AN INVESTIGATION OF GENE ACTION AND GENOTYPE $\times$ ENVIRONMENT INTERACTION IN TWO CROSSES OF *NICOTIANA RUSTICA* BY TRIPLE TEST CROSS AND INBRED LINE ANALYSIS

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SUMMARY

Data from two random samples of inbred lines and from the two sets of the triple test cross in which these inbreds are crossed to the pure-breeding parents and F_1 of the cross from which they were derived, one involving material derived from the cross between varieties 1 and 5 of *Nicotiana rustica* and the other material from the cross between varieties 2 and 12, are analysed and the results compared to those reported earlier. Detection of epistasis and the estimation of the additive and dominance components of variation among the triple test cross families is based on the orthogonal analysis of Jinks and Perkins (1970) while the additive component is also estimated directly from the inbred families. Tests are carried out to detect genotype $\times$ micro-environment interaction in the L_1 and L_2 families of the triple test cross and in the inbred families and the interaction partitioned into that involving additive and dominance gene action. Their relationship with the corresponding additive and dominance components of mean performance is investigated by linear regression analysis.

As expected the material from the $V_1 \times V_5$ cross segregates at loci the alleles of which display large additive effects but little or no dominance and epistasis while dominance and epistasis are larger components of the genetic variation in $V_2 \times V_{12}$ cross. In both crosses, the micro-environmental interaction involves mainly the additive genetic component. For some characters there is evidence of independent segregation of genes controlling environmental sensitivity.

Estimates of the additive genetic component D from the triple test cross and the inbred families, are consistent for all the characters in both crosses. The triple test cross analysis, therefore, provides satisfactory estimates of the genetic variation among a random set of inbred lines, even for those characters which display non-allelic interactions.

1. INTRODUCTION

THE triple test cross breeding programme, an extension of North Carolina Design III (Comstock and Robinson, 1952) proposed by Kearsey and Jinks (1968) and subsequently extended by Jinks, Perkins and Breese (1969) and Jinks and Perkins (1970), has been extensively applied to detect and estimate the components of the genetic variation in material derived from crosses between varieties 1 and 5 and 2 and 12 of the Birmingham *Nicotiana rustica* collection (Perkins and Jinks, 1970, 1971; Jayasekara, 1974; Pooni, 1976, and Pooni and Jinks, 1976). Detection of genotype $\times$ environment interaction both with the macro and micro-environments has also been

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carried out and attempts made to partition these interactions into those involving the additive and the dominance action of the genes (Perkins and Jinks, 1970). All these studies, however, were largely limited to illustrating the new techniques for detecting and estimating the genetical and genotype $\times$ environment interaction components of variation as exemplified by the analysis of flowering time and final height. A comprehensive survey of the genetic variation in these *Nicotiana rustica* crosses has therefore been undertaken using the optimal material, namely, random inbred lines derived from them.

2. THE EXPERIMENT

The experiment consists of two separate triple test crosses. The first, based on material derived from the cross between varieties 1 and 5 of *Nicotiana rustica*, was initiated during 1972/73 by crossing V_1 and V_5 and their F_1 (1×5) to each of the 82, F_{11} inbreds derived by single seed descent from the F_2 of the $V_1 \times V_5$ cross (Perkins and Jinks, 1973) to give the L_1 , L_2 and L_3 families of a triple test cross, respectively. Each of these 82×3

TABLE 1

A list of the morphological and seed characters scored for the present material

Character		Description
1	H_1	Plant height (cm) at 2 weeks after planting in the field
2	H_2	Plant height (cm) at 4 weeks after planting in the field
3	H_3	Plant height (cm) at 6 weeks after planting in the field
4	FT	Flowering time in days from the date of sowing
5	HFT	Height in cm at the time of flowering
6	CL	Corolla length in cm of the first flower
7	SSP	Stamen-stigma positioning in the first flower
8	LL	Length of the largest leaf blade at flowering time (cm)
9	LW	Width of the largest leaf blade at flowering time (cm)
10	LS	Plant diameter across the largest pair of leaves at flowering time (cm)
11	FH	Height of the plant at the end of the season (cm)
12	CN	Number (count) of seed bearing capsules at the end of the season
13	SW	Weight of the total seed produced by 10 randomly chosen capsules of a plant ($g \times 10^{-4}$)
14	ASW	Hundred seed weight for each plant
15	TSN	Total seed number per plant in thousands

crosses and the selfs of the 82 inbreds were raised in a single experiment during the summer of 1973. The experiment was divided into two equal blocks and five individually randomised plants were raised for each family in each block. Data were recorded for the 15 morphological and seed characters listed in table 1.

The second triple test cross was based on material derived from the cross between varieties V_2 and V_{12} . Again the 60, F_7 inbreds derived by single seed descent from the F_2 generation of the $V_2 \times V_{12}$ cross (see Jinks, Jayasekara and Boughey, 1977) were crossed to V_2 , V_{12} and their F_1 (12×2) to produce the L_1 , L_2 and L_3 families of a triple test cross, respectively. These 180 families together with the 60 inbred selfs were grown during 1975 in a single experiment with two blocks. Five individually randomised plants were raised for each family in each block. The material, however, was scored for only eight of the 15 characters listed in table 1.

3. THE EPISTATIC, ADDITIVE AND DOMINANCE COMPONENTS

The tests for epistatic, additive and dominance components were those described by Jinks and Perkins (1970) in which the appropriate block (replicate) interaction is used to test the significance of the three components if this interaction is itself significant against the error derived from the variation within families. The results obtained for the test for epistasis are given in table 2 for both crosses.

TABLE 2

*Variance ratios testing the significance of epistasis ($\bar{L}_{11} + \bar{L}_{21} - 2\bar{L}_{31}$ variance) in the triple test cross analyses of the material from $V_1 \times V_5$ and $V_2 \times V_{12}$ crosses of *Nicotiana rustica* varieties*

Character	$V_1 \times V_5$ cross	$V_2 \times V_{12}$ cross
H ₁	1.26 ^{NS}	1.95**
H ₂	1.38 ^{NS}	2.72***
H ₃	1.29 ^{NS}	3.00***
FT	1.03 ^{NS}	1.78***
HFT	< 1.00 ^{NS}	1.09 ^{NS}
LL	< 1.00 ^{NS}	1.46**
LW	1.03 ^{NS}	1.23 ^{NS}
LS	1.03 ^{NS}	—
FH	1.14 ^{NS}	1.75**
CL	1.37*	—
SSP	< 1.00 ^{NS}	—
CN	< 1.00 ^{NS}	—
SW	1.24 ^{NS}	—
ASW	1.30*	—
TSN	< 1.00 ^{NS}	—

^{NS} $P > 0.05$; * $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P < 0.001$; — = results not available.

The between sums (additive) and between differences (dominance) mean squares provide estimates of σ_m^2 and σ_{m1}^2 (hereafter referred to as σ_s^2 and σ_d^2), which in the absence of epistasis and linkage disequilibrium in this special case of randomly inbred populations with equal gene frequencies, equal $\frac{1}{4}D = \frac{1}{4}\Sigma d^2$ and $\frac{1}{4}H = \frac{1}{4}\Sigma h^2$, respectively (Kearsey and Jinks, 1968). In the presence of epistasis, however, these expectations include epistatic terms and these estimates of D and H become:

$$\begin{aligned}
 D &= \Sigma d_i^2 + \frac{1}{4}\Sigma i_{jk}^2 + \frac{1}{16}\Sigma j_{jk}^2 + \frac{1}{9}\Sigma l_{jk}^2 + \Sigma d_j \Sigma j_{jk}^* - \frac{2}{3}[\Sigma d_j \Sigma j_{kj}]^* + \frac{1}{3}[\Sigma i_{jk} l_{jk}] \\
 &\quad - \frac{2}{3}[\Sigma j_{jk} j_{kj}] + \frac{1}{2}\Sigma j_{jk} j_{js} + [\Sigma j_{jk} (\frac{2}{9}\Sigma j_{sk} - \frac{1}{3}\Sigma j_{ks} - \frac{1}{3}\Sigma j_{sj})]; \\
 H &= \Sigma h_i^2 + \frac{1}{2}\Sigma i_{jk}^2 + \frac{1}{2}\Sigma l_{jk}^2 + \frac{1}{4}\Sigma j_{jk}^2 + \Sigma l_{jk} (h_j + h_k)^* - [\Sigma i_{jk} (h_j + h_k)]^* \\
 &\quad - [\Sigma i_{jk} l_{jk}] + \frac{1}{2}[\Sigma j_{jk} j_{kj}] + \frac{1}{2}[\Sigma i_{jk} (\Sigma i_{js} + \Sigma i_{ks})] \\
 &\quad + \frac{1}{2}[\Sigma i_{jk} (\Sigma l_{js} + \Sigma l_{ks})] + \frac{1}{2}[\Sigma l_{jk} (\Sigma l_{js} + \Sigma l_{ks})]
 \end{aligned}$$

All the genetic effects are as defined by Mather and Jinks (1971) on the F_∞ metric (Van der Veen, 1959). The expectations given in square brackets ([]) are dependent on the coefficient of gene association and the asterisked co-products alone may change their direction with the type of epistasis present (Pooni, 1976).

The variation among the inbred families included in these experiments can be partitioned into three items; between inbred families, inbred

families $\times$ blocks and the error derived from the variation within families and the appropriate tests of significance applied. The significance of the "between inbred families" component provides an independent test of $D = \Sigma d_i^2$ and a direct estimate of its value. In the presence of epistasis this estimate of D will equal $\Sigma d_i^2 + \Sigma i_{jk}^2$.

The estimates of D obtained from the triple test cross and from the inbred families and the estimates of H obtained from the triple test cross are listed for both the crosses in table 3.

4. MICRO-ENVIRONMENTAL INTERACTION

The L_1 and L_2 families in both triple test crosses being F_1 families show no segregation. The variation within each family is entirely environmental in origin and in the absence of micro-environmental interactions these variances are expected to be homogeneous over all L_{1i} or L_{2i} families since all are then estimates of E_1 , the additive environmental variance. A significant heterogeneity between the "within" variances of L_{1i} or L_{2i} families is therefore evidence of differential genotypic sensitivity to the micro-environmental variation. This is also true for the variation within the true breeding lines. Any differential genotypic sensitivity among the true-breeding lines, however, can only arise from interactions with additive genetic effects while the differential sensitivity of the L_1 or L_2 families may involve dominance effects also.

Two estimates of within family variance (one from each block) are available for any inbred, L_{1i} or L_{2i} family for most of the characters and these have been pooled for individual families before carrying out the Bartlett test of homogeneity. Characters CN, SW, ASW and TSN, however, were scored only for the first block and for these the test of homogeneity was carried out on the single estimate of the variance.

The results of the Bartlett test for both the crosses are given in table 4 as $\chi^2_{(n-1)}$ values and their significances. These tests, however, only detect the presence of genotype $\times$ micro-environmental interactions, and they do not indicate their cause. Such interactions can arise from pleiotropic effects of the genes segregating for mean performance or by segregation at independent loci which control environmental sensitivity only. Furthermore, the loci controlling mean performance and sensitivity may or may not be in linkage equilibrium. Pleiotropy and linkage disequilibrium will produce a relationship between the mean performance (family mean) and sensitivity (within family variance). If a linear regression analysis is therefore carried out using the family mean as independent and the standard deviation as dependent variable, for the inbred families the regression mean square will indicate the degree of linear dependence of the additive genetic $\times$ micro-environment interaction on the additive genetic variation and the remainder mean square, the degree of independent control of this interaction. For all except four of the characters both mean squares can be tested against the families $\times$ blocks interaction mean square which provides an estimate of error for the standard deviations.

The genotype $\times$ micro-environment interaction present amongst L_{1i} and L_{2i} families, on the other hand, can be partitioned between the additive genetic and dominance effects (Perkins and Jinks, 1971) and their linear

TABLE 3
Estimates of *D* and *H* for the various characters obtained from the triple test cross analysis and estimates of *D* from the inbred families for each cross

Character	$V_1 \times V_5$ TTC			$V_1 \times V_6$ inbreds			$V_2 \times V_{12}$ TTC			$V_2 \times V_{12}$ inbreds		
	D	H	D	D	H	D	D	H	D	D	H	D
H ₁	1.09 ± 0.49	0.56 ± 0.34	1.40 ± 0.31	3.74 ± 0.74	0.62 ± 0.25	2.97 ± 0.58						
H ₂	13.38 ± 3.91	4.22 ± 2.74	15.08 ± 3.02	36.51 ± 7.22	7.23 ± 2.53	28.49 ± 5.45						
H ₃	108.10 ± 25.90	23.58 ± 15.76	101.48 ± 20.34	254.82 ± 50.52	63.51 ± 18.07	237.05 ± 45.21						
FT	23.75 ± 4.95	1.77 ± 2.20	23.02 ± 4.63	55.97 ± 10.91	18.72 ± 4.51	63.72 ± 12.13						
HFT	149.36 ± 30.29	8.66 ± 13.82	132.05 ± 25.13	337.15 ± 68.74	124.30 ± 29.04	287.54 ± 55.77						
LL	2.81 ± 0.69	−0.32 ± 0.35	4.66 ± 0.86	15.15 ± 3.00	1.27 ± 0.55	11.53 ± 2.25						
LW	3.65 ± 0.87	−0.21 ± 0.49	4.90 ± 0.92	19.10 ± 3.78	2.55 ± 0.82	12.27 ± 2.40						
LS	14.89 ± 4.00	0.58 ± 2.07	26.78 ± 5.03	—	—	—						
FH	187.26 ± 35.64	23.79 ± 14.33	190.11 ± 34.71	467.43 ± 91.77	209.38 ± 43.95	373.21 ± 70.96						
CL	0.0050 ± 0.001	0.0020 ± 0.0004	0.0043 ± 0.0008	—	—	—						
SSP	0.203 ± 0.039	0.028 ± 0.021	0.183 ± 0.034	—	—	—						
CN	1381.8 ± 375.4	60.44 ± 241.3	2027.2 ± 412.5	—	—	—						
SW	0.0167 ± 0.006	0.0096 ± 0.0058	0.0182 ± 0.0053	—	—	—						
ASW	0.0004 ± 0.0001	0.0001 ± 0.0001	0.0004 ± 0.0001	—	—	—						
TSN	3079.2 ± 799.8	1267.6 ± 588.6	2114.6 ± 470.9	—	—	—						

+ Estimates non-significant against error.

TABLE 4

Significance of genotype $\times$ micro-environmental variation within L_{1i} , L_{2i} and inbred families as detected by Bartlett's test of heterogeneity for various characters scored on the material from $V_1 \times V_5$ and $V_2 \times V_{12}$ crosses

Character	$V_1 \times V_5$ material			$V_2 \times V_{12}$ material		
	L_1 fams	L_2 fams	Inbreds	L_1 fams	L_2 fams	Inbreds
	$\chi^2_{(81)}$	$\chi^2_{(81)}$	$\chi^2_{(81)}$	$\chi^2_{(59)}$	$\chi^2_{(59)}$	$\chi^2_{(59)}$
H_1	104.08*	115.41**	165.13***	87.04*	50.71 ^{Ns}	133.06***
H_2	100.21 ^{Ns}	118.67**	165.20***	141.96*	53.38 ^{Ns}	178.08***
H_3	103.24*	68.13 ^{Ns}	115.66***	93.99**	98.78***	101.52***
FT	117.70**	126.08***	230.23***	103.71***	199.38***	231.25***
HFT	138.74***	76.49 ^{Ns}	200.00***	137.03***	135.32***	147.10***
LL	95.10 ^{Ns}	76.78 ^{Ns}	115.67***	66.55 ^{Ns}	81.74*	104.22***
LW	102.67 ^{Ns}	95.73 ^{Ns}	112.52***	82.87**	75.37 ^{Ns}	100.45***
LS	97.35 ^{Ns}	68.80 ^{Ns}	117.02***	—	—	—
FH	110.38*	88.85 ^{Ns}	126.20***	104.61***	71.99 ^{Ns}	129.46***
CL	104.15*	98.45 ^{Ns}	72.10 ^{Ns}	—	—	—
SSP	86.76 ^{Ns}	58.06 ^{Ns}	431.02***	—	—	—
CN	109.33**	119.23*	108.14**	—	—	—
SW	110.99*	100.70 ^{Ns}	131.60***	—	—	—
ASW	80.59 ^{Ns}	97.06 ^{Ns}	122.58***	—	—	—
TSN	105.96*	131.52***	176.03***	—	—	—

^{Ns} $P > 0.05$; * $P = 0.05-0.01$; ** $P = 0.01-0.001$; *** $P < 0.001$; — results not available.

relationship determined independently by regressing $\frac{1}{2}(\sigma L_{1i} + \sigma L_{2i})$ on to $\frac{1}{2}(\bar{L}_{1i} + \bar{L}_{2i})$ and $\frac{1}{2}(\sigma L_{1i} - \sigma L_{2i})$ on to $\frac{1}{2}(\bar{L}_{1i} - \bar{L}_{2i})$ respectively. Again, with four exceptions the regression and remainder mean squares can be tested for their significance against the corresponding blocks interaction mean squares. The results of these analyses are given in tables 5 and 6 for the $V_1 \times V_5$ and $V_2 \times V_{12}$ crosses respectively. For the four characters CN, SW, ASW and TSN (in the $V_1 \times V_5$ cross) the regression mean squares have been tested against the corresponding remainder mean squares.

5. INTERPRETATION AND CONCLUSION

(i) Gene action

Reference to table 2 and to the estimates of H in table 3 shows that for the material derived from the $V_1 \times V_5$ cross epistasis and dominance effects are either non-significant or of marginal significance only. On the other hand, there is ample evidence of an additive component of variation which is highly significant for all the characters irrespective of the source of its estimate. This material therefore segregates at loci, the alleles of which display little dominance or epistasis but exhibit comparatively large additive effects. Similar results for this material have been reported by Perkins and Jinks (1970) and Jinks and Perkins (1970) for two characters, flowering time (FT) and final height (FH).

For the material from the $V_2 \times V_{12}$ cross there is significant epistasis for six out of the eight characters (table 2) and the estimates of the additive and dominance components are highly significant for all characters (table 3). Non-allelic interaction and dominance therefore constitute a common feature of the genetic variation in this cross. The estimates of additive (D) and dominance (H) components, however, will not be the true magnitudes

TABLE 5

The direction and variance ratios testing the significance of the linear and non-linear components of $\frac{1}{2}(\sigma L_{11} + \sigma L_{21})$, $\frac{1}{2}(\sigma L_{11} - \sigma L_{21})$ and the inbred standard deviations when each was regressed on to $\frac{1}{2}(\bar{L}_{11} + \bar{L}_{21})$, $\frac{1}{2}(\bar{L}_{11} - \bar{L}_{21})$ and inbred means, respectively for the characters scored on material from the $V_1 \times V_3$ cross

Character	Triple test cross						Inbred families					
	Sums			Differences			Linear (1)			Remainder (80)		
	Linear (1)			Linear (1)			Linear (1)			Linear (1)		
	Direction	Significance	Remainder (80)	Direction	Significance	Remainder (80)	Direction	Significance	Direction	Significance	Direction	Significance
H ₁	+	44.86***	< 1.00Ns	+	< 1.00Ns	< 1.00Ns	+	< 1.00Ns	+	48.45***	+	1.55*
H ₂	+	48.63***	1.06Ns	+	< 1.00Ns	< 1.00Ns	+	< 1.00Ns	+	57.89***	+	1.71*
H ₃	+	1.20Ns	1.11Ns	+	< 1.00Ns	< 1.00Ns	+	< 1.00Ns	+	1.54Ns	+	1.10Ns
FT	+	25.10***	< 1.00Ns	+	10.50***	< 1.00Ns	+	< 1.00Ns	+	42.43***	+	< 1.00Ns
HFT	+	27.70***	< 1.00Ns	+	5.95*	< 1.00Ns	+	< 1.00Ns	+	45.10***	+	< 1.00Ns
LL	+	< 1.00Ns	1.52Ns	—	1.27Ns	1.11Ns	+	1.95Ns	+	1.95Ns	+	1.85**
LW	+	1.65Ns	1.67*	—	< 1.00Ns	1.35Ns	+	9.92**	+	1.53Ns	+	1.59*
LS	—	1.49Ns	1.38Ns	—	< 1.00Ns	< 1.00Ns	+	< 1.00Ns	+	1.69Ns	+	1.69*
FH	—	1.22Ns	< 1.00Ns	—	< 1.00Ns	1.14Ns	+	< 1.00Ns	—	< 1.00Ns	—	< 1.00Ns
CL	+	< 1.00Ns	< 1.00Ns	—	< 1.00Ns	< 1.00Ns	—	< 1.00Ns	—	14.90***	—	1.15Ns
SSP	—	10.95***	1.12Ns	—	—	—	+	2.51Ns	+	2.51Ns	—	—
CN	+	12.91***	—	+	4.24*	—	+	< 1.00Ns	+	< 1.00Ns	—	—
SW	+	2.91Ns	—	—	3.07Ns	—	+	1.88Ns	+	1.88Ns	—	—
ASW	+	1.74Ns	—	—	2.63Ns	—	+	63.14***	+	63.14***	—	—
TSN	+	24.59***	—	+	10.79**	—	+	—	+	—	+	—

Ns P = 0.05; * P = 0.05-0.01; ** P = 0.01-0.001; *** P < 0.001; — results not available.

TABLE 6

The direction and variance ratios testing the significance of the linear and non-linear components of $\frac{1}{2}(\sigma L_{11} + \sigma L_{21})$, $\frac{1}{2}(\sigma L_{11} - \sigma L_{21})$ and inbred standard deviations when each was regressed on to $\frac{1}{2}(\bar{L}_{11} + \bar{L}_{21})$, $\frac{1}{2}(\bar{L}_{11} - \bar{L}_{21})$ and inbred means, respectively for the characters scored on the material from the $V_3 \times V_{12}$ cross.

Character	Triple test cross						Inbred families			
	Sums			Differences			Linear (1)		Remainder (58)	
	Linear (1)		Remainder (58)		Linear (1)		Linear (1)		Linear (1)	
	Direction	Significance	Significance	Direction	Significance	Significance	Direction	Significance	Direction	Significance
H ₁	+	5.90*	<1.00Ns	+	2.42Ns	<1.00Ns	+	82.43***	+	1.32Ns
H ₂	+	13.44***	<1.00Ns	+	1.56Ns	<1.00Ns	+	85.69***	+	<1.00Ns
H ₃	+	<1.00Ns	1.37Ns	—	<1.00Ns	<1.00Ns	+	15.17***	+	<1.00Ns
FT	+	18.08***	<1.00Ns	+	6.03*	<1.00Ns	+	7.75**	+	1.01Ns
HFT	+	23.02***	1.40Ns	+	8.06**	2.00**	+	37.46***	+	1.25Ns
LL	+	<1.00Ns	1.59*	—	<1.00Ns	1.24Ns	+	5.04*	+	<1.00Ns
LW	+	3.59Ns	1.57*	+	<1.00Ns	1.42Ns	+	1.14Ns	+	1.12Ns
FH	+	12.46***	1.15Ns	+	<1.00Ns	1.46Ns	+	12.31***	+	1.69*

Ns P>0.05; * P = 0.05-0.01; ** P = 0.01-0.001; *** P<0.001.

of Σd_i^2 and Σh_i^2 as they will contain the epistatic effects given earlier (see Section 3).

The two estimates of D , one from the triple test cross and the other from the analysis of the inbred families, are consistent in magnitude for all characters in both crosses (table 3). Both estimate Σd_i^2 in the absence of epistasis, but in its presence they are affected by non-allelic interactions in different ways as shown by the expectations in Section 3 (Pooni, 1976). It follows, therefore, that in the present data the contributions of the epistatic effects to these two estimates of D must be of the same order of magnitude in every case. Thus over two quite contrasting crosses and widely differing characters the estimate of D from the triple test cross is always a satisfactory estimate of the genetic variation among the random inbred lines even in the presence of epistasis.

(ii) *Genotype $\times$ micro-environment interaction*

The results in table 4 confirm the widespread occurrence of genotype $\times$ micro-environment interactions in both crosses. However, the material from $V_2 \times V_{12}$ cross seems to be the more interactive in that 19 of the 24 tests conducted show significant heterogeneity among the within family variances compared with 28 out of 45 tests for the material from the $V_1 \times V_5$ cross. Furthermore, most of this environmental sensitivity is positively related to mean performance (tables 5 and 6). This can only arise from pleiotropy or strong linkage disequilibrium at most of the loci controlling mean performance and environmental sensitivity. Evidence for independent segregation at loci controlling environmental sensitivity is confined to a few cases where the remainder mean square is found to be significant against the error (tables 5 and 6). Independent segregation of mean performance and genotypic sensitivity to micro-environmental variation is also reported by Perkins and Jinks (1973) for some morphological characters recorded on $V_1 \times V_5$ material.

It can also be seen from table 4 that the $\chi^2_{(n-1)}$ for heterogeneity more often takes a significant value for the inbred family variances than for those of the L_{1i} or L_{2i} families for both crosses. Furthermore, the inbred families also display a more marked linear dependence. It must be remembered, however, that the $\chi^2_{(n-1)}$ for heterogeneity have different expectations in the inbred and L_1 and L_2 families. In the inbred families the genotype $\times$ environment interactions have the expectation of $\Sigma g d_{ij}^2$ while in the L_1 and L_2 families they are $\frac{1}{4}\Sigma g_{dij}^2 + \frac{1}{4}\Sigma g_{hij}^2 - \frac{1}{2}\Sigma g_{dij}g_{hij}$ and $\frac{1}{4}\Sigma g_{dij}^2 + \frac{1}{4}\Sigma g_{hij}^2 + \frac{1}{2}\Sigma g_{dij}g_{hij}$ respectively, where g_{dij} is the interaction with the additive genetic effect and g_{hij} the interaction with the dominance effect (Perkins and Jinks, 1970). Similarly, the variation in mean performance on to which they are regressed has the expectation Σd_i^2 for the inbreds, $\frac{1}{4}\Sigma d_i^2 + \frac{1}{4}\Sigma h_i^2 - \frac{1}{2}\Sigma d_i h_i$ for the L_1 families and $\frac{1}{4}\Sigma d_i^2 + \frac{1}{4}\Sigma h_i^2 + \frac{1}{2}\Sigma d_i h_i$ for the L_2 families.

Finally, dominance $\times$ micro-environment interactions are rarely significant in this material and whenever they are they always display a significant linear relationship with the dominance deviations for the mean performance. The performance of the heterozygotes is therefore more stable than that of the corresponding homozygotes in both the crosses and

any differences in sensitivity there are in the heterozygotes are largely associated with differences in mean performance.

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