COMPARISON OF ASSOCIATED AND DISPERSED TESTERS IN THE TRIPLE TEST CROSS

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SUMMARY

The theoretical consequences of using inbred testers for an F_2 and F_∞ triple test cross in which the allelic differences are associated as opposed to dispersed are described for four situations of increasing complexity that arise from the presence of non-allelic interaction and a linkage disequilibrium either singly or jointly. The theoretical expectations are confirmed by analyses of two F_∞ triple test crosses on a random sample of 60 inbred families from the cross of varieties 2 and 12 of *Nicotiana rustica* for which the inbred testers are the two varieties and the two extremes of the 60 inbred families in respect of final height and flowering time.

In the presence of non-allelic interaction and a linkage disequilibrium between interacting or non-interacting genes, the expectations of the mean squares in the analysis of variance of a triple test cross and of the estimates of the additive genetic, dominance and epistatic components obtained from them, differ characteristically according to whether a dispersed or an associated pair of inbred testers have been used. The pattern of the differences can, therefore, be used to detect these complex effects.

Comparison of the corresponding mean squares and estimates from the two F_∞ triple test crosses shows that non-allelic interactions and a linkage disequilibrium are present but there is no significant evidence that the disequilibrium involves interacting genes.

1. INTRODUCTION

Comparison of the basic generations of a matched pair of crosses whose pure breeding parents display association and dispersion for the same alleles at the same loci provides sensitive tests for the presence of epistasis and linkage disequilibrium (Pooni and Jinks, 1982). In this paper we extend this comparison to the triple test cross (Kearsey and Jinks, 1968). In the absence of epistasis and a linkage disequilibrium the expectations of the components of variation in a triple test cross analysis are the same irrespective of whether the alleles are associated or dispersed in the pure breeding testers L_1 and L_2 . In their presence this is no longer true as we shall show by deriving the appropriate theoretical expectations. Comparative triple test cross analyses of the same population, a random sample of highly inbred lines from the cross of varieties 2 and 12 of *Nicotiana rustica*, using dispersed and associated testers will be used to illustrate the theory.

2. THEORETICAL EXPECTATIONS

Expectations have been obtained for a single pair of loci at which the alleles are either associated ($AABB$ and $aabb$) or dispersed ($AAbb$ and $aaBB$) in the pure breeding testers. The populations under test are the F_2 and F_∞ generations of a cross between two pure breeding lines in which

TABLE 1

Differences between the expected variances for the additive genetic comparisons in an F_2 and F_∞ triple test cross when the alleles at a pair of loci are associated in the L_1 and L_2 testers and when they are dispersed in these testers. The differences are given for four models of increasing complexity (1 to 4) and all the variances on which they are based have been adjusted so that they equal $D = d_a^2 + d_b^2$ for model 1

Comparison	Model	F_2	F_∞
Linkage disequilibrium			
Epistasis			
1. No	No	0	0
2. Yes	No	0	0
3. No	Yes	$-\frac{4}{3}i_{ab}i_{ba} - \frac{4}{3}(d_a i_{ba} + d_b i_{ab}) + \frac{1}{3}i_{ab}^2 1_{ab}$	$-\frac{4}{3}i_{ab}i_{ba} - \frac{4}{3}(d_a i_{ba} + d_b i_{ab}) + \frac{1}{3}i_{ab}^2 1_{ab}$
4. Yes	Yes	$\frac{1}{3}(3-8p+4p^2)(j_{ab}^2 + j_{ba}^2) + \frac{1}{3}(6-2p)i_{ab}i_{ba}$ $-\frac{1}{12}(3+2p)(d_a i_{ba} + d_b i_{ab})$ $+\frac{1}{3}(6-16p+8p^2)(d_a i_{ab} + d_b i_{ba}) + \frac{1}{2}(p-4p^2+4p^3)1_{ab}^2$ $+\frac{2}{3}[2p-7p(1-p)+10p(1-p)^2+p(1-2p)^3]i_{ab}1_{ab}$	$\frac{(3-2p)(1-2p)}{3(1+2p)}(j_{ab}^2 + j_{ba}^2) - \frac{(6+8p-8p^2)}{3(1-2p)}i_{ab}i_{ba}$ $+\frac{4p(1-2p)+2(1-2p)^2}{3(1+2p)}(d_a i_{ab} + d_b i_{ba})$ $-\frac{8-2(1-2p)^2}{3(1+2p)}(d_a i_{ba} + d_b i_{ab})$ $+\frac{8p(3-2p)}{3(1+2p)^2}i_{ab}^2 1_{ab}$
Additive genetic			
$\bar{L}_{11} + \bar{L}_{21} + \bar{L}_{31}$	1. No	0	0
	2. Yes	0	0
$\bar{L}_{11} + \bar{L}_{21} + R\bar{L}_{31}$	3. No	$i_{ab}i_{ba} - (d_a i_{ba} + d_b i_{ab}) + \frac{1}{4}i_{ab}^2 1_{ab}$	$-d_a i_{ba} - d_b i_{ab} + \frac{1}{2}i_{ab}^2 1_{ab} - i_{ab}i_{ba}$
	4. Yes	$(1-p)(1-2p)(j_{ab}^2 + j_{ba}^2) - 2(1-p)i_{ab}i_{ba}$ $+ 2(1-p)(1-2p)(d_a i_{ab} + d_b i_{ba}) - 2(1-p)(d_a i_{ba} + d_b i_{ab})$ $-\frac{1}{8}p^2\{4(1-2p)^2 + (1-2p)^3 + (1-p)^2(1-2p)^2\}i_{ab}^2$ $+\frac{1}{8}p^2\{1(1-2p)\{(4-5p)-p(1-p)-10(1-p)^3\}1_{ab}^2$ $-\frac{1}{4}[p-11p(1-p)+25p(1-p)^2-35p(1-p)^3$ $+ 16p(1-p)^4 - 12p(1-p)^2]i_{ab}1_{ab}$	$\frac{(1-2p)(1-p)}{1+2p}(j_{ab}^2 + j_{ba}^2) + \frac{2(1-2p)(1-p)}{1+2p}$ $\times (d_a i_{ab} + d_b i_{ba}) - \frac{2(1-p)(1-2p)}{1+2p}(d_a i_{ba} + d_b i_{ab})$ $- 2(1-p)i_{ab}i_{ba} + \frac{8p(1-p)}{(1+2p)^2}i_{ab}^2 1_{ab}$

[illegible]

the alleles at these pair of loci are dispersed. Four levels of complexity of the genetical variation in these populations are considered:

- (a) No epistasis and linkage equilibrium.
- (b) No epistasis and linkage disequilibrium.
- (c) Epistasis and linkage equilibrium.
- (d) Epistasis and linkage disequilibrium.

The differences between the expected variances derived from the standard comparisons used in triple test cross analysis for the associated and dispersed testers using the standard symbols of biometrical genetics (Mather and Jinks, 1982) are tabulated as follows:

Table 1: the additive genetic comparisons ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$), ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{R}\bar{L}_{3i}$), ($\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i} + \bar{R}\bar{L}_{3i}$), ($\bar{L}_{1i} + \bar{L}_{2i}$), ($\bar{L}_{3i}$), ($\bar{R}\bar{L}_{3i}$) and ($\bar{L}_{3i} + \bar{R}\bar{L}_{3i}$).

Table 2: the epistasis comparisons ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$), ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{R}\bar{L}_{3i}$) and ($\bar{L}_{1i} + \bar{L}_{2i} - \bar{L}_{3i} - \bar{R}\bar{L}_{3i}$) and the dominance comparison ($\bar{L}_{1i} - \bar{L}_{2i}$).

To make all of these expectations directly comparable, irrespective of the number and coefficients of the L_{1i} , L_{2i} , L_{3i} and $R\bar{L}_{3i}$ family means involved in their derivation and whether they relate to an F_2 or an F_∞ population, they have been adjusted so that the epistatic comparisons equal $I = i_{ab}^2$ and the additive genetic and dominance comparisons equal $D = d_a^2 + d_b^2$ and $H = h_a^2 + h_b^2$ for a linkage equilibrium and no epistasis. For example, the first comparison in table 1 is $\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i}$ which has an expected mean square in the standard analysis of variance of $\sigma^2 + 3r\sigma_s^2$, where σ^2 is the error component, r is the number of replicates and σ_s^2 is the "sums" component which on the simplest model has the expectation $\frac{1}{2}D$ for an F_2 and $\frac{1}{4}D$ for an F_∞ triple test cross. The adjusted variances of table 1 are, therefore $8\sigma_s^2$ for the F_2 and $4\sigma_s^2$ for the F_∞ and the differences tabulated are $8[(\sigma_s^2 \text{ for the associated testers}) - (\sigma_s^2 \text{ for the dispersed testers})]$ for the F_2 and half of this for the F_∞ .

Reference to tables 1 and 2 shows that in the absence of epistasis (models 1 and 2) the expectations of the additive genetic component are independent of whether the alleles are associated or dispersed in the inbred testers, L_1 and L_2 . Hence in the absence of epistasis estimates of the additive component D are expected to be the same irrespective of the distribution of the alleles between the testers. Furthermore, if the additive genetic component is obtained from the $\bar{L}_{3i}$, $\bar{R}\bar{L}_{3i}$ and $\bar{L}_{3i} + \bar{R}\bar{L}_{3i}$ comparisons it is independent of the allelic distribution between the testers even in the presence of epistasis provided that there is no linkage disequilibrium among the interacting alleles.

In contrast the expectation of the dominance comparison and hence the estimate of the dominance component H is independent of the allelic distribution between the testers only if neither epistasis nor a linkage disequilibrium are present. On the other hand, the expectations of the epistasis comparisons are independent of the allelic distribution between the testers irrespective of whether epistasis or a linkage disequilibrium are present.

For the additive genetic and dominance comparisons these expectations can be directly extended to many pairs of loci, each pair contributing the difference specified in tables 1 and 2. This is not, however, the case for all of the epistasis comparisons. In the presence of epistasis (models 3 and 4) the overall epistasis variance for 1 degree of freedom after adjustment has

TABLE 2

Differences between the expected variances for the epistatic and dominance comparisons in an F_2 and F_∞ triple test cross when the alleles at a pair of loci are associated in the L_1 and L_2 testers and when they are dispersed in these testers. The differences are given for four models of increasing complexity (1 to 4) and all the variances on which they are based have been adjusted so that epistasis equals $1 = i_{ab}^2$ and dominance $H = h_a^2 + h_b^2$ for model 1

Comparison	Model	F_2	F_∞
Epistasis	Linkage disequilibrium		
1.	No	Overall epistasis sets $\times$ epistasis	0 0
2.	Yes	Overall epistasis sets $\times$ epistasis	0 0
3.	No	Overall epistasis sets $\times$ epistasis	0 0
4.	Yes	Overall epistasis sets $\times$ epistasis	0 0
Dominance			
1.	No	0	0
2.	Yes	$-4(1-2p)h_a h_b$	$-\frac{4(1-2p)}{1+2p} h_a h_b$
3.	No	$\frac{1}{2} i_{ab} i_{ba} - 2i_{ab} 1_{ab} - 2(h_a + h_b) i_{ab}$	$i_{ab} i_{ba} - 2i_{ab} 1_{ab} - 2(h_a + h_b) i_{ab}$
4.	Yes	$-4(1-2p)h_a h_b - (1-2p)(i_{ab}^2 + 1_{ab}^2)$	$-\frac{4(1-2p)}{1+2p} h_a h_b - \frac{(1-2p)}{1+2p} (i_{ab}^2 + 1_{ab}^2)$
		$-2i_{ab} 1_{ab} - 2(h_a + h_b) i_{ab} + 2p(2-5p+4p^2) i_{ab} i_{ba}$	$-2(h_a + h_b) i_{ab} - \frac{8p}{1+2p} i_{ab} 1_{ab}$
			$+\frac{8p}{(1+2p)^2} i_{ab} i_{ba}$

the general form $[r_i \sum_i \frac{1}{2} k(k-1)]^2$ (Mather and Jinks, 1982) where r_i , the coefficient of association and dispersion equals 1 when all contributing pairs are associated, 0 when associated and dispersed pairs are contributing equally and -1 when all contributing pairs are dispersed. The maximum difference between the adjusted epistasis variances for models 3 and 4 is, therefore, $(\sum_i \frac{1}{2} k(k-1))^2$.

The patterns of expected differences for the additive and dominance comparisons in tables 1 and 2 provide diagnostic tests for a linkage disequilibrium and non-allelic interactions. For example:

- (a) If no difference is significant, neither a linkage disequilibrium nor non-allelic interaction is making a significant contribution (model 1).
- (b) If only the dominance comparison difference is significant, a linkage disequilibrium involving loci which are not displaying non-allelic interactions is making a significant contribution (model 2).
- (c) If all differences are significant with the exception of those for the additive genetic comparisons $\bar{L}_{3i}$, $\overline{RL}_{3i}$ and $(\bar{L}_{3i} + \overline{RL}_{3i})$, non-allelic interactions are making a significant contribution but there is no linkage disequilibrium (model 3).
- (d) If all differences are significant, there is a linkage disequilibrium involving loci displaying non-allelic interactions (model 4).

Because h_a , h_b , i_{ab} , j_{ab} , j_{ba} and l_{ab} can all take sign, the signs of the differences are not particularly helpful in discriminating between the various models. One exception is the dominance comparison for model 2. With dominance in the same direction at the linked loci the difference is negative but if it is in opposite directions the difference is positive.

3. MATERIAL AND EXPERIMENTAL DESIGN

Allelic differences for flowering time and final height are relatively dispersed between varieties 2 and 12 of *Nicotiana rustica*. Estimates of their coefficient of association/dispersion by the method of Jayasekara and Jinks (1976) were 0.52 and 0.35, respectively (Pooni and Jinks, 1982) where 0 is complete dispersion and 1 complete association. Among the random sample of the 60 inbred families derived by single seed descent from the F_2 of the cross of V2 and V12 by Perkins and Jinks (see Jinks, Jayasekara and Boughay, 1977) were two inbred lines D10 and D17 which had the extreme combination of both characters with coefficients of association/dispersion of 0.77 for flowering time and 1.00 for final height (Pooni and Jinks, 1982).

Two F_∞ triple test crosses were set up in 1974 using the 60D inbred families and V2, V12 and their reciprocal F_1 's as the dispersed set of testers and D10, D17 and their reciprocal F_1 's as the associated set of testers with respect to flowering time and final height. Five plants of each of the 60×8 test cross families and of the 60D families were raised in 1975 in each of two replicate blocks in which all 2700 plants in each block were individually randomised and scored for the two characters. Because there were no significant block interactions the five plants of each family in each block were pooled in the analyses.

The standard triple test cross design using V2, V12 and one F_1 ($V2 \times V12$) as testers, which can be extracted from the 1975 experiment, has

previously been described and analysed by Pooni, Jinks and Jayasekara (1978). The very small differences between the estimates presented in their table 3 and the corresponding ones presented later in this paper are due to the pooling of the two blocks.

4. RESULTS

The relevant mean squares of the triple test cross analysis including the alternative comparisons that are available for the additive genetic and epistasis components are given in tables 3 and 4. They are standardised on the means of the ten individuals in each family. With but two exceptions, epistasis $\times$ sets ($\bar{L}_{1i} + \bar{L}_{2i} - 2R\bar{L}_{3i}$) comparison and overall epistatic ($\bar{L}_{1i} + \bar{L}_{2i} - 2R\bar{L}_{3i}$) comparison using the V2 $\times$ V12 testers for flowering time, all the mean squares are significant ($P \leq 0.05$) most of them highly so ($P \leq 0.001$). Apart from the epistatic comparisons where the significances are higher for the D10 $\times$ D17 than for the V2 $\times$ V12 testers there is no suggestion that the different testers are affecting the sensitivity of the tests.

Whether or not estimates of the additive genetic, dominance and epistatic components of variation differ significantly according to whether

TABLE 3

Mean squares and tests of significance for the additive genetic comparisons of an F_{∞} triple test cross with dispersed (V2, V12) and associated (D10, D17) inbred testers

Inbred testers	Item	d.f.	Flowering time			Final height		
			MS	$\chi^2_{(n)}$	P	MS	$\chi^2_{(n)}$	P
(i) $(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i})$ Comparison								
V2 V12	Between sets	59	48.23	1293	***	370.07	1060	***
	Within families	1608	2.20			20.59		
D10 D17	Between sets	59	34.86	1238	***	382.69	1068	***
	Within families	1606	1.66			21.13		
(ii) $(\bar{L}_{1i} + \bar{L}_{2i} + R\bar{L}_{3i})$ Comparison								
V2 V12	Between sets	59	44.39	1196	***	373.13	1071	***
	Within families	1605	2.16			20.55		
D10 D17	Between sets	59	32.39	1062	***	381.74	1080	***
	Within families	1604	1.84			20.86		
(iii) $(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i} + R\bar{L}_{3i})$ Comparison								
V2 V12	Between sets	59	60.43	1431	***	496.15	1224	***
	Within families	2143	2.50			23.91		
D10 D17	Between sets	59	47.63	1471	***	533.93	1336	***
	Within families	2142	1.91			23.58		
(iv) $(\bar{L}_{1i} + \bar{L}_{2i})$ Comparison								
V2 V12	Between sets	59	31.83	1227	***	245.45	1042	***
	Within families	1070	1.53			13.90		
D10 D17	Between sets	59	19.74	820	***	234.00	872	***
	Within families	1068	1.42			15.83		
(v) $(\bar{L}_{3i} + R\bar{L}_{3i})$ Comparison								
V2 V12	Between sets	59	32.09	547	***	286.02	497	***
	Within families	1069	3.46			33.92		
D10 D17	Between sets	59	33.09	810	***	341.95	644	***
	Within families	1074	2.41			31.34		

*** $P \leq 0.001$

TABLE 4

Mean squares and tests of significance for the epistasis and dominance comparisons of an F_{∞} triple test cross with dispersed (V2, V12) and associated (D10, D17) inbred testers

Inbred testers	Item	d.f.	Flowering time			Final height		
			MS	$\chi^2_{(n)}$	P	MS	$\chi^2_{(n)}$	P
<i>Epistasis</i>								
(i) $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$ Comparison								
V2 V12	Overall epistasis†	1	19.61	7	**	228.36	6	*
	Epistasis × sets	59	3.04	63	NS	40.03	87	*
	Within families	1608	2.85			27.22		
D10 D17	Overall epistasis	1	103.97	21	***	595.45	14	***
	Epistasis × sets	59	4.94	153	***	41.77	93	**
	Within families	1606	1.90			26.43		
(ii) $(\bar{L}_{1i} + \bar{L}_{2i} - 2R\bar{L}_{3i})$ Comparison								
V2 V12	Overall epistasis	1	14.45	3	NS	275.02	6	*
	Epistasis × sets	59	5.34	113	***	43.79	95	**
	Within families	1605	2.79			27.15		
D10 D17	Overall epistasis	1	28.82	5	*	1023.15	23	***
	Epistasis × sets	59	5.46	143	***	43.29	99	***
	Within families	1604	2.26			25.90		
(iii) $(\bar{L}_{1i} + \bar{L}_{2i} - \bar{L}_{3i} - R\bar{L}_{3i})$ Comparison								
V2 V12	Overall epistasis	1	24.16	6	*	368.65	9	**
	Epistasis × sets	59	3.93	93	***	40.17	99	***
	Within families	2139	2.50			23.91		
D10 D17	Overall epistasis	1	93.14	17	***	1183.79	27	***
	Epistasis × sets	59	5.22	161	***	42.92	107	***
	Within families	2140	1.91			23.58		
<i>Dominance</i>								
(i) $(\bar{L}_{1i} - \bar{L}_{2i})$ Comparison								
V2 V12	Between sets	59	11.98	462	***	118.51	503	***
	Within families	1070	1.53			13.90		
D10 D17	Between sets	59	6.61	275	***	62.40	233	***
	Within families	1068	1.42			15.83		

*** $P \leq 0.001$; ** $0.001 < P \leq 0.01$; * $0.01 < P \leq 0.05$; NS $P > 0.05$.

† MS for 1 d.f. were tested as V.R. against the between sets MS for 59 d.f. whenever the latter were significant.

dispersed (V2 and V12) or associated (D10 and D17) inbred testers are used can be determined by the maximum likelihood procedures described by Pooni, Jinks and Pooni (1980, page 186). The χ^2 for one degree of freedom testing these differences are given in table 5. Only three differences are significant ($P \leq 0.05$). One is the epistasis × sets $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$ comparison for flowering time noted earlier which is significantly larger for the associated testers. The other two are the dominance component for both characters, which are significantly smaller for the associated testers.

Finally, estimates of the additive genetic (D) and dominance components (H) derived from the various comparisons are given in table 6 along with the estimate of D obtained directly from the 60D family means. The reduction in the estimates of H when associated testers are used is particularly marked but none of the estimates of D differ significantly from one another.

TABLE 5

Tests of significance of the differences between the F_{∞} triple test cross comparisons for the dispersed (V2, V12) and associated (D10, D17) inbred testers based on the goodness of fit of models which assume no difference

Comparison		Flowering time		Final height	
		$\chi^2_{(1)}$	<i>P</i>	$\chi^2_{(1)}$	<i>P</i>
<i>Difference epistatic components</i>					
$(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$	Overall epistasis	0.46	NS	0.20	NS
	Epistasis $\times$ sets	6.37	*	0.06	NS
$(\bar{L}_{1i} + \bar{L}_{2i} - 2R\bar{L}_{3i})$	Overall epistasis	0.11	NS	0.00	NS
	Epistasis $\times$ sets	0.21	NS	0.01	NS
$(\bar{L}_{1i} + \bar{L}_{2i} - \bar{L}_{3i} - R\bar{L}_{3i})$	Overall epistasis	0.34	NS	0.27	NS
	Epistasis $\times$ sets	2.35	NS	0.08	NS
<i>Difference additive genetic components</i>					
$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i})$		1.41	NS	0.02	NS
$(\bar{L}_{1i} + \bar{L}_{2i} + R\bar{L}_{3i})$		1.37	NS	0.01	NS
$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i} + R\bar{L}_{3i})$		0.78	NS	0.08	NS
$(\bar{L}_{1i} + \bar{L}_{2i})$		3.19	NS	0.05	NS
$(\bar{L}_{3i} + R\bar{L}_{3i})$		0.06	NS	0.51	NS
<i>Difference dominance components</i>					
$(\bar{L}_{1i} - \bar{L}_{2i})$		4.75	*	5.99	***

For *p* values see table 4.

TABLE 6

Estimates of additive genetic (*D*) and dominance (*H*) components obtained from F_{∞} triple test cross comparisons using dispersed (V2, V12) and associated (D10, D17) inbred testers and of the additive genetic component of the F_{∞} families (P_i)

Inbred testers	Comparison	Flowering time	Final height
<i>Additive genetic component</i>			
V2 V12	$\bar{P}_i$	63.79 $\pm$ 12.12	372.91 $\pm$ 70.93
	$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i})$	61.37 $\pm$ 11.84	465.97 $\pm$ 90.85
	$(\bar{L}_{1i} + \bar{L}_{2i} + R\bar{L}_{3i})$	56.31 $\pm$ 10.90	470.11 $\pm$ 91.60
	$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i} + R\bar{L}_{3i})$	58.13 $\pm$ 11.16	472.24 $\pm$ 91.35
	$(\bar{L}_{1i} + \bar{L}_{2i})$	60.59 $\pm$ 11.72	463.09 $\pm$ 90.39
	$(\bar{L}_{3i} + R\bar{L}_{3i})$	57.26 $\pm$ 11.82	504.20 $\pm$ 105.36
D10 D17	$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i})$	44.27 $\pm$ 8.56	482.08 $\pm$ 93.95
	$(\bar{L}_{1i} + \bar{L}_{2i} + R\bar{L}_{3i})$	40.73 $\pm$ 7.95	481.17 $\pm$ 93.72
	$(\bar{L}_{1i} + \bar{L}_{2i} + \bar{L}_{3i} + R\bar{L}_{3i})$	45.72 $\pm$ 8.77	510.35 $\pm$ 98.31
	$(\bar{L}_{1i} + \bar{L}_{2i})$	36.62 $\pm$ 7.26	436.33 $\pm$ 86.18
	$(\bar{L}_{3i} + R\bar{L}_{3i})$	61.36 $\pm$ 12.19	621.22 $\pm$ 125.95
<i>Dominance component</i>			
V2 V12	$(\bar{L}_{1i} - \bar{L}_{2i})$	20.90 $\pm$ 4.42	209.22 $\pm$ 43.66
D10 D17	$(\bar{L}_{1i} - \bar{L}_{2i})$	10.38 $\pm$ 2.44	93.14 $\pm$ 23.02

5. CONCLUSIONS

The genetical components of variation for flowering time and final height in the $V2 \times V12$ cross obtained from the triple test cross using $V2$ and $V12$ as the inbred testers agree with those from previous analyses based upon an F_2 triple test cross (Jinks and Perkins, 1970, Jinks and Pooni, 1980), an F_∞ triple test cross (Pooni, Jinks and Jayasekara, 1978), F_2 and backcross families (Pooni and Jinks, 1982) and F_3 families (Jinks and Pooni, 1980). There are, however, significant differences between the two F_∞ triple test crosses described in this paper attributable to the use, for the first time, of relatively associated inbred testers, $D10$ and $D17$, which results in the halving of the dominance components (tables 4 and 6). From the theoretical expectations in table 2 and the diagnostic tests based upon them (section 2) it is clear that this halving of H must be due to a linkage disequilibrium arising from an excess of repulsion linkages between alleles whose dominance deviations have the same sign.

Epistasis of the i , j and l types is detected by the appropriate comparisons in both triple test crosses but with higher levels of significance where the associated testers, $D10$ and $D17$, are used (table 4). There are, however, no significant differences between the estimates of the additive genetic component that could be attributed to the type of testers. On the basis of the diagnostic tests in section 2 there is, therefore, no evidence that the linkage disequilibrium involves alleles that are displaying non-allelic interactions. This conclusion must reflect the relative insensitivity of the test since there is evidence of repulsion linkages between loci at which there are non-allelic interactions for flowering time and final height in the $V2 \times V12$ cross (Pooni and Jinks, 1982).

That the insensitivity resides in the test rather than in the data will be shown by analyses presented in a further paper where the information from the two triple test crosses is combined rather than contrasted to illustrate the influence of allele distribution between the inbred testers.

6. REFERENCES

- JAYASEKARA, N. E. M. AND JINKS, J. L. 1976. Effect of gene dispersion on estimates of components of generation means and variances. *Heredity*, **36**, 31–40.
- JINKS, J. L., JAYASEKARA, N. E. M. AND BOUGHEY, H. 1977. Joint selection for both extremes of mean performance and of sensitivity to a macro-environmental variable. II. Single seed descent. *Heredity*, **39**, 345–355.
- JINKS, J. L. AND PERKINS, J. M. 1970. A general method for the detection of additive, dominance and epistatic components of variation. III. F_2 and backcross populations. *Heredity*, **25**, 419–429.
- JINKS, J. L. AND POONI, H. S. 1980. Comparing predictions of mean performance and environmental sensitivity of recombinant inbred lines based upon F_3 and triple test cross families. *Heredity*, **45**, 305–312.
- KEARSEY, M. J. AND JINKS, J. L. 1968. A general method for the detection of additive, dominance and epistatic components of variation for metrical traits. I. Theory. *Heredity*, **23**, 403–409.
- MATHER, K. AND JINKS, J. L. 1982. *Biometrical Genetics* (Third edition). Chapman and Hall, London.
- POONI, H. S. AND JINKS, J. L. 1982. Comparative analysis of association and dispersion crosses to detect linkage and epistatic components of variation. *Heredity*, **49**, 211–220.

- POONI, H. S., JINKS, J. L. AND JAYASEKARA, N. E. M. 1978. An investigation of gene action and genotype $\times$ environmental interaction in two crosses of *Nicotiana rustica* by triple test cross and inbred line analysis. *Heredity*, **41**, 83–92.
- POONI, H. S., JINKS, J. L. AND POONI, G. S. 1980. A general method for the detection and estimation of additive, dominance and epistatic variation for metrical traits. IV. Triple test cross analysis for normal families and their selfs. *Heredity*, **44**, 177–192.