

TRIPLE TEST CROSS ANALYSIS IN TWO WHEAT CROSSES

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SUMMARY

Modified triple test cross analysis described by Jinks and Perkins (1970) has been applied to the study of additive, dominance and epistatic components of genetic variance for five metric traits, namely final plant height, ear length, number of spikelets per spike, number of grains per spike and grain yield per plant, in two wheat crosses (Kalyan Sona \times Norteno 67 and Norteno 67 \times WL 212). The results of the analysis reveal that the epistatic component is an important element in both the crosses for all the five characters.

1. INTRODUCTION

Most genetic models, particularly those for second-degree statistics, which have been developed to estimate the components of continuous variation, have as one of their simplifying assumptions the absence of epistasis. This assumption may be true for some characters in some populations but not for others. Very few analyses, however, provide a valid test for this. A good genetic model, in fact, is that which enables the breeder to have precise and unbiased estimates of all the components of genetic variance. A design which is a simple extension of the design III of Comstock and Robinson (1952) has been proposed by Kearsey and Jinks (1968). This design, known as "triple test cross", provides not only a precise test for epistasis but also gives unbiased estimates of additive (D) and dominance (H) components if epistasis is absent. Further, this approach is independent of both the gene frequencies and the mating system of the population to be investigated.

Jinks and Perkins (1970) have suggested a modification in the triple test cross analysis and applied it to F_2 and backcross populations of *Nicotiana rustica*. In the modified analysis, all comparisons among the three kinds of progeny means, namely $\bar{L}_{1i}(F_2 \times P_1)$, $\bar{L}_{2i}(F_2 \times P_2)$ and $\bar{L}_{3i}(F_2 \times F_1)$, are orthogonal to one another and, in the absence of epistasis, the L_3 families are used to provide additional information about the additive component.

2. MATERIALS AND METHODS

(i) *Experimental design*

Twenty plants were randomly chosen from each of the two F_2 's, namely Kalyan Sona \times Norteno 67 and Norteno 67 \times WL 212. In each F_2 the 20 plants were backcrossed, as male parent, to the same three testers, P_1 , P_2 and F_1 ($P_1 \times P_2$), where P_1 and P_2 are the varieties Kalyan Sona and

Norteno 67 for the F_2 of the cross between them and the varieties Norteno 67 and WL 212 for the F_2 of the cross between these two varieties. Sixty families (from each original cross), thus obtained, were raised in completely randomised blocks with three replications. From each family in each replication, five plants were randomly tagged. Each of these tagged plants was scored for five characters, namely, final plant height, ear length, number of spikelets per spike, number of grains per spike and grain yield per plant. Data for analysis were, therefore, based on 180 values, each being the mean of five plants and the corresponding variances of these sets of five plants.

Jinks and Perkin's (1970) analysis was applied to detect epistasis and to test and estimate additive and dominance components of genetic variation.

(ii) *Test for epistasis*

For the test of epistasis, twenty values of $L_{1i} + L_{2i} - 2L_{3i}$, for $i = 1$ to 20 were obtained for each of the three replicates. After summing over the replicates, the sum of twenty squared deviations of $L_{1i} + L_{2i} - L_{3i}$ from zero for 20 degrees of freedom, that is, sum of squares due to epistasis, was obtained. Sum of squares due to replicate error, that is, the error for testing the significance of epistasis, was obtained for 40 degrees of freedom. A further estimate of the error variance was obtained by the mean variance within the L_1 , L_2 and L_3 types of families for 720 degrees of freedom.

This analysis was, however, pursued further. The epistasis sum of squares for 20 degrees of freedom could be partitioned into an item for 1 degree of freedom, testing for i type epistasis (homozygote \times homozygote interactions) and an item for 19 degrees of freedom testing for j and l types of epistasis (homozygote \times heterozygote and heterozygote \times heterozygote interactions, respectively). Similarly, the sum of squares due to replicate error for 40 degrees of freedom could be subdivided into two items, namely replicates and epistasis \times replicates, respectively, for 2 and 38 degrees of freedom.

(iii) *Test and estimation of additive and dominance components*

Additive and dominance components were estimated, assuming no epistasis. The 20 sums of means of the families yielded a variance of sums for 19 degrees of freedom. Similarly, the variance of differences was obtained further for 19 degrees of freedom. Variances of sums \times replicates and differences \times replicates were obtained each for 38 degrees of freedom.

3. RESULTS

(i) *Epistasis*

Significant epistasis was recorded for all the five characters in both the triple test crosses (table 1). Further partitioning of the epistasis item, however, revealed that overall epistasis (i type) was not significant for the character spikelets per spike in the first triple test cross (K. Sona \times Norteno 67) and for final plant height, ear length and spikelets per spike in the second (Norteno 67 \times WL 212). Whereas the item replicate error was significant for all the characters in both triple test crosses except for yield

per plant in first cross and ear length in the second cross, the item replicates was insignificant for all the traits in both the sets except for final plant height and spikelets per spike in the second triple test cross. Epistasis \times replicate interaction was significant for all the characters in both the triple test crosses except for yield per plant in the first cross.

TABLE 1

Analysis of variance to test for epistasis in two triple test crosses, 1 (K. Sona \times Norteno 67) and 2 (Norteno 67 \times WL212) for five characters in wheat

Item	d.f.		Final plant height	Ear length	Spikelets per spike	Grains per spike	Yield per plant
Epistasis ($L_{1i} + L_{2i} - 2L_{3i}$)	1	20	48.475**	1.639***	4.875***	185.254***	48.232***
	2	20	131.042**	1.983***	4.890*	336.304***	38.581***
(a) Overall epistasis (<i>i</i> type)	1	1	89.361***	9.624***	0.982	58.081*	127.939***
	2	1	65.775	1.213	0.136	1535.121***	43.864***
(b) Epistasis (<i>j</i> and <i>l</i> type)	1	19	46.323**	1.218***	5.080**	191.968***	44.035***
	2	19	134.478**	2.024**	5.141**	273.209***	38.302***
Replicate error	1	40	17.000***	0.345*	1.500***	16.880**	4.680
	2	40	41.995***	0.555	2.095***	18.950***	6.760***
(a) Replicates	1	2	0.260	0.280	0.385	1.255	0.835
	2	2	32.740**	0.490	4.140**	21.825	5.140
(b) Epistasis \times replicates	1	38	17.880***	0.350*	1.555***	17.700**	4.880
	2	38	42.480***	0.620*	1.985***	18.795***	6.845***
Within families within replicates	1	720	8.026	0.230	0.738	9.770	3.590
	2	720	7.050	0.419	0.893	9.144	3.324

* $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P < 0.001$.

(ii) *Additive and dominance components*

In the absence of epistasis analysis of variance for sums and differences provides direct tests of the significance of the additive (significance of sums) and dominance component (significance of differences). Both items, the sums and differences, were significant in both the triple test crosses for all the characters studied (table 2). Accordingly, the components *D* and *H* were significant for all the traits in both the sets (table 3). As regards the relative magnitudes of additive and dominance components, estimates of *D* were higher than those of *H* for all the traits except final plant height in the first triple test cross. The second triple test cross, however, presented a quite different picture. In this, higher estimates of *D* (as compared to those of *H*) were recorded only for one character, namely ear length. The remaining four characters gave relatively higher estimates of *H*. But since both the crosses gave evidence of significant epistasis for all the five characters, these estimates of *D* and *H* were biased by epistasis to an unknown extent. Only one character final plant height gave higher estimates of *H* (as compared to those of *D*) with a large epistasis in both the crosses, indicating that the additive component of genetic variation is relatively less important for this character. The item sums \times replicates, was significant in both the triple test crosses for all the five traits. Differences \times replicates interaction

was also significant for all the characters except for grains per spike in the first triple test cross and ear length in the second triple test cross.

TABLE 2

Analysis of variance to detect additive and dominance components in two triple test crosses (TTC) for five characters in wheat

Item	d.f.	Final plant height	Ear length	Spikelets per spike	Grains per spike	Yield per plant
TTC 1 (K. Sona × Norteno 67):						
(a) Analysis of sums ($L_{1i} + L_{2i} + L_{3i}$)						
Replicates	2	102.250***	0.175	17.650***	37.500*	5.050
Sums (Additive component)	19	144.084***	5.275***	13.071***	672.953***	102.460***
Sums × replicates	38	14.470**	0.470***	2.515***	28.750***	16.138***
Within families	720	8.026	0.230	0.738	9.770	3.590
(b) Analysis of differences ($L_{1i} - L_{2i}$)						
Differences (Dominance component)	19	142.674***	1.927***	2.895*	213.771***	38.605***
Differences × replicates	38	19.000***	0.475***	1.510***	12.230	10.224***
Within families	480	7.203	0.238	0.698	9.694	3.529
TTC 2 (Norteno 67 × WL 212):						
(a) Analysis of sums ($L_{1i} + L_{2i} + L_{3i}$)						
Replicates	2	8.450	2.475**	0.525	1.200	0.260
Sums (Additive component)	19	118.416**	6.109***	8.448***	360.575***	58.388***
Sums × replicates	38	38.945***	0.600*	1.995***	14.715*	9.915***
Within families	720	7.050	0.419	0.898	9.144	3.324
(b) Analysis of differences ($L_{1i} - L_{2i}$)						
Differences (Dominance component)	19	136.483**	1.460**	5.778***	317.230***	99.877***
Differences × replicates	38	41.745***	0.375	1.345*	15.290**	9.050***
Within families	480	6.877	0.670	0.856	9.339	3.406

* $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P < 0.001$.

TABLE 3

Estimates of additive (D) and dominance (H) components in two triple test crosses for five characters in wheat

Item	Final plant height	Ear length	Spikelets per spike	Grains per spike	Yield per plant
TTC 1 (K. Sona × Norteno 67):					
<i>D</i>	115.212***	4.271***	9.383***	572.627***	76.731***
<i>H</i>	164.899***	1.936***	1.847*	268.721***	37.841***
TTC 2 (Norteno 67 × WL 212):					
<i>D</i>	70.641**	4.897***	5.736***	307.431***	43.087***
<i>H</i>	126.317**	1.447**	5.911***	402.587***	121.103***

* $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P < 0.001$.

4. DISCUSSION

The results of the present study reveal that all the three kinds of variances, namely additive, dominance and epistatic, are significant for all the char-

acters in both the triple test crosses. Absence of significant *i* type epistasis for the character spikelets per spike in the first and for final plant height, ear length and spikelets per spike in the second triple test cross, however, indicates that overall epistasis is a relatively minor component of epistasis for these characters. Because of the bias caused by epistasis no precise conclusion can be drawn about the relative importance of the three components of genetic variation on the basis of the biased estimates of *D* and *H*. However, high estimates of *H* combined with the large mean square for epistasis for final plant height in both the crosses indicate that probably epistatic and dominance components are relatively more important for the control of this character. The two triple test crosses gave contrasting results with regard to the relative magnitudes of *D* and *H*, except for the characters final plant height and ear length.

These results indicate that an epistatic component plays an important role in governing all the five characters studied in these wheat crosses. Therefore, this component cannot be ignored when one is formulating breeding plans to improve wheat populations for economic traits. If the presence of epistasis is ignored in wheat populations (which has been a general trend in the past), one would not only lose information about epistasis but also the estimates of additive and dominance components would be biased as they are in the present crosses and, therefore, could be misleading. Further, the detection and estimation of epistasis would enable the breeder to determine the genetic cause of heterosis with greater reliance.

5. REFERENCES

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