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Linear and non-linear regression analysis of genotype × environment interactions in pearl millet

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Summary. Regression analysis was computed on the grain yield of 15 single cross F_1 hybrids of pearl millet (*Pennisetum typhoides* (Burm.) S. & H.) evaluated in 20 environments at 19 sites in India to assess the nature of genotype × environment interactions. Linear, quadratic, cubic, two- and three-intersecting straight line models were examined for fit. The interactions of six hybrids viz. MH 110, MH 113, MH 114, MH 115, MH 120 and MBH 110 were explained by the linear regression model. The response of the remaining nine hybrids was largely non-linear. The two- and three-intersecting straight line models fit better than the quadratic and cubic models and explained non-linearity of response. The two-intersecting straight line models fit for 6 hybrids MH 106, MH 107, MH 112, MH 116, MH 117 and BJ 104. The response of MH 109 was best explained by a three-intersecting straight line model, but there still existed a significant remainder variation. The truncation of environmental range by assuming moving division points was more efficient than the fixed division points for the segmental regression models. The stability of hybrid varieties on the best fitting model has been discussed.

Key words: *Pennisetum typhoides* (Burm.) S. & H. – Pearl millet – Linear and non-linear regression analysis – Genotype × environment interaction

Introduction

The conventional regression analysis (Yates and Cochran 1938; Finlay and Wilkinson 1963; Eberhart and Russell 1966; Perkins and Jinks 1968a, b) assumes a linear relationship between genotype × environment (GE) interactions and the additive environmental values (e_j). When, however, this relationship is largely non-linear (Perkins and Jinks 1968a, b, 1973; Verma et al. 1978; Jinks and Pooni 1979; Pooni and Jinks 1980; Mariani et al. 1983; Virk et al. 1986) the simple regression analysis no longer retains its full predictive utility. Non-linear GE interactions can be investigated either by fitting curvilinear (quadratic, cubic, etc.) or segmental regression (two- or three-intersecting straight lines) models. While fitting segmental regression models, the environmental range may be divided by assuming fixed division points for all genotypes (Verma et al. 1978; Mariani et al. 1983) or by using moving division points where the truncation points are genotype specific and are determined by the change in response over the environmental range. In this paper we examine various regression models for investigating the responses of different pearl millet hybrids to changes in the environment in respect to grain yield. Further, the method of Jinks and Pooni (1979) will be extended to three-intersecting straight lines model (Virk and Virk 1986) and the stability parameters will be computed for classifying varieties according to their level of adaptation.

Materials and methods

Fifteen single cross F_1 hybrids of pearl millet were evaluated in 20 environments at 19 sites with 2 fertility levels at one of the sites in India during 1981 under the All-India Coordinated Pearl Millet Improvement Project (AICMIP). In each of the 20 environments, a randomized complete block design with three replicate blocks and 5 m long plots of 6 rows was used. A uniform spacing of 50 cm between rows and 10 cm between plants within rows was maintained. The grain yield in q/ha was recorded at maturity.

Jinks and Pooni (1979) investigated the effect of thresholds on the regression analysis of genotype×environment interactions by examining a situation in which each genotype had an upper limit to its phenotypic response; further change in the environment in the direction that increased the expression would evoke no further response. Presently, we shall examine a situation in which each genotype has both lower and upper limits to its phenotypic expression, and further change in the environment in either direction will evoke no response. We shall assume that these limits, like any other property of the phenotype, will differ between genotypes and will be subjected to genotypic control. The response of each genotype to an environmental range can then be represented by three intersecting-straight lines. From the poorest environment to the environment in which response starts, the straight line will have a slope of zero; thereafter it will have a positive slope. When this genotype ceases to respond in the above average environment the regression slope will again be zero. Since the genotype is the limiting factor leading to phenotypic expression, the average phenotype of all of the genotypes grown in that environment will serve as an environmental index (Yates and Cochran 1938; Finlay and Wilkinson 1963; Perkins and Jinks 1968a; Perkins and Jinks 1973; Jinks and Pooni 1979). The consequence of measuring the environmental value (e_j) in this way will be that the average response of all the genotypes over the whole range should have a slope of one. The response of the genotypes must, therefore, deviate symmetrically on either side of this value. In the 3 segments of an environmental range, with 3 rates of response ($b<1$, $b=1$ and $b>1$), it should be possible to detect 27 types of triplet combinations of rates of response in the 3 segments. Further, there is every likelihood that a genotype with below average response in the poor environments ($b<1$), favourable response in the average environments ($b \geqq 1$) and still greater response in the most favourable environments ($b>1$) may exist. A genotype with such a combination of rates of response accompanied by a desirable mean performance would be preferred by plant breeders and we shall call it an ideal genotype. Furthermore, genotypes with specific adaptations can be identified by various combinations of regression slope in the three segments.

The analyses have proceeded by fitting linear, quadratic, cubic, two-intersecting straight line and three-intersecting straight line models of the regression of the phenotype of each genotype on to dependent e_j values. The analyses up to two-intersecting straight line models have been described by Jinks and Pooni (1979). By comparing the residual mean squares a best fitting triplet of straight lines – (1) $Y=a_I+b_I x$, (2) $Y=a_{II}+b_{II} x$, and (3) $Y=a_{III}+b_{III} x$ – were selected from all possible triplets: (1) $Y \ldots Y_i$, (2) $Y_i+1 \ldots Y_{n-3}$, and (3) $Y_i+4 \ldots Y_n$, where i varies from 3 to (n-6). In this way there are (n-7) (n-8)/2 possible triplet combinations.

A single straight line model was rejected in favour of quadratic, cubic, two-lines and three-lines regression, only if this resulted in a significant reduction in the residual mean squares. When quadratic, cubic and two-lines met these criteria, the three-intersecting straight lines were subjected to more stringent criterion, the result being a reduction in the residual mean squares significantly greater than that achieved by the quadratic, cubic and two-intersecting straight lines.

Results and discussion

The 20 test environments were widely diverse as the environmental values (e_j) varied from −14.62 for Durgapura to 22.85 for Mahua (Table 1). The joint regression analysis (Perkins and Jinks 1968a) showed that significant differences existed among the hybrids in respect to grain yield. The hybrids, however, interacted significantly with the environments (Table 2). Both heterogeneity among regressions and remainder mean squares were significant but the former was not significantly greater than the latter.

Apparently the non-linear GE interaction component was important and the analysis must account for it. Therefore, linear, quadratic, cubic, two- and three-intersecting straight line models were fitted in order to identify the best fitting model for each hybrid.

For 6 hybrids – MH 110, MH 113, MH 114, MH 115, MH 120 and MBH 110 – all GE interaction was attributable to the linear component with non-significant remainder mean squares. The stability parameters of these hybrids are given in Table 3. The hybrid MBH 110 with high yield is specifically suited to

Table 1. Environmental indices (e_j) for grain yield (q/ha) of 15 pearl millet hybrids tested in 20 environments

Ser. no.	Environment	e_j
1	Durgapura	– 14.62
2	Paiyur	– 11.95
3	Jodhpur	– 11.84
4	Kovilpatti	– 9.94
5	Kanpur	– 9.86
6	Bijapur	– 6.31
7	Coimbatore	– 6.13
8	Aurangabad	– 5.77
9	Vizianagaram	– 3.47
10	Patancheru (Low fertility)	– 1.51
11	Palem	– 1.35
12	Jamnagar	2.55
13	Dhule	3.57
14	Rahuri	4.99
15	Patancheru (High fertility)	5.10
16	Jalna	5.69
17	Hissar	10.96
18	Ludhiana	11.69
19	Pantnagar	15.34
20	Mahua	22.85

Table 2. Joints regression analysis for 15 pearl millet hybrids tested in 20 environments

Item	df	Mean squares
Genotypes (G)	14	61.45**
Environments (E)	19	1,528.87**
G×E	266	19.01**
Heterogeneity of regressions	14	27.54**
Remainder	252	18.53**
Error	560	9.27

** Significant at the 1% probability level

Table 3. Mean ($\bar{X}_i$) grain yield (q/ha), linear regression coefficient (b_i), standard error of regression (SE b_i), remainder mean squares ($S^2_{d_i}$) and overall mean for pearl millet hybrids

Hybrid	Environment no.	$\bar{X}_i$	b_i	SEb_i	$S^2_{d_i}$	Overall mean
Single line regression						
MH 110	1–20	21.11	0.98	0.08	11.56	21.11
MH 113	1–20	20.93	0.99	0.07	10.56	20.93
MH 114	1–20	18.28	0.88	0.06	7.66	18.28
MH 115	1–20	21.68	1.10	0.09	14.16	21.68
MH 120	1–20	19.14	0.84	0.08	14.00	19.14
MBH 110	1–20	23.63	1.23**	0.07	9.47	23.63
Two-lines regression						
MH 106	1–9	16.24	2.18**	0.26	13.72	23.71
	10–20	29.82	1.05	0.19		
MH 107	1–17	20.60	1.26*	0.12		
	18–20	35.74	1.48[a]	0.72	14.53	22.87
MH 112	1–13	15.21	1.13	0.16		
	14–20	26.60	1.40	0.18	9.44	19.20
MH 116	1–11	16.28	1.55**	0.16		
	12–20	30.57	1.36	0.25	12.55	22.71
MH 117	1–16	18.39	1.10*	0.11		
	17–20	35.85	2.44	0.23	8.20	21.88
BJ 104	1–17	17.41	1.01	0.12		
	18–20	41.97	0.44[a]	0.95	15.02	21.09
Three-lines regression						
MH 108	1–4	13.67	3.01[a]	0.86		
	5–15	22.54	1.18	0.29	24.47**	24.29
	16–20	36.65	0.10[a]	0.50		
MH 109	1–13	16.51	0.94	0.12		
	14–16	20.38	7.36[a]	4.16	13.38	20.93
	17–20	35.67	0.96[a]	0.81		
MH 119	1–8	10.13	0.03[a]	0.42		
	9–16	23.04	0.26[a]	0.39	23.06**	21.81
	17–20	42.71	0.85[a]	0.96		

*, ** Significant at the 5% and 1% probability level, respectively, from unity
[a] Nonsignificant from zero

favourable environments because of its above average response ($b_i > 1.0$). The remaining five hybrids possess general adaptation since their b_i values are unity with $S^2_{d_i} \simeq 0$.

Fit tests for the various regression models for hybrid varieties where the single linear regression model was inadequate are presented in Tables 4 and 5. Items 1 and 2 correspond to linear regression and remainder mean squares for each hybrid variety at 1 and 18 df, respectively. The reduction in the remainder sum of squares (SS) attributable to adding a quadratic term for 1 df is nonsignificant for all hybrids (Tables 4 and 5) except for MH 108 (Table 5). The reduction in the remainder SS of the linear regression attributable to fitting the cubic regression instead of single line for 2 df (item 6) was significant for MH 106, MH 116, MH 117 and MH 119 hybrids. The reduction in the remainder SS of the quadratic (item 4) attributable to fitting cubic regression rather than the quadratic regression for 1 df (item 5) was significant for five hybrids, namely MH 106, MH 116, MH 117, BJ 104 and MH 119. The reduction in the remainder SS of the linear regression attributable to fitting the best pair of intersecting straight lines instead of a single straight line for 2 df (item 9) was highly significant for all nine hybrids (Tables 4 and 5). The reduction in the remainder SS of the quadratic (item 4) attributable to fitting of two-intersecting straight lines rather than a quadratic regression for 1 df (item 8) was also significant for all nine hybrids. The remainder mean squares from the two-intersecting straight lines regression (item 10, Table 5) was significant for three hybrids, namely MH 108, MH 109 and MH 119. Therefore, three-intersecting straight line model was fitted for them. The reduction in the remainder SS of the linear, quadratic, cubic and two-intersecting straight lines regression attributable to fitting the best triplet of intersecting straight lines instead of a linear, quadratic, cubic and two-intersecting straight lines regression for 4, 3, 2 and 2 df, respectively, was significant for all three hybrids as indicated by items 14, 13, 12 and 11, respectively, in Table 5.

The relative efficiency computed as the ratio of remainder mean squares showed that the two-lines regression model was superior to linear regression by 11%–126% and by 11%–113% to the quadratic regression for the six hybrids MH 106, MH 107, MH 112, MH 116, MH 117 and BJ 104. The superiority of the three-lines model over the two-lines model was 3%–23% for the three hybrids MH 108, MH 109 and MH 119.

The estimates of stability parameters on the best fitting model are given in Table 3. Of the six hybrids for which two-intersecting straight lines was the best fit, BJ 104 and MH 107 reached their upper limit of response between the environmental values of 10.96 and 11.69 (Table 1). The hybrid MH 117 increased its linear rate of response in favourable environments and is specifically suitable for above average environments. Since its response is average in average conditions but is greater than unity in favourable conditions (along with a high mean yield), it is a desirable variety from a plant breeder's point of view. On the other hand, the hybrids MH 106, MH 107 and MH 116 show a unit response in favourable environments but an above average response in poor environments. As their rate of response reaches a threshold in average environments, they are specifically suitable for poor environments.

Although a three-intersecting line model gave the best fit for MH 108, MH 109 and MH 119 hybrids, there existed a significant remainder mean squares for MH 108 and MH 119. The hybrid MH 109 showed a

Table 4. Goodness of fit (mean squares) of the linear, quadratic, cubic and two-intersecting straight line models of the regression for six pearl millet hybrids where single linear regression model was inadequate

Ser. no.	Item	df	MH 106	MH 107	MH 112	MH 116	MH 117	BJ 104
1	Linear regression	1	1,832.40**	2,031.00**	1,442.80**	2,008.10**	2,152.50**	2,403.20**
2	Remainder	18	22.22**	19.90**	16.50*	18.55**	18.50**	16.61*
3	Reduction to quadratic	1	20.95	21.93	10.65	3.49	28.14	4.16
4	Remainder	17	22.29**	19.78**	16.84*	19.44**	17.46*	17.34*
5	Reduction to cubic	1	36.60*	4.53	23.94	84.75**	74.94**	38.73*
6	Reduction to cubic	2	28.78*	13.23	17.29	44.12**	51.54**	21.44
7	Remainder	16	21.40**	20.74**	16.40*	15.35*	13.86	16.00*
8	Reduction to two-lines	1	159.46**	103.86**	135.34**	129.60**	165.33**	54.44*
9	Reduction to two-lines	2	90.20**	62.89**	72.99**	66.54**	96.73**	29.30*
10	Remainder	16	13.72	14.53	9.44	12.55	8.20	15.02
11	Error	560	9.27	9.27	9.27	9.27	9.27	9.27

*, ** Significant at the 5% and 1% probability level, respectively

Table 5. Goodness of fit (mean squares) of the linear, quadratic, cubic, two- and three-intersecting straight line models of the regression for three hybrids where two-intersecting straight lines regression model was inadequate

Ser. No.	Item	df	MH 108	MH 109	MH 119
1	Linear regression	1	1,542.00**	1,439.30**	2,694.00**
2	Remainder	18	28.77**	20.93**	30.52**
3	Reduction to quadratic	1	52.09*	17.69	29.47
4	Remainder	17	27.40**	21.12**	30.58**
5	Reduction to cubic	1	0.10	22.78	58.97*
6	Reduction to cubic	2	26.09	20.23	44.22**
7	Remainder	16	29.11**	21.01**	28.81**
8	Reduction to two-lines	1	63.56**	84.31**	79.04**
9	Reduction to two-lines	2	57.82**	51.00**	54.25**
10	Remainder	16	25.14**	17.17*	27.55**
11	Reduction to three-lines	2	29.63*	43.68**	58.99**
12	Reduction to three-lines	2	61.56**	74.45**	69.03**
13	Reduction to three-lines	3	41.07**	57.23**	65.68**
14	Reduction to three-lines	4	43.83**	47.33**	56.62**
15	Remainder	14	24.47**	13.38	23.06**
16	Error	560	9.27	9.27	9.27

*, ** Significant at the 5% and 1% probability level, respectively

Table 6. Relative efficiency (%) values of fitting two-lines vs. single line regression models, keeping the best fitting pair of any one genotype as constant for all other hybrids in turn, along with ordered serial number of the environments for each of the two segments, for six hybrids where two-lines regression model was adequate. See Table 1 for environmental index number

Ser. no.	Serial no. of environments in		Hybrids					
	Segment I	Segment II	MH 106	MH 107	MH 112	MH 116	MH 117	BJ 104
1	1– 9	10–20	162**	94	89	109*	94	95
2	1–17	18–20	89	137**	98	100	181**	111*
3	1–13	14–20	91	113*	175**	92	95	94
4	1–11	12–20	96	95	94	146**	95	94
5	1–16	17–20	93	101	97	105	225**	106

*, ** Significant at the 5% and 1% probability level, respectively

unit response in the first segment and nonsignificant (from zero) response in the second and third segments. It is, therefore, the best adapted hybrid from Durgapura to Dhule (1 to 13 in Table 1) conditions. Its yield, although high in the remaining environments, did not show a corresponding rate of improvement.

It has been shown that none of the hybrids, with the exception of MH 117, met all the criteria of an ideal variety defined earlier on two- and three-line models. However, the fitting of intersecting straight lines models was effective in accounting for the non-linear component of GE interaction and in identifying hybrids adapting to specific environments.

We have assumed that the response threshold value (s) is the specific property of each hybrid variety. Therefore, fixation of truncation point(s) near zero environmental value (Verma et al. 1978) or by constructing fiducial limits of mean (Mariani et al. 1983) may not be as efficient as assuming a moving truncation point (s) for each genotype in fitting two- and three-intersecting straight line models (Jinks and Pooni 1979). It is shown in Table 1 that truncation points differ over hybrids; only for MH 116 was the truncation point near the zero environmental value. The five distinct truncation points for the six hybrids that two-lines model fit were used for each of the hybrid varieties for investigating the effect of fitting a common truncation point. The relative efficiency (%) values are given in Table 6. Neither environmental classification provides a suitable truncation point for all hybrids. Similar results were obtained for the three-lines model. Obviously, the truncation point (s) is the specific property of a genotype which must be allowed to take its own value in the environmental range.

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