followed by large scale inter-mating in the first segregating generation. A set of desirable genotypes selected in further generation can be advanced to homozygosity. Multiple crosses heterotic due to additive genetic and additive interaction effects in their F_1 , can be advanced by inter-mating of the segregating progeny at random to cut down effectively the long time usually taken to breed a variety by traditional methods in self-pollinated crops. Such an insurance is hardly available in the population improvement programme of JENSEN (1970).

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ABSTRACT

Single and multiple crosses of triticales made according to specific designs of mating were evaluated for a set of quantitative characters. Parents and hybrids were characterised as genetically close as possible using the components of combining ability. A high (H) or low (L) status was assigned to the overall general and specific combining ability of parents and hybrids. The methods adopted were found to be repeatable and non-arbitrary. The magnitude of heterosis was related to the status of parents and grandparents in multiple crosses. It was found that $H \times L$ was superior to $H \times H$ as heterotic single crosses and potential as female parents of three- and four- way crosses. $(HXL) \times H$, $(HXL) \times L$, $(HXL) \times (HXH)$, $(HXL) \times (HXL)$ were found to produce heterotic crosses with low or non-significant epistatic effects.

RIASSUNTO

Stima del potenziale genetico di incroci multipli nel Triticale

Incroci singoli e multipli di Triticale eseguiti secondo programmi specifici di combinazione sono stati valutati per un gruppo di caratteri quantitativi. I genitori e gli ibridi venivano caratterizzati geneticamente quanto più vicini possibile usando le componenti dell'attitudine combinatoria. Uno status alto (H) o basso (L) è stato assegnato all'attitudine combinatoria generale e specifica dei genitori e degli ibridi. I metodi usati sono apparsi riproducibili e non arbitrari. L'ampiezza dell'eterosi è stata correlata allo status dei genitori e dei progenitori in incroci multipli. È stato rilevato che $H \times L$ era superiore a $H \times H$ come incroci eterotici singoli e potenziali come genitori femminili di incroci a tre e a quattro vie. $(H \times L) \times H$, $(H \times L) \times L$, $(H \times L) \times (H \times H)$, $(H \times L) \times (H \times L)$ hanno mostrato di produrre incroci eterotici con effetti epistatici bassi o non significativi.