NON-LINEAR GENOTYPE $\times$ ENVIRONMENT INTERACTIONS

II. STATISTICAL MODELS AND GENETICAL CONTROL

H. S. POONI, and J. L. JINKS

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

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SUMMARY

Jinks and Pooni (1979) showed that when a single linear regression fails, two intersecting linear regressions are the most widely applicable model of the relationship between the interaction of genotype and environment and the additive environmental value e_j . In theory two overlapping linear regressions should be a more appropriate model where many factors contribute to the interaction. We have therefore compared the goodness-of-fit of models based upon linear, quadratic, two overlapping linear and two intersecting linear regressions to the final heights of 81 inbred lines derived from the cross of varieties 1 and 5 of *Nicotiana rustica* raised in 15 environments, and of 60 inbred lines derived from the cross of varieties 2 and 12 of the same species raised in 14 environments. As controls, the same models have to be fitted to varieties 1 and 5 and their F_1 and varieties 2 and 12 and their F_1 , raised in the majority of these environments.

The results of these analyses confirm the strictly linear relationships previously reported for varieties 1 and 5 and their F_1 . But as a result of segregation at many loci non-parental kinds of non-linear relationships occur among the inbred lines derived from this cross. They also confirm that for varieties 2 and 12 and their F_1 two intersecting linear regressions provide the best fitting model of their responses to environmental differences. Among the inbred lines from this cross are found segregants with non-parental kinds of linear and quadratic relationships. Of the five regression models examined two intersecting linear regressions provide the best fitting model for the largest number of genotypes.

1. INTRODUCTION

JINKS and Pooni (1979) have described an analysis of genotype $\times$ environment interactions that compares the goodness-of-fit of linear, quadratic and two intersecting-straight-line models for the regression of the phenotypic response of a genotype to changes in the environment as measured by the additive environmental values e_j . They used this analysis to confirm that the responses of varieties 1 and 5 of *Nicotiana rustica* and their F_1 were strictly linear while those of varieties 2 and 12, their F_1 and inbred selections derived from them could best be described by two intersecting linear regressions with different slopes. This was partly but not wholly due to the occurrence of thresholds in the responses of some genotypes to further improvement in the environment.

In this paper we extend the analysis to include comparisons of five different regression models by adding to the existing three, two further models based upon two overlapping-straight-lines. These are expected to be more appropriate than two intersecting-straight-lines where many factors contribute to the response. At the same time we shall use the analysis

to investigate the variation in environmental sensitivity within two large random samples of inbred lines derived from the crosses between varieties 1 and 5 and 2 and 12. As controls we shall use the same analysis to investigate the environmental sensitivities of these parental varieties and their F_1 's when raised in the same environments as the inbred lines.

2. THEORY AND METHODS

In our previous paper we have shown that the same genotype may respond differently in different parts of the environmental range and consequently require two regression equations, with differing means, " a "s, and linear regression coefficients, " b "s. In fitting these regressions we assumed that a complete switch-over from one to the other took place between the pair of environments which minimised the remainder mean square. This procedure can be presented in a matrix form as:

$$y_i = a_1 D_i + a_2 (1 - D_i) + \{b_1 D_i + b_2 (1 - D_i)\} x_i + U_{1i} D_i + U_{2i} (1 - D_i)$$

where a_1 , a_2 , b_1 and b_2 are the regression parameters; y_i and x_i the dependent and independent variable vectors; U_{1i} and U_{2i} the remainder vectors for the two regressions and D_i a discrete vector of coefficients with values of 0 and 1 respectively below and above the change-over point between the two sets of environments. Our method therefore assumes a complete independence of two sets of environments and their dependent genotypic scores and provides a unique solution for either group of data.

Switch-over between the two regressions, however, may not be so abrupt and in fact may take place gradually. This is likely when the response of a genotype is dependent on many factors. In these circumstances the two regressions will overlap and make a proportionate contribution to the phenotypic values over the whole range of environments. Clearly D_i which represents a step function will not satisfy these requirements and has to be replaced by some continuous function which allows the contributions of two regressions to vary from environment to environment. One obvious functional form of such an approximate function is the cumulative normal integral (Goldfeld and Quandt, 1972). Here the step function D_i is replaced by the C.N.I. from $-\infty$ to $(x_i - x_0)/\sigma$. Again we can maximise the regression sum of squares by changing the reference environment x_0 by environmental scores between $x_{(3)}$ and $x_{(n-3)}$ and estimate the various parameters.

We can estimate a_1 , a_2 , b_1 and b_2 by using the new method (which we will call overlapping-lines) and compare the results with our previous method, intersecting-straight-lines, as each estimation process takes 4 degrees of freedom. We can also assume $a_1 = a_2 = a$ and estimate two regression coefficients with the same " a " and compare the improvement over a single linear regression with that obtained from a quadratic regression which also has two regression coefficients and one " a ". However, for both overlapping-lines and intersecting-straight-lines we have to use the conservative test of significance by multiplying the observed probability by $(n - 5)$ before deciding the level of significance (Jinks and Pooni, 1979).

3. MATERIAL

The data we shall analyse are of four kinds which are classified into two groups as follows:

Group 1 includes two pure-breeding varieties V1 and V5 of *Nicotiana rustica* from the Birmingham collection of varieties (Mather and Vines, 1952), their F₁ cross and a random sample of 81 inbred lines obtained from the F₂ of the same cross by single-seed-descent (Perkins and Jinks, 1973). This material was grown during the 1970-79 period in a number of environments including different sites and varying sowing dates and planting densities. In total the random inbreds were raised in 15 environments while the parents and F₁ generation were included in only 11 of them.

Group 2 includes the parental varieties V2 and V12 and their F₁ and a random sample of 60 inbred lines derived by single-seed-descent from its F₂ (Jinks, Jayasekara and Boughey, 1977). The material was raised in 14 environments during the 1972-79 period. Again the inbreds were grown in all fourteen environments while the parents and F₁ generation were only raised in the first ten.

While further descriptions of the 29 environments are provided in table 1, the details of some individual experiments which constitute parts of these

TABLE 1

Description of the environments used for the material from the V1×V5 and the V2×V12 respectively. Parental varieties and the F₁'s of the two crosses were only raised in environments 1 to 11 and 16 to 25 respectively

Environment Number	Season	Site	Treatment	e _j -order
V1×V5 material				
1	1971	University	S1, ND	9
2			S1, HD	4
3			S2, ND	5
4			S2, HD	3
5			S3, ND	13
6			S3, HD	8
7			S4, ND	15
8			S4, HD	14
9	1970	University	ND	12
10	1973	University	ND	11
11	1979	University	ND	6
12	1974	University	ND	7
13	1976	Avoncroft	HD	1
14	1977	University	ND	2
15	1977	University	ND	10
V2×V12 material				
16	1972	University	S1, ND	10
17			S1, HD	4
18			S2, ND	9
19			S2, HD	6
20			S3, ND	13
21			S3, HD	8
22			S4, ND	14
23			S4, HD	12
24	1975	University	ND	3
25	1979	University	ND	7
26	1975	Avoncroft	ND	5
27	1976	University	ND	2
28	1977	University	ND	1
29	1978	University	ND	11

† HD = High density; ND = Normal density; S1 to S4 successive sowings.

environments have already been reported elsewhere (Jayasekara, 1974; Pooni, Jinks and Pooni, 1980; Boughey and Jinks, 1978 and Boughey, Jinks, Coombs and Shufflebotham, 1978). Individual plant randomisation was used throughout and each genotype had a minimum of 8 replicate plants in any one environment.

The character we have selected for analysis is the final plant height (FH) in cm. and we shall fit our models to each of the four sets of data using their own additive environmental, e_j , values.

4. RESULTS

(i) Parental varieties and their F_1 generations

The family means of the two pairs of inbred varieties (V1 and V5 and V2 and V12) and their F_1 generations ($V1 \times V5$ and $V2 \times V12$) for each environment, have been tabulated in table 2. Both sets of means are also ranked (ascending order) for the e_j values based on the means of the parental varieties.

TABLE 2

The mean final height (in cm) of the parental varieties and F_1 's for the cross of $V1 \times V5$ and $V2 \times V12$ when raised in environments which are cross referenced in respect of the e_j values to the list in table 1

Environment Number	V1 $\times$ V5 material			e_j -order	Environment Number	V2 $\times$ V12 material			e_j -order
	V1	V5	F_1			V1	V5	F_1	
1	111.00	122.00	130.00	8	16	108.40	148.00	160.50	10
2	101.63	109.00	119.50	5	17	93.80	133.50	150.15	3
3	96.63	110.75	118.50	4	18	108.80	134.90	157.35	7
4	79.88	91.38	102.88	1	19	99.50	131.10	149.85	4
5	109.25	125.75	135.38	9	20	111.60	135.40	168.65	8
6	95.75	110.50	117.88	2	21	105.60	125.70	156.70	5
7	115.00	134.38	141.50	10	22	110.70	137.90	169.00	9
8	117.38	139.50	140.13	11	23	104.70	133.80	162.55	6
9	105.85	120.95	130.65	6	24	82.00	118.43	139.14	1
10	102.69	129.68	131.25	7	25	93.88	127.16	148.39	2
11	98.80	107.72	120.40	3					

The two sets of data have been subjected to linear, quadratic, overlapping-lines (both with common "a" and two "a"s) and intersecting-straight-lines regression analyses. The results obtained for each genotype in each set are summarised in tables 3 and 4, respectively. The items listed are linear regression (for 1 d.f.); improvement attributable to fitting a quadratic regression (1 d.f.) and two overlapping regression lines (1 d.f.); and overall improvements (over linear regression) attributable to fitting two overlapping-straight-lines with different "a"s (2 d.f.) and two intersecting-straight-lines (2 d.f.). Each mean square is tested for its significance against the corresponding within genotype within environment mean square.

There are, of course, five remainder mean squares corresponding with the five different regressions. Only one of these is, however, tabulated and tested for significance, namely, that for the two intersecting-straight-lines which invariably has the smallest value. The other four remainders can be

TABLE 3

Goodness-of-fit of the linear, quadratic, two overlapping- and two intersecting-straight-lines models for the regression of varieties V1 and V5 and their F₁ generation on e_j in eleven environments using within genotypes within environment mean square as the error

Genotype	Category	Item	DF	MS	VR	Probability
V1	One <i>a</i> and one <i>b</i>	Linear regression	1	1055.2	231	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	5.37	1.17	>0.05
		{ Overlapping lines	1	5.25	1.15	>0.05
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	3.64	0.79	>0.05
		{ Intersecting lines	2	5.85	1.28	>0.05
		Remainder	7	6.32	1.38	>0.05
Error		158	4.57			
Regression equation $\bar{Y} = 103.08$, $\hat{\sigma} = 0.8539 \pm 0.0548$. Environmental range -25.07 to 17.74						
V5	One <i>a</i> and one <i>b</i>	Linear regression	1	1900.7	298	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	5.37	0.84	>0.05
		{ Overlapping lines	1	5.25	0.82	>0.05
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	3.64	0.57	>0.05
		{ Intersecting lines	2	5.85	0.92	>0.05
		Remainder	7	6.32	0.99	>0.05
Error		186	6.37			
Regression equation $\bar{Y} = 118.33$, $\hat{\sigma} = 1.1461 \pm 0.0645$. Environmental range -25.07 to 17.74						
F ₁	One <i>a</i> and one <i>b</i>	Linear regression	1	1289.9	213	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	0.21	0.08	>0.05
		{ Overlapping lines	1	0.82	0.14	>0.05
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	4.29	0.71	>0.05
		{ Intersecting lines	2	7.42	1.22	>0.05
		Remainder	7	2.61	0.43	>0.05
Error		211	6.06			
Regression equation $\bar{Y} = 126.19$, $\hat{\sigma} = 0.9441 \pm 0.0768$. Environmental range -25.07 to 17.74						

readily obtained by appropriate manipulation of the sums of squares as, Remainder SS = Total SS_y - regression SS.

Table 3 shows that for all three genotypes the single linear regression is the only item which is significantly greater than the error mean squares. Undoubtedly therefore V1, V5 and their F₁ display only rectilinear responses to any change in the e_j value. These results support the earlier conclusions of Bucio Alanis, Perkins and Jinks (1969) and Jinks and Pooni (1979). However, while the regression coefficients for varieties V1, V5 and their F₁ are in the same rank order in the earlier and present set of environments the latter show smaller deviations from the mean.

Table 4 shows that the regression mean squares for two overlapping-lines with separate "*a*" values are significant for V2 and F₁ but only the regression mean squares for the intersecting-straight-lines produce significant improvements over linear regression for all three genotypes. The remainder mean squares are also always non-significant for the two intersecting-straight-lines while for the two overlapping-lines it is highly significant for the F₁ generation. Overall, therefore two intersecting straight lines is a better model for these three genotypes.

TABLE 4

Goodness-of-fit of the linear, quadratic, two overlapping- and two intersecting-straight-lines models for the regression of varieties V1 and V12 and their F₁ on e_j in ten environments using within genotype within environment mean square as the error

Genotype	Category	Item	DF	MS	VR	Probability†
V2	One <i>a</i> and one <i>b</i>	Linear regression	1	722.3	152	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	13.64	2.87	>0.05
		{ Overlapping lines	1	15.16	3.18	(>0.05)
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	24.21	5.09	(<0.05)
		{ Intersecting lines	2	30.70	6.44	(<0.05)
		Remainder	6	5.14	1.08	>0.05
		Error	104	4.76		
Regression equations (1) $\bar{Y}_1 = 92.29$, $\hat{b}_1 = 1.0570 \pm 0.1825$. (2) $\bar{Y}_2 = 108.30$, $\hat{b}_2 = 0.4058 \pm 0.2406$. <i>e_j</i> limits -17.03 to -1.94, -1.59 to 10.96						
V12	One <i>a</i> and one <i>b</i>	Linear regression	1	468.7	76	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	13.64	2.22	>0.05
		{ Overlapping lines	1	15.16	2.47	(>0.05)
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	24.21	3.94	(>0.05)
		{ Intersecting lines	2	30.70	5.00	(<0.05)
		Remainder	6	5.14	0.84	>0.05
		Error	104	6.14		
Regression equations (1) $\bar{Y}_1 = 127.55$, $\hat{b}_1 = 0.9430 \pm 0.1825$. (2) $\bar{Y}_2 = 135.95$, $\hat{b}_2 = 1.5942 \pm 0.2406$. <i>e_j</i> limits -17.03 to -1.94, -1.59 to 10.96						
F ₁	One <i>a</i> and one <i>b</i>	Linear regression	1	631.5	117	<0.001
	One <i>a</i> and two <i>b</i> 's	{ Quadratic	1	2.05	0.38	>0.05
		{ Overlapping lines	1	6.88	1.27	(>0.05)
	Two <i>a</i> 's and two <i>b</i> 's	{ Overlapping lines	2	32.25	6.53	(<0.05)
		{ Intersecting lines	2	58.38	10.81	(<0.001)
		Remainder	6	10.00	1.85	>0.05
		Error	236	5.40		
Regression equations (1) $\bar{Y}_1 = 152.02$, $\hat{b}_1 = 0.9910 \pm 0.1985$. (2) $\bar{Y}_2 = 166.05$, $\hat{b}_2 = -1.8760 \pm 0.3728$. <i>e_j</i> limits -17.03 to 4.61, 6.26 to 10.96						

† The probabilities for overlapping- and intersecting-straight-lines (bracketed) are corrected for the number of (5) pairs of lines examined in choosing the best.

(ii) *Random inbreds*

(a) *From cross V1 × V5*

As the two sets of inbred lines were produced by single-seed-descent from randomly chosen F₂ individuals they will display the results of segregation both for the allelic differences controlling mean plant height and for those controlling their response to environmental change. As a first approximation this segregation should result in a bivariate normal distribution of the mean plant heights and environmental sensitivities of the inbred lines around the corresponding mean values for the parental varieties (Jinks and Pooni, 1976, 1980). The results of fitting the five different regression models to the responses of the inbred segregants to the additive environmental differences will, however, depend on the nature of the genetical control of environmental sensitivity. For example, the responses

of the inbreds from the cross between varieties 1 and 5 will fit the strictly linear regression model which was adequate for their parental varieties if either an allelic difference at a single locus controls all of the differences in environmental sensitivity or the allelic differences at the two or more controlling loci produce similar differences in environmental sensitivity to all of the environmental variables. In all other circumstances, for example, if the allelic difference at each of the controlling loci produces a pattern of differences in response to the various environmental variables that is unique to itself, the linear regression model will not be adequate for all of the inbred segregants (Mather, 1975) and in general, the greater the number of controlling loci and the greater the diversity of the patterns of response they individually control, the more varied and more complex will be the regression models that are required to describe adequately the environmental sensitivities of a random sample of inbred segregants.

The results of fitting the five different regression models to the 81 inbred lines derived from the cross of varieties 1 and 5 raised in 15 environments using the overall means in each environment as dependent e_i values are presented in tables 5 and 6. Each of the 81 lines was initially tested for the

TABLE 5

Extended joint regression analysis of the linear (heterogeneity of regressions), quadratic, two overlapping lines and two intersecting-straight-lines regression models for the 81 random inbreds derived from V1×V5 cross. Each of these components together with the overall remainder mean square is tested against an error which is the pooled within genotypes within environment mean square

Category	Item	DF	MS	$\chi^2_{(DF)}$	Probability†
One a and one b	Joint regression (Environments)	14	14,416.32		
	Heterogeneity of regression	80	118.74	869	<0.001
One a and two b 's	Quadratic regression	81	78.76	584	<0.001
	Overlapping lines	81	97.16	720	(<0.001)
Two a 's and two b 's	Overlapping lines	162	65.59	1031	(<0.001)
	Intersecting lines	162	109.86	1628	(<0.001)
	Remainder	878	32.01	2571	<0.001
	Error	12,879	10.93		

† Bracketed probabilities are already multiplied by $n-5$, (10) the number of pairs of regression lines used for selecting the best.

goodness-of-fit of the five models using the same analysis as that performed on the parental varieties (tables 3 and 4). The 81 individual analyses in respect of the linear regression model were then combined using the standard joint regression analysis of Yates and Cochran (1938) in which the Joint Regression sum of squares is identical with the Environment sum of squares for 14 degrees of freedom and the Heterogeneity of Regression sum of squares for 80 degrees of freedom arises from the differences among the 81 individual linear regressions. To these sums of squares (table 5) we have added four new items; namely, the additional sums of squares accounted for by fitting a quadratic regression and overlapping regressions (single a) in the 81 individual analyses, each for a total of 81 degrees of freedom, and for

TABLE 6

Classification of the 81 inbreds from $V1 \times V5$ cross into three groups based on the goodness-of-fit of the regression models. The quadratic group is subdivided into those with positive and negative regression coefficients and the two-line regression group is cross-classified according to whether $b_1 < b_2$ or $b_1 > b_2$ and the pair of e_i values between which the changeover occurs

Model	Changeover range	Category	Inbred lines
(1) Linear regression	—	—	4, 9, 12, 15, 19, 20, 33, 39, 48, 49, 53, 61, 65, 71, 77, 80
(2) Quadratic regression	(a) —	positive	18, 21, 35, 41, 55, 59, 66, 69, 78, 79
	(b) —	negative	1, 2, 13, 14, 31, 32, 51, 57, 62, 67, 68, 75
(3) Two-line regression	(a) -16.61 to -5.24	$b_1 > b_2$	42
		$b_1 < b_2$	28
	(b) -5.24 to -1.97	$b_1 > b_2$	44, 62
		$b_1 < b_2$	5, 10, 36, 70
	(c) -1.97 to -1.70	$b_1 > b_2$	3, 24, 72,
		$b_1 < b_2$	6
	(d) -1.70 to -1.20	$b_1 > b_2$	29, 38, 54, 74
		$b_1 < b_2$	17
	(e) -1.20 to 0.23	$b_1 > b_2$	6, 50
		$b_1 < b_2$	64
	(f) 0.23 to 5.31	$b_1 > b_2$	82
		$b_1 < b_2$	43, 58
	(g) 5.31 to 5.62	$b_1 > b_2$	25, 34, 40, 52, 60
		$b_1 < b_2$	56, 63, 73, 81
	(h) 5.62 to 9.47	$b_1 > b_2$	22, 23, 47, 76
		$b_1 < b_2$	8
	(i) 9.47 to 9.49	$b_1 > b_2$	46
		$b_1 < b_2$	27
	(j) 9.49 to 12.43	$b_1 > b_2$	11, 26, 45
		$b_1 < b_2$	37

fitting the overlapping regressions (two a 's) and intersecting regressions in the 81 individual analyses each for a total of 162 degrees of freedom. Also tabulated is the pooled remainder sums of squares, for 878 degrees of freedom, of the 81 individual analyses after fitting the intersecting regressions. All of the corresponding mean squares have been tested against the within genotype within environment error mean square for 12,879 degrees of freedom (table 5).

Every item in table 5 is highly significant against the error. Not only, therefore, do the 81 inbred lines differ significantly in their linear responses but some also require quadratic, two overlapping or intersecting lines or even more complex regression models to describe adequately their responses to the environmental differences.

From the initial regression analyses carried out on the 81 inbred lines individually we can identify for each line which of the five regression models is the most satisfactory. To simplify the presentation of the results in table 6 the 81 inbred lines have been classified into three groups. The first consists of 16 lines where a single linear regression is adequate, the second of 22 lines where a quadratic regression gives the best fit and the third of the remaining 43 lines where one of the two overlapping or intersecting lines models is required. The quadratic group is subdivided into those with a positive (10) and those with a negative (12) quadratic regression coefficient. Similarly, the two line group is cross-classified according to whether $b_1 > b_2$ or $b_2 > b_1$

and the pair of environments (e_j values) between which the changeover from b_1 to b_2 occurs.

(b) *From cross V2×V12*

The analyses described in the last section have also been carried out on the 60 inbred lines derived from the cross between varieties 2 and 12 raised in 14 environments. The results summarised in table 7 and 8 show that all

TABLE 7

Extended joint regression analysis of the linear (heterogeneity of regression), quadratic, two overlapping regressions and two intersecting-straight-lines regression models for the 60 inbreds derived from V2×V12 cross. Each of these components including the remainder mean square is tested against the pooled error

Category	Item	DF	MS	$\chi^2_{(DF)}$	Probability†
One a and one b	Joint regression	13	5,686.25		
	Heterogeneity of regressions	59	130.64	1039	<0.001
One a and two b 's	Quadratic regression	60	30.93	250	<0.001
	Overlapping lines	60	41.18	333	(<0.001)
Two a 's and two b 's	Overlapping lines	120	34.80	563	(<0.001)
	Intersecting lines	120	89.44	1446	(<0.001)
	Remainder	588	30.27	2399	<0.001
	Error	10,260	7.42		

† See table 5.

TABLE 8

Classification of the 60 inbreds from V2×V12 cross into three groups based on the goodness-of-fit of the regression model. The quadratic group is subdivided into those with positive and negative regression coefficients and the two-line regression group is cross-classified according to whether $b_1 > b_2$ or $b_1 < b_2$ and the pair of e_j values between which the changeover occurs

Model	Changeover range	Category	Inbred lines
(1) Linear regression	—	—	14, 19, 29, 45, 49, 54, 59
(2) Quadratic regression	(a) —	positive	52
	(b) —	negative	36, 44, 57
(3) Two lines regression	(a) -9.40 to -7.58	$b_1 > b_2$	9, 22, 34
		$b_1 < b_2$	23, 47
	(b) -7.58 to -2.52	$b_1 > b_2$	—
		$b_1 < b_2$	11, 21, 43
	(c) -2.52 to -1.54	$b_1 > b_2$	6, 7, 13, 17, 26, 53
		$b_1 < b_2$	1, 16, 40, 51
	(d) -1.54 to -0.05	$b_1 > b_2$	25, 32, 46, 55
		$b_1 < b_2$	5
	(e) -0.05 to 2.18	$b_1 > b_2$	—
		$b_1 < b_2$	10, 24, 41
	(f) 2.18 to 4.21	$b_1 > b_2$	—
		$b_1 < b_2$	2, 3, 35
	(g) 4.21 to 6.28	$b_1 > b_2$	18, 30, 60
		$b_1 < b_2$	20, 56, 58
	(h) 6.28 to 6.92	$b_1 > b_2$	15, 33, 37, 38, 39, 42, 50
		$b_1 < b_2$	4, 12, 27, 28, 48
	(i) 6.92 to 8.67	$b_1 > b_2$	8
		$b_1 < b_2$	31

the items in the extended joint regression analysis are again highly significant. The 60 inbred lines, therefore, differ in their linear responses but in addition some require quadratic, two overlapping or intersecting lines and even more complex regression models to describe adequately their responses to the environmental differences.

The regression analyses of the 60 inbred lines individually again allow them to be divided into five classes on the basis of the best fitting model and these are summarised in table 8 which shows that 7, 4 and 49 inbred lines fall into the linear, quadratic and two-line groups respectively.

5. DISCUSSION

(i) *Parental varieties and their F_1 's*

The present results (table 3) confirm those obtained previously (Bucio Alanis, Perkins and Jinks, 1969 and Jinks and Pooni, 1979) in showing that varieties 1 and 5 and their F_1 respond linearly to environmental differences. The physical treatments that produced the present set of environments (table 1) are completely different from the set of 16 environments used by Bucio Alanis *et al.* (1969) and described by Bucio Alanis (1966). Nevertheless the mean and spread of additive environmental values within the two sets are the same. The present analyses, therefore, extend the number of physical treatments but not the range of environmental values over which the linear relationship holds.

The present results (table 4) also agree with those of previous analyses of varieties 2 and 12 and their F_1 (Jinks and Pooni, 1979) to the extent that the best fitting regression model is two intersecting-straight-lines. The results, however, differ in detail. In the previous analyses variety 2 and the F_1 had an increased response relative to variety 12 in the above average environments while in the present analyses they show a decreased response (table 4). The most likely explanation is differences between the two sets of environments.

Reference to table 1 and to tables 1 and 7 of Jinks and Pooni (1979) shows that by restricting our present analyses to the ten environments in which the random inbred lines derived from the cross of varieties 2 and 12 were also raised, only 8 of the 32 environments used in the previous analyses could be included. Furthermore these 8 environments all have e_j values which are high, ranking 19, 20, 21, 24, 25, 26, 28 and 29 among the 32 environments. The 10 environments of the present analyses cannot therefore be regarded as a random sample of the total environments available. They are, in fact, a set of well above average environments. It appears, therefore, that the increase in the rate of response of variety 2 and the F_1 relative to variety 12 between the poorest and the better environments is not maintained in the best environments which constitute the majority of the environments used in the present analyses. This suggests that the correct model over all of the environments would be three intersecting-straight-lines with the second of the three lines for variety 2 and the F_1 having a higher slope than the first and third. Our analyses could only pick out whichever pair of straight lines gave the smallest remainder mean square but since the best fitting pair of straight lines would still be inadequate this remainder mean square would be significant. This is precisely the result our earlier analyses of all 32 environments gave (Jinks and Pooni, 1979). Equally, if we analyse the response in one half of the environmental range,

only the two intersecting-straight-lines model should be adequate which is, of course, what we find in the present analyses.

(ii) *Random inbreds*

Random samples of inbred lines derived from a single cross are expected to include parental types and recombinants produced by genetic segregation. Their relative proportions will depend on the number of loci at which the parental varieties differ and the strength of any linkages among them. The parental types, in respect of the loci controlling environmental sensitivity, are expected to show the same response to environmental differences as the parental varieties themselves. The responses shown by the recombinants, on the other hand, may differ from those of the parental varieties both in degree and in kind. They may fit the same regression model as their parental varieties and differ solely in their rate of response or they may fit one of the alternative regression models, depending upon the nature of the genetical control of environmental sensitivity.

Among the 81 inbred lines derived from the cross of varieties 1 and 5 only 16 fit the kind of regression model, *i.e.*, linear regression, that is adequate for the parental lines and their F_1 (tables 3 and 6). Among these, however, only four have linear regression coefficients which do not differ significantly from that of either variety 1 or variety 5, two being indistinguishable from variety 1 and two from variety 5. Hence four of the inbred lines have the parental type of response to environmental differences and 77 a non-parental response. These relative frequencies are compatible with a minimal estimate of 5 gene loci, or more strictly effective factors, controlling the segregation for environmental sensitivity in this cross (Jinks, Caten, Simchen and Croft, 1966).

Among the 60 inbred lines derived from the cross of varieties 2 and 12, 49 fit the kind of regression model *i.e.*, two line regression model, that is adequate for the parental varieties and their F_1 (tables 4 and 8). But while it is clear that the 11 inbred lines that fit either the linear or quadratic regression models are non-parental recombinants there is no single criterion for deciding which of the 49 that fit one of the two line regression models are also non-parental.

One of the aims of the present paper was to compare four different regression models for non-linear responses to environmental differences. The results show that of these the two intersecting-straight-lines model accounts for the greatest mean square and hence leaves the smallest remainder mean square for the largest number of genotypes (tables 4 to 8). It would appear, therefore, that non-linear responses most frequently arise from a sharp discontinuity in the rate of linear response at some point on the environmental range.

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