Heredity (1979), **43** (1), 57-70

NON-LINEAR GENOTYPE × ENVIRONMENT INTERACTIONS ARISING FROM RESPONSE THRESHOLDS

1. PARENTS, F_1s AND SELECTIONS

J. L. JINKS and H. S. POONI

Department of Genetics, University of Birmingham, Birmingham B15 2TT, U.K.

Received 12.ii.79

SUMMARY

Examples of genotype × environment interactions in *Nicotiana rustica* that appear to be simply linearly related to the additive environmental value (e_j) and others in which this does not appear to be the case have been analysed by testing the goodness-of-fit of linear, quadratic and two intersecting-straight-line models of this relationship. In varieties 1 and 5 and their F_1 cross there is no significant improvement in goodness-of-fit over the linear model from either the quadratic or the two straight-line models. In a stratified sample of 10 inbred lines derived from this cross a pair of intersecting-straight-lines was the best model for the only two inbreds to show significant non-linearity. In varieties 2 and 12, their F_1 cross and the four inbred selections derived from it, the best fit is always obtained with the two intersecting-straight-lines. The reasons, however, differ for the different genotypes. In variety 2 it is because the linear rate of response is relatively higher in the better than in the poorer environments, in variety 12 it is because of a change in the reverse direction, while in the F_1 it is because the rate of response more than doubles in the very best environments. Among the four inbreds it is because one of them, D10, reaches a limit to its response in the environments with above average e_j values while of the remaining three inbreds two increase their linear responses in these environments while the third shows a small decrease.

While, therefore, two intersecting-straight-lines appear to be a widely applicable model of the relationship between the interaction of genotype and environment and the additive environmental value, in only one case, D10, which is a low mean performance and low environmental sensitivity selection, is the use of this model necessitated by a genotypic limit to further response to environmental improvement.

1. INTRODUCTION

IN a series of papers initiated by Bucio Alanis in 1966, biometrical genetical analyses of genotype × environment interactions were presented which exploited the empirical finding that these interactions were a linear function of the additive environmental effects in the generations derived from an initial cross between varieties 1 and 5 of *Nicotiana rustica* (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966; Bucio Alanis *et al.*, 1969; Perkins and Jinks, 1973). By enabling the genotype × environment interactions to be partitioned into those involving the additive, dominance and epistatic action of the genes these analyses permitted the prediction of the magnitude of the linear function across generations as well as the mean phenotype of any generation in any environment within the range over which the linear relationship held.

While there is no comparable analysis of any other cross, the literature now contains many reports, too numerous to cite individually, of linear relationships between genotype × environment interactions and some environmental index (see, for example, reviews by Freeman, 1973; Hill, 1975). There are many others, however, as was shown by Perkins and Jinks (1968*a*, *b*, and 1973) with *Nicotiana rustica* material, where the relationship is non-linear. In this paper we shall analyse one such example, namely, inbred selections from a cross between varieties 2 and 12 of *N. rustica* and show that in this material a significant part of the non-linearity results from thresholds in the response of genotypes to environmental change. At the same time we shall use the same analytical procedures to examine whether thresholds are operating in our previously published data.

2. THEORY AND METHOD

To investigate the effect of thresholds on the regression analysis of genotype × environment interactions we shall examine a simple situation in which each genotype has an upper limit to its phenotypic expression beyond which further change in the environment in the direction that increased the expression will evoke no further response. We shall assume that this limit, like any other property of the phenotype, will differ between genotypes and will be subject to genotypic control. In the simplest case the response of each genotype to an improving environment can then be represented by two intersecting-straight-lines. From the poorest environment to the environment in which further response ceases the straight-line will have a positive slope, thereafter it will have a slope of zero.

Response curves to increasing nutrient levels, which fit this simple expectation, have been reported by Boyd, *et al.*, (1976) along with procedures for comparing the goodness-of-fit of this intersecting-straight-line model relative to that obtained with linear, polynomial, inverse polynomial and exponential models. These authors also note that intersecting-straight-lines is the model of response expected from Liebig's (1855) " Law of the Minimum " and Blackman's subsequent " Limiting Factors " (1905) which describe the joint effects of several environmental factors. In our case the genotype will be the limiting factor leading to a constant phenotypic expression beyond a certain value of the environmental index, because, in general, we shall have no measure of an environment's value other than the average phenotype of all or some of the genotypes grown in that environment (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Bucio Alanis, 1966; Perkins and Jinks, 1968*a*; Bucio Alanis *et al.*, 1969; Perkins and Jinks, 1973).

The consequence of having to measure the environmental values (e_j) in this way can be examined by considering the simple case of two genotypes (A and B) raised in a number of environments. We shall assume that genotype A shows the same linear response to environmental change over the whole environmental range while genotype B ceases to respond in above-average environments. If we now have to use the mean phenotype of A and B in each environment to measure the value of e_j, the response of B, that is, its regression on e_j, will be completely described by two intersecting-straight-lines with positive and zero slopes in the poorer and better environments, respectively.

Because of the way e_j is defined the average response of A and B over the whole environmental range must have a slope of one. The response curves of A and B must, therefore, deviate symmetrically either side of this value. Thus at the environmental value at which B changes its slope from say b_2 to zero the slope of A must change from b_1 to b_1+b_2 to keep its symmetry with the corresponding value for B. Hence the response of A will be completely described by two intersecting-straight-lines both with positive slope; the line in the better environments having a slope $1+\frac{b_2}{b_1}$ times larger than its original value of b_1.

If in our example we extend the upper end of the environmental range beyond the point where A is able to respond further the response of A and B when regressed on e_j will remain unchanged. Because of the way e_j is measured, A, unlike B, can never have a zero slope when regressed on e_j.

These relationships for two genotypes can be extended to three or more genotypes raised in a number of environments when regressed on to e_j. The average response of all genotypes must still be a straight-line of unit slope. The responses of the individual genotypes must still, therefore, be symmetrical around this value. Hence, when the first of n genotypes stops responding to an increase in e_j each of the remaining n–1 genotypes must on average increase their rates of response by $1+\frac{b_1}{\sum_2^n b_i}$. More generally, when r genotypes ($r = 1$ to n) have reached the limit of their response each of the remaining $n-r$ genotypes which are still responding will, on average, have increased their initial rate of response by $1+\frac{\sum_1^r b_i}{\sum_{r+1}^n b_i}$. The remaining $n-r$ genotypes will, therefore, on average show a steadily accelerating response to any further increase in e_j as r increases from 1 to $n-1$.

In the general case some of the r genotypes may show a reduced rather than a zero response to an improvement in the environment leading to a significant deviation between their linear responses in better and poorer environments. In these circumstances the remaining $n-r$ genotypes must increase their responses on average by a factor of $1+\frac{\sum_1^r c_i}{\sum_{r+1}^n b_i}$ where c_i is the absolute change in the linear slope of the *ith* of the r genotypes.

If only one of a number of genotypes reaches its limit within the range of e_j values, or alternatively, two or more genotypes reach their limits but at the same e_j value then a pair of intersecting-straight-lines will account for the response of each of the genotypes. If, however, two or more genotypes reach their limits but do so at different e_j values then it is unlikely that a pair of intersecting-straight-lines will account for the response of any genotype that has not reached its limit. This is because the responses of these genotypes will, on average, accelerate at each environmental value at which an additional genotype reaches its limit. The responses of such genotypes are, therefore, more likely to fit a polynomial, for example, a quadratic curve.

The analyses have, therefore, proceeded by fitting linear, quadratic and two intersecting-straight-line models of the regression of the phenotype of each genotype on to, with two exceptions, dependent e_j values. The method for fitting two intersecting-straight-lines is that described by Boyd, Yuen and Needham (1976) and we are indebted to P. E. Sparrow, Rothamsted Experimental Station, Harpenden, Herts, for a copy of his computer programme which we have modified for use on the ICL 1906A of the University of Birmingham Computer Centre. By comparing the residual mean squares, a best fitting pair of straight lines (1) $Y = a_{\mathrm{I}} + b_{\mathrm{I}}x$ and (2) $Y = a_{\mathrm{II}} + b_{\mathrm{II}}x$ were selected from all possible pairs (1) $y \ldots y_i$ and (2) $y_i + 1 \ldots y_n$ where i is given every value from 3 to $n-3$. However, a single straight-line was rejected in favour of the best fitting pair only if this resulted in a significant reduction of the residual mean square and a significant difference between b_{I} and b_{II}. For reasons given earlier we did not follow Boyd *et al.* (1976) in rejecting pairs of lines in which $b_{\mathrm{I}} < b_{\mathrm{II}}$ since this as well as $b_{\mathrm{I}} > b_{\mathrm{II}}$ is expected in our case.

Similarly, a single straight-line was rejected in favour of a quadratic, or higher-order polynomial, only if this resulted in a significant reduction in the residual mean square and the quadratic (or higher order) regression coefficient was significant. Where the quadratic met these criteria the two intersecting-straight-lines were subject to a more stringent criterion, namely, that they must result in a reduction in the residual mean square which was significantly greater than that achieved by the quadratic.

For the linear and quadratic regression analyses the normal tests of significance apply. It can be argued, however, that in seeking the best pair of intersecting-straight-lines by examining all $n-5$ possible pairs a more stringent test of significance should be applied. A conservative test in which the probability (P) obtained from the normal test of significance is multiplied by $n-5$ wherever P is less than 0.05 has therefore been used throughout. If $(n-5)$ $P < 0{\cdot}05$ there can be little doubt that the best pair of intersecting-straight-lines is a more appropriate model than either the linear or quadratic regressions.

3. MATERIAL

The data we shall analyse are of four kinds and they are listed below in the order in which we shall present their analysis in section 4.

(i) Inbred varieties 1 and 5 of *N. rustica* and their F_1 cross raised in 16 seasons between 1946 and 1964. Details of the sources of these data have been given by Bucio Alanis (1966) and the data are summarised in table 1 in Bucio Alanis *et al.*, (1969).

(ii) A stratified sample of 10 inbred lines from the random sample of 82 of the B inbreds produced by single seed descent from the F_2 of the cross between varieties 1 and 5 by Perkins and Jinks raised in eight environments consisting of all combinations of four sowing dates and two planting densities. These data have been previously analysed by Perkins and Jinks (1973) and by Verma *et al* (1978).

(iii) Four inbred selections, D5, D8, D10 and D21 from the random sample of 60 of the D inbreds produced by single seed descent from the F_2 of the cross between varieties 2 and 12 of *N. rustica* by Perkins and Jinks raised in 27 environments. The four were chosen to represent the range of mean performance and environmental sensitivity among the D inbreds. Although selected on different criteria three of these lines, D5, D10 and D21 are among the later selections of Jinks *et al.* (1977) and Boughey and Jinks (1978). The 27 environments are the first 27 of the 34 listed in table 1. They represent attempts over a number of years to produce the most diverse range of environments possible with the variables at our disposal.

TABLE 1

Descriptions of the 34 *environments used for the data sets* (*iii*) *and* (*iv*), *sections* 3 *and* 4. *Where the fertiliser application, sowing date or planting density deviate from the standard this is indicated under treatment. Superimposed on these treatments are seasonal and site differences*

Environment	Season	Site	Treatment*
1	1973	Winterbourne	Ca, N
2			Ca, K
3			Ca, N, P
4			Ca
5			Ca, N, P, K
6			Ca, N, K
7			Ca, P
8			Ca, P, K
9			P, K
10			P
11			N, K
12			N, P, K
13			Nil
14			N, P
15			K
16			N
17	1972	University	S1
18			S1, HD
19			S2
20			S2, HD
21			S3
22			S3, HD
23			S4
24			S4, HD
25	1975	Avoncroft	
26	1976	University	
27	1975	University	
28	1969	University	S1
29			S2
30	1951	Winterbourne	
31	1952	Winterbourne	
32	1953	Winterbourne	
33	1970	University	S1
34			S2

* Sowing date (S), planting density (D) and fertiliser applications (Ca, N, P and K) are the standard ones for *N. rustica* experiments unless otherwise stated.

(iv) Varieties 2, 12 and their F_1 cross raised in 32 of the environments listed in table 1.

The character we shall analyse in every case is final plant height in cm. The mean final height of each genotype in each environment in the previously unreported experiments (set 3 and environments 1–29, 33 and 34 of set 4) is based on at least eight completely randomised replicate plants.

4. Results

(i) *V1, V5 and their F_1 in 16 environments*

To illustrate our method of comparing linear, quadratic and two intersecting-straight-line models and to test more rigorously earlier conclusions (Bucio Alanis *et al.*, 1969) we have reanalysed the regression of varieties 1 and 5 and their F_1 on e_j derived from the mean of V1 and V5 in each environment. The results of the regression analyses for each genotype are summarised in table 2.

Table 2

Comparison of goodness-of-fit of linear, quadratic and two intersecting-straight-line models of the regression of varieties 1, 5 and their F_1 on e_j for 16 environments. (See Bucio Alanis et al., *1969, table 1, for data.) The items used as denominators in the F tests are given in brackets*

Genotype	Item	d.f	M.S.	F	P
Variety 1	1. Linear regression	1	209·93	95·33(2)	***
	2. Remainder	14	2·20		
	3. Quadratic regression	1	1·36	< 1·0 (4)	NS
	4. Remainder	13	2·27		
	5. Two-lines	2	4·45	2·43(7)	NS
	6. Two-lines	1	7·53	4·12(7)	NS
	7. Remainder	12	1·83		
	Best equation $\bar{V}_{1j} = 41{\cdot}31+0{\cdot}6476\ (\pm 0{\cdot}0663)e_j$				
Variety 5	1. Linear regression	1	915·71	415·33(2)	***
	2–7. As for V_1				
	Best equation $\bar{V}_{5j} = 47{\cdot}09+1{\cdot}3524\ (\pm 0{\cdot}0663)e_j$				
F_1	1. Linear regression	1	765·56	832·13(2)	***
	2. Remainder	14	0·92		
	3. Quadratic regression	1	0·04	< 1·0 (4)	NS
	4. Remainder	13	0·99		
	5. Two-lines	2	0·91	< 1·0 (7)	NS
	6. Two-lines	1	1·79	1·94(7)	NS
	7. Remainder	12	0·92		
	Best equation $F_{1j} = 49{\cdot}69+1{\cdot}2366\ (\pm 0{\cdot}0429)e_j$				

*** $P \leqq 0{\cdot}001$; NS $P > 0{\cdot}05$.

With 16 environments there are 15 d.f. for the regression analysis of each genotype. Items 1 and 2 of each analysis are the linear regression and remainder mean squares for 1 and 14 d.f., respectively. For each genotype the linear regression is highly significant when tested against the remainder as previously reported (Bucio Alanis *et al.*, 1969). The reduction in the remainder sum of squares attributable to adding a quadratic term to the regression for 1 d.f. (item 3) is not significant for any of the three genotypes when tested against the new remainder mean square for 13 d.f. (item 4). Similarly, the reduction in the remainder sum of squares of the linear regression (item 2) attributable to fitting the best pair of intersecting-straight-lines instead of a single straight-line for 2 d.f. (item 5) is also not significant against the remainder mean square, which now has 12 d.f. (item 7), for any genotype either on the normal or the conservative test. Nor is the reduction in the remainder sum of squares of the quadratic regression (item 4) attributable to fitting these two intersecting-straight-lines rather than a quadratic regression for 1 d.f. (item 6) significant against this remainder (item 7).

Clearly we cannot improve significantly on linear regressions for these three genotypes and the best fitting regression equations given in table 2 remain those given by Bucio Alanis *et al.* (1969, table 9).

(ii) *Stratified sample of 10 inbred lines in eight environments*

Following a reanalysis of these data of Perkins and Jinks (1973) Verma *et al.* (1978) have claimed that there are different linear regressions in the below average and the above average environments. Since this is the only claim in the literature that two intersecting-straight-lines provide a better model of genotype × environment interactions than a single straight-line we shall re-examine it.

Verma *et al.* (1978) did not apply statistical criteria of the kind laid down in section 2 to distinguish between alternative models. Furthermore, they included one of the intermediate environments in both the below- and above-average sets of environments. To test their claims objectively we have, therefore, fitted linear, quadratic and two intersecting-straight-line models to the regression of each of the 10 genotypes on the eight dependent e_j values as described in section 2. The results summarised in table 3 have been condensed from the seven items of the full analyses in table 2 to the four unique items 1, 3, 6 and 7.

TABLE 3

Comparisons of goodness-of-fit of linear, quadratic and two intersecting-straight-line models of the regression of 10 inbred lines from the V1 × V5 *cross on* e_j *for eight environments using the within genotype within environment mean square as the error*

	Mean squares				
Inbred genotype	Linear regression 1 d.f.	Quadratic component 1 d.f.	Two-line regression† 1 d.f.	Remainder 4 d.f.	Error 56 d.f.
1	764·3***	16·00 NS	77·31* (0·032)	14·66 NS	11·05
2	575·8***	26·32 NS	1·47 NS	34·10 NS	17·34
3	515·1***	80·34*	107·29** (0·017)	60·77**	13·10
4	1001·4***	0·18 NS	107·70*** (0·001)	26·35*	7·79
5	925·9***	0·74 NS	16·59 NS	6·07 NS	9·68
6	227·2***	4·78 NS	30·69 NS	9·00 NS	31·87
7	1640·1***	40·62 NS	37·01 NS	16·60 NS	12·83
8	833·7***	5·73 NS	59·78 NS	21·16 NS	16·53
9	1022·8***	0·02 NS	7·24 NS	23·51 NS	22·23
10	1008·9***	95·03 NS	33·79 NS	11·58 NS	27·64

*** $P<0{\cdot}001$; ** $P = 0{\cdot}01-0{\cdot}001$; * $P = 0{\cdot}05-0{\cdot}01$; NS $P>0{\cdot}05$.

† The probability in brackets is corrected for the number of pairs of lines examined (3) in choosing the best.

For each genotype there is also an additional item, an error mean square for 56 degrees of freedom derived from replicates within environments. Because this item is heterogeneous ($\chi_9^2 = 55{\cdot}66, P<0{\cdot}001$) it cannot be pooled over genotypes but for each genotype it is the appropriate error for testing the significance of the other four items. For every one of the 10 genotypes the linear regression is highly significant but only for genotypes 1, 3 and 4 is there any evidence that one of the alternative models might be better. The evidence is strongest for genotype 3 where the quadratic regression is significantly better than the linear and the best pair of intersecting-straight-lines is significantly better than both even on the conservative test (P = 0·017). There is still, however, a significant remainder mean square suggesting that a more complex model is required. The evidence is weakest for genotype 1 where the quadratic regression is not significantly better than the linear and the best pair of intersecting-straight-lines is significantly better than both on the normal test but only marginally better than the quadratic (P = 0·032) and no longer significantly better than the linear ($P>0{\cdot}05$) on the conservative test. For only genotypes 3 and 4, therefore, is there convincing evidence that two intersecting-straight-lines is the best of the three models tested and for these genotypes the significant remainder

TABLE 4

The mean final heights of the 4 D selections raised in 27 environments ranked in order of their dependent e_j *values and cross referenced with the treatments that produced them in table 1*

e_j	Environmental treatment (table 1)	Inbred means			
		D5	D8	D10	D21
−42·10	1	37·60	67·60	45·60	62·10
−41·75	4	39·60	73·20	48·00	53·50
−30·50	6	45·50	84·60	52·20	77·00
−30·32	7	48·50	82·20	54·50	74·80
−26·40	2	57·80	83·80	61·20	72·90
−24·85	13	51·50	85·20	61·30	83·70
−22·75	10	52·40	95·20	64·50	78·20
−18·85	15	57·80	99·30	68·20	80·60
−18·50	3	65·30	100·80	57·60	83·60
−16·37	14	65·90	102·40	68·00	79·50
−14·82	9	60·10	102·60	70·20	89·10
−13·82	16	68·90	103·50	65·40	88·20
−9·75	8	69·90	101·30	71·10	100·00
5·25	11	83·90	124·80	83·70	109·90
5·28	5	87·40	122·90	75·60	116·50
7·71	26	84·30	138·97	80·27	108·57
11·35	12	87·30	138·50	91·50	109·40
15·42	18	84·56	150·80	75·10	132·50
18·84	25	89·04	154·97	89·37	123·26
21·21	27	102·17	150·70	77·87	135·40
22·63	20	89·60	159·40	75·90	146·90
29·37	17	98·89	174·60	76·89	148·38
29·75	22	107·50	163·20	81·20	148·40
31·41	24	110·22	159·50	80·10	157·10
33·25	19	105·60	173·80	79·00	155·90
35·78	21	111·70	169·80	83·50	159·40
43·50	23	116·60	181·30	79·00	178·40

mean squares suggest that a still more complex model is required. Neither of these genotypes has reached a limit to its response, genotype 3 showing an increase in its response and genotype 4 a decrease in its response between the poorer and the better environments.

(iii) *D5, D8, D10 and D21 in 27 environments*

These data, which have not been previously reported are presented in table 4. The 27 environments are given in ascending order of their dependent e_j values and the treatments which produced them are numbered to correspond with the list in table 1. The results of the goodness-of-fit tests of the three regression models for each of the four genotypes are given in table 5. Again they are condensed to items 1, 3, 6 and 7 of the full

TABLE 5

Comparisons of goodness-of-fit of linear, quadratic and two intersecting-straight-line models of the regression of 4D inbred selections on e_j *for 27 environments*

Genotype	Item	d.f.	M.S.	χ^2	P†
D5	Linear regression	1	14404·77	1990	***
	Quadratic regression	1	1·99	0·27	NS
	Two-line regression	1	67·79	9·36	**
					(0·05–0·01)
	Remainder	23	14·70	46·70	**
	Error	273	7·24		
Best equation	(1) 62·58+0·9722***(±0·0492)e_j		(2) 101·59+1·1453***(±0·1852)e_j		
with e_j limits	−42·10 to 11·35		15·42 to 43·50		
D8	Linear regression	1	32713·20	5209	***
	Quadratic regression	1	22·56	3·59	NS
	Two-line regression	1	199·87	31·83	***
					(<0·001)
	Remainder	23	16·63	60·91	***
	Error	273	6·28		
Best equation	(1) 95·29+1·1404***(±0·0613)e_j		(2) 159·63+1·2073***(±0·1416)e_j		
with e_j limits	−42·10 to 5·28		7·71 to 43·50		
D10	Linear regression	1	2862·52	791	***
	Quadratic regression	1	543·26	150·07	***
	Two-line regression	1	118·66	32·78	***
					(<0·001)
	Remainder	23	15·48	98·35	***
	Error	270	3·62		
Best equation	(1) 65·82+0·7338***(±0·0557)e_j		(2) 79·79+0·02620 NS (±0·1725)e_j		
with e_j limits	−42·10 to 11·35		15·42 to 43·50		
D21	Linear regression	1	30425·04	3351	***
	Quadratic regression	1	398·82	43·92	***
	Two-line regression	1	129·35	14·25	***
					(0·01–0·001)
	Remainder	23	24·32	61·60	***
	Error	273	9·08		
Best equation	(1) 83·31+1·1333***(±0·0870)e_j		(2) 141·97+1·9074***(±0·1532)e_j		
with e_j limits	−42·10 to 5·28		7·71 to 43·50		

*** P ≦ 0·001; ** 0·001<P ≦ 0·01; * 0·01<P ≦ 0·05; NS P>0·05.

† The probability in brackets is corrected for the number of pairs of lines examined (22) in choosing the best.

analyses of table 2 with the addition of an error mean square derived from replicates within environments. In every case two intersecting-straight-lines give significantly the best fit. For D10 and D21 a quadratic gives a significantly better fit than a linear regression but the best pair of straight lines is a significantly better fit than either. The regression equations for the best pair of lines for each genotype and the range of e_j values over which each line fits are given in table 5.

Inbred D10 is the only genotype to reach its limit within the range of environments. It does so between environmental values 11·35 and 15·42 (environments 12 and 18 of table 1). Above these values its rate of response is not significantly different from zero. Inbred D5, on the other hand, increases its linear rate of response between these two environments. In the below average environments, however, D5 and D10 have similar mean performances and linear rates of response.

TABLE 6

Comparisons of goodness-of-fit of linear, quadratic and two intersecting-straight-line models of the regression of D8 and D21 on e_j *values for 27 environments with the two lines intersecting between* e_j = *11·35 and 15·42*

Genotype	Item	d.f.	M.S.	χ^2	P†
D8	Linear regression	1	32713·20	5209	***
	Quadratic regression	1	22·56	3·59	NS
	Two-line regression	1	112·12	17·85	***
	Remainder	23	20·55	75·26	***
	Error	273	6·28		

Regression equations (1) $100{\cdot}40+1{\cdot}2576^{***}(\pm 0{\cdot}0629)e_j$
(2) $163{\cdot}81+1{\cdot}0964^{***}(\pm 0{\cdot}2039)e_j$

Genotype	Item	d.f.	M.S.	χ^2	P†
D21	Linear regression	1	30425·04	3351	***
	Quadratic regression	1	398·82	43·92	***
	Two-line regression	1	124·16	13·67	***
	Remainder	23	24·54	62·16	***
	Error	273	9·08		

Regression equations (1) $86{\cdot}33+1{\cdot}0363^{***}(\pm 0{\cdot}0729)e_j$
(2) $148{\cdot}56+1{\cdot}7315^{***}(\pm 0{\cdot}2059)e_j$

† See table 5.

The two higher performing inbreds, D8 and D21, both increase their linear responses between environmental values 5·28 and 7·71 (environments 5 and 26 of table 1) which are slightly lower than the e_j values at which D5 and D10 change their responses. Below these e_j values D8 and D21 have almost the same rates of response while above them D21 has the much greater response.

That all four genotypes change their slopes between consecutive pairs of the 27 environmental values suggests that the simple threshold model presented in section 2 may be applicable. This model, which assumes no sampling errors, predicts that all the changes in slope will occur at the same environmental value as a result of the one genotype ceasing to respond at that value. We can, of course, investigate the consequences of insisting that all four genotypes change their slopes between the same pair of environments. The pair chosen on this occasion would be, e_j = 11·35 and 15·42 because it gives the maximum reduction in the remainder mean square over all four genotypes. The appropriate pair of intersecting-straight-lines for D5 and D10 remain those presented in table 5 while those for D8 and D21 are presented in table 6. For D21 this new pair of intersecting-straight-lines give almost exactly the same goodness-of-fit as the best pair of lines in table 5. For D8, however, the new pair are not as good as the best pair but they are still highly significantly better than the linear and the quadratic regression.

If we now compare the regression slopes in the environmental range −42·10 to 11·35 with those in the range 15·42 to 43·50, the effect of D10 reaching a threshold between environmental values 11·35 to 15·42 on the average regression slopes of the other three genotypes is exactly as predicted by the simple theoretical model in section 2. The effect on the individual genotypes, however, varies markedly; D5 and D21 increase their slopes in the better environments by 18 and 67 per cent respectively, D8, on the other hand, reduces its slope by 13 per cent.

TABLE 7

The mean final heights of varieties 2, 12 and their F_1 raised in 32 environments ranked in order of their e_j values and cross-referenced with the treatments that produced them in table 1

e_j	Environmental treatment (table 1)	V2	V12	F_1
−48·72	1	40·30	59·00	63·50
−47·47	4	44·50	57·30	68·20
−38·02	6	47·10	73·60	78·65
−32·92	13	49·50	81·40	83·75
−32·32	7	51·80	80·30	90·05
−30·57	2	54·30	81·30	96·40
−27·12	10	52·10	90·40	95·50
−26·37	15	50·90	93·10	99·95
−21·32	9	56·80	97·30	104·95
−19·57	3	67·20	90·40	106·55
−17·37	16	67·80	94·20	105·95
−16·87	14	69·70	93·30	103·95
−16·47	8	68·60	95·20	120·15
−3·82	11	68·50	120·60	133·40
−0·52	5	88·20	107·50	133·85
7·61	25	90·12	121·85	143·35
8·18	12	86·40	126·70	147·20
9·32	31	85·09	130·30	159·64
15·28	18	93·80	133·50	150·15
16·93	20	99·50	131·10	149·85
17·28	22	105·60	125·70	156·70
17·71	30	97·79	134·37	170·43
18·86	28	98·78	135·69	150·70
20·88	24	104·70	133·80	162·55
23·48	19	108·80	134·90	157·35
25·13	21	111·60	135·40	168·65
25·74	33	108·12	140·10	165·80
25·93	23	110·70	137·90	169·00
29·83	17	108·40	148·00	160·50
30·37	34	113·82	143·66	168·20
37·62	29	116·76	155·23	183·55
49·33	32	127·76	167·64	219·33

Fitting these pairs of intersecting-straight-lines accounts for a highly significant portion of the non-linearity in the response of these four genotypes to environmental change. However, a significant residual non-linearity remains even after fitting the best pairs of such lines as is shown by the significant remainder mean squares in table 5.

(iv) *V2, V12 and their F_1 in 32 environments*

These data, most of which have not previously been reported are given in table 7 and the tests of goodness-of-fit of the regression models using the dependent e_j values for V2 and V12 and the same values as independent e_j's for their F_1 are summarised in table 8. Although a quadratic is significantly better than the linear regression for V2 and V12 a pair of intersecting-straight-lines is the best of the three models for all three genotypes. Nevertheless it does not account for all of the non-linearity in response (see significant remainder mean square in table 8). Over the whole range of environments V12 has a higher rate of response than V2 but whereas

TABLE 8

Comparisons of goodness-of-fit of linear, quadratic and two intersecting-straight-line models of the regression of varieties 2, 12 and their F_1 on e_j for 32 environments

Genotype	Item	d.f.	M.S.	χ^2	P†
Variety 2	Linear regression	1	20276·0	9795	***
	Quadratic regression	1	24·96	12·06	***
	Two-line regression	1	119·43	57·70	*** (<0·001)
	Remainder	28	13·88	187·75	***
	Error	568	2·07		

Best equation (1) $49{\cdot}70+0{\cdot}5080^{***}(\pm 0{\cdot}0727)e_j$ (2) $95{\cdot}55+0{\cdot}9391^{***}(\pm 0{\cdot}0479)e_j$
with e_j limits $-48{\cdot}72$ to $-21{\cdot}32$ $-19{\cdot}57$ to $49{\cdot}33$

Variety 12	Linear regression	1	25031·7	6896	***
	Quadratic regression	1	24·96	6·88	*
	Two-line regression	1	119·43	32·90	*** (<0·001)
	Remainder	28	13·88	107·06	***
	Error	425	3·63		

Best equation (1) $79{\cdot}30+1{\cdot}4920^{***}(\pm 0{\cdot}0727)e_j$ (2) $127{\cdot}70+1{\cdot}0609^{***}(\pm 0{\cdot}0479)e_j$
with e_j limits $-48{\cdot}72$ to $-21{\cdot}32$ $-19{\cdot}57$ to $49{\cdot}33$

F_1	Linear regression	1	42923·4	16259	***
	Quadratic regression	1	7·48	2·83	NS
	Two-line regression	1	542·67	205·56	*** (<0·001)
	Remainder	28	29·52	313·09	***
	Error	911	2·64		

Best equation (1) $126{\cdot}29+1{\cdot}3680^{***}(\pm 0{\cdot}0437)e_j$ (2) $182{\cdot}89+2{\cdot}8580^{***}(\pm 0{\cdot}2154)e_j$
with e_j limits $-48{\cdot}72$ to $25{\cdot}93$ $29{\cdot}83$ to $49{\cdot}33$

*** $P \leqq 0{\cdot}001$; ** $0{\cdot}001 < P \leqq 0{\cdot}01$; * $0{\cdot}01 < P \leqq 0{\cdot}05$; NS $P > 0{\cdot}05$.

† The probability in brackets is corrected for the number of pairs of lines examined (27) in choosing the best.

the rate of response of V2 increases in environments better than $e_j = -19{\cdot}57$ (environment 3 in table 1) that of V12 decreases.

The F_1 is different again. A single straight-line fits all but the very best environments ($e_j > 29{\cdot}83$) but in the latter its rate of response is more than doubled. Because the F_1 is regressed on to an independent e_j this increase is not offset by a corresponding decrease in the rate of response of either of the other genotypes (see section 2).

5. Conclusion

By testing the goodness-of-fit of linear, quadratic and two interacting-straight-line models of the response of different genotypes in respect of their final heights, to changes in the environment, as measured by the additive environmental component e_j, we have arrived at the following conclusions:

(i) Previous claims that the genotype × environment interaction of varieties 1 and 5 and their F_1 over 16 seasons are linear functions of e_j are confirmed by this more rigorous test.

(ii) There is some statistical support for the claim that inbred lines from the V1 × V5 cross show different linear responses to e_j in above- and below-average environments in that a pair of intersecting-straight-lines is the best of the three models for two of the ten inbreds examined.

(iii) The responses of each of the four selected inbreds from the V2 × V12 cross to a very wide range of environments are best accounted for by pairs of intersecting-straight-lines, the points of intersection occurring within a narrow range of environments for all four inbreds. Over almost all of the above average range of environments one of the inbreds, D10, shows no significant response, since the other three inbreds continue to respond linearly in these environments the genotype of D10 must be the limiting factor. The average increase in the linear response of the remaining three inbreds in the better environments is a direct and predictable result of the lack of response of D10 over these environments. That, however, these three inbreds show very different changes in their responses is a genuine reflection of their genotypic differences.

(iv) Although two intersecting-straight-lines also give the best fit to the responses of the parents (V2 and V12) and F_1 of the cross from which the D inbreds were derived to the same wide range of environments none of these genotypes shows a zero response over the better environments. Variety 12, the parent with the higher mean performance, however, shows a reduced linear response in all except the poorer environments. In contrast the high performing F_1 doubles its rate of response in the very best environments. It is quite clear, therefore, that only genotypes such as D10 with low mean performances approach a zero response in the better environments. Nevertheless, all the material originating from varieties 2 and 12 show a non-linearity in their response when regressed on to e_j values and much but not all of this is best accounted for by fitting different linear regressions in the lower and upper ends of the environmental range.

Acknowledgments.—We are indebted to Dr R. J. Brumpton, Dr Hilarie Boughey, Dr N. E. M. Jayasekara and J. W. Stenhouse, all of whom have provided observations on material derived from varieties 2 and 12.

6. References

BLACKMAN, F. F. 1905. Optima and limiting factors. *Annals of Botany*, *19*, 281-295.

BOUGHEY, H., AND JINKS, J. L. 1978. Joint selection for both extremes of mean performance and of sensitivity to a macroenvironmental variable. III. The determinants of sensitivity. *Heredity*, *40*, 363-369.

BOYD, D. A., YUEN, LOWSING T. K., AND NEEDHAM, P. 1976. Nitrogen requirement of cereals. I. Response curves. *J. agric. Sci. Camb.*, *87*, 149-162.

BUCIO ALANIS, L. 1966. Environmental and genotype–environmental components of variability. I. Inbred lines. *Heredity*, *21*, 387-397.

BUCIO ALANIS, L., AND HILL, J. 1966. Environmental and genotype–environmental components of variability. II. Heterozygotes. *Heredity*, *21*, 399-405.

BUCIO ALANIS, L., PERKINS, J. M., AND JINKS, J. L. 1969. Environmental and genotype–environmental components of variability. V. Segregating generations. *Heredity*, *24*, 115-127.

FINLAY, K. W., AND WILKINSON, G. N. 1963. The analysis of adaptation in a plant breeding programme. *Aust. J. Agric. Res.*, *14*, 742-754.

FREEMAN, G. H. 1973. Statistical methods for the analysis of genotype–environment interactions. *Heredity*, *31*, 339-354.

HILL, J. 1975. Genotype–environment interaction—a challenge for plant breeding. *J. Agric. Sci. Camb.*, *85*, 477-493.

JINKS, J. L., JAYASEKARA, N. E. M., AND BOUGHEY, H. 1977. Joint selection for both extremes of mean performance and of sensitivity to a macroenvironmental variable. II. Single seed descent. *Heredity*, *39*, 345-355.

VON LIEBIG, J. 1855. *Die Grundsatze der Agricultur-chemie.* Braunschweig.

PERKINS, J. M., AND JINKS, J. L. 1968*a*. Environmental and genotype–environmental components of variability. III. Multiple lines and crosses. *Heredity*, *23*, 339-356.

PERKINS, J. M., AND JINKS, J. L. 1968*b*. Environmental and genotype–environmental components of variability. IV. Non-linear interactions for multiple inbred lines. *Heredity*, *23*, 525-535.

PERKINS, J. M., AND JINKS, J. L. 1973. The assessment and specificity of environmental and genotype–environmental components of variability. *Heredity*, *30*, 111-126.

VERMA, M. M., CHAHAL, G. S., AND MURTY, B. R. 1978. Limitations of conventional regression analysis—a proposed modification. *Theor. App. Genet.*, *53*, 89-91.

YATES, F., AND COCHRAN, W. G. 1938. The analysis of groups of experiments. *J. Agric. Sci. Camb.*, *28*, 556-580.