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Genetic Analyses for Certain Plant and Ear Characters in Pearl Millet Top-Crosses[1]

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Summary. Combining ability and the genetics of tiller number, days taken to flower and ear thickness were studied in top-cross progenies of pearl millet. General combining ability seemed to be more important for all the characters. The prevalence of epistatic variation, presumably of the type additive × additive, additive × dominance and dominance × dominance gene effects, with a non-significant contribution of additive and dominance components of genetic variance, was observed for tiller number. For days taken to flower, the importance of additive genetic variance was greater than that of the dominance component with directional dominance towards the recessive allele. However, for ear thickness, the existence of additive genetic variability together with the additive × additive type of genic interaction was suggested.

An appreciable effect of epistasis on $\hat{D}$ and $\hat{H}_1$ components was observed for tiller number, whereas this effect was not so marked for other characters.

Introduction

Genetic variation in quantitative traits could arise from additive, dominant or epistatic gene effects. Various methods of analysis have been suggested to detect the presence of such variation (Mather, 1949; Hayman, 1954; Jinks, 1954; Anderson and Kempthorne, 1954; Hayman and Mather, 1955; and Hayman, 1958). All these analyses involve either successive and backcross generations of a cross or all possible crosses involving a known number of parental lines. Recently, Jinks *et al.* (1969) proposed a design which consists of crossing each of n inbred lines to two inbred testers, chosen because they are the opposite extreme phenotypes available for the character under investigation, to yield $2n$ progenies. They developed a special test for detecting epistasis and demonstrated that the new analysis with $2n$ progenies yields the same information as the full diallel analysis.

The present study deals with combining ability and the genetics of certain plant and ear characters as observed by the new analysis in top-cross progenies of pearl millet (*Pennisetum typhoides* [Burm.] Stapf & Hubb.).

Materials and Methods

Initially, 17 genetically diverse pearl millet inbred lines were crossed with three cytoplasmic-genetic male steriles, $L107A$, $L103A$ and $L67A$, and 51 top-cross progenies were obtained. These male steriles are true breeding homozygous lines maintained by sib mating with their sterility maintainers. The 51 top-cross progenies, together with the parental inbred lines, were grown at the plant breeding experimental farm, Ludhiana, in a randomized block design of four replications, during the summer, 1965. Data for a number of quantitative characters were recorded on ten random plants in each row and then averaged on a single plant basis. Of the three testers, $L103A$ and $L67A$ proved to be the phenotypically extreme lines for tiller number, days taken to flower and ear thickness. The array of crosses involving male sterile $L107A$ was, therefore, excluded from the present analysis. Line × tester analyses for combining ability were made according to Kempthorne (1957). The heterogeneity of the variance of $\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i$ against the error variance (variance within crosses) was used as a test for the presence of epistasis (Jinks *et al.*, 1969). Where $\bar{L}_{1i}$ is the mean of the progeny of the cross between the ith inbred parent and the tester L_1, $\bar{L}_{2i}$ is the mean of the progeny of the cross between the ith inbred parent and the tester L_2, and $\bar{P}_i$ is the mean of the ith inbred parent. Additive ($\hat{D}$) and dominance ($\hat{H}_1$) components of genetic variance were estimated by utilizing the extension of the design III of Comstock and Robinson (1952) as presented by Kearsey and Jinks (1968). The form of the analysis of variance of such a design is given below:

Analysis of variance for sums and differences

Source of variation	d. f.	ems
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$)	$n - 1$	$\sigma^2 + 2r\sigma^2_m$
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$)	$n - 1$	$\sigma^2 + 2r\sigma^2_{ml}$
Within crosses	$n(r - 1)$	σ^2

where n and r are the number of inbred parents and replications, respectively. σ^2_m is the variance due to inbred parents ($= \frac{1}{4}\hat{D}$), and σ^2_{ml} is the variance due to inbred parents × testers interaction ($= \frac{1}{4}\hat{H}_1$).

The covariance of $\bar{L}_{1i} + \bar{L}_{2i}$ (sum) on $\bar{L}_{1i} - \bar{L}_{2i}$ (difference) for all values of i provided an estimate of $\hat{F}$, which measures the sum of products of the d and h terms (Jinks *et al.*, 1969). Both the magnitude and the sign of $\hat{F}$ provide information about the magnitude and direction of dominance. The significance of $\hat{F}$ was seen from the test

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Table 1. *Mean values of parents and F_1's for different characters*

Parent	Parental means			F_1 means					
	Tiller number	Days to flower	Ear thickness	Tiller number		Days to flower		Ear thickness	
				L103A	*L67A*	*L103A*	*L67A*	*L103A*	*L67A*
Ghana 73	3.65	54.5	2.67	4.32	3.77	57.0	55.3	2.62	3.40
Droa 20	3.32	71.3	3.63	3.92	3.55	57.3	61.0	2.83	3.88
IP 139−75	4.56	65.3	2.93	4.35	3.40	60.0	65.5	2.52	3.48
Georgia 37	3.12	73.5	2.02	3.67	3.07	60.5	66.0	2.06	2.86
Georgia 48	4.57	62.5	2.04	3.72	4.27	58.3	59.0	2.05	2.67
Georgia 485	3.94	66.3	2.01	4.32	3.67	60.5	61.0	2.03	2.73
Georgia 507	3.75	60.5	2.37	4.20	4.02	57.0	60.0	2.29	3.04
D3	3.85	67.3	2.03	4.52	3.17	57.3	62.5	2.07	2.73
BIL-1	4.60	60.5	2.13	5.32	3.67	56.5	62.8	2.19	2.56
T 55−33	3.70	59.0	2.69	4.55	3.55	57.5	56.8	2.63	3.14
T 55−56	2.72	65.0	2.26	4.20	4.12	55.5	61.5	2.16	2.88
S 350−122	4.75	66.0	2.02	5.32	3.57	59.3	63.5	2.14	3.07
(*D54*^{4} × *S530*)−20	3.15	58.8	2.65	4.25	3.67	58.8	56.5	2.71	3.71
D55−2	3.85	73.0	4.08	4.30	2.47	58.8	66.5	3.61	4.12
L107B	1.37	66.0	2.37	4.35	2.82	62.5	65.5	2.71	3.29
L103B	3.70	63.8	2.10	4.22	3.52	58.5	60.0	2.09	2.72
L67B	1.32	70.5	2.91	4.27	2.65	61.0	64.8	2.59	3.33
S.E.	0.29	1.29	0.07	0.34		1.42		0.11	

of significance of $\hat{r}_{sum/diff}$ for $(n - 3)$ degrees of freedom (Jinks *et al.*, 1969).

Results and Discussion

Significant differences were observed among F_1's for different characters. Mean performance of parents and of their F_1's is presented in Table 1. The variances due to females, males and females × males interaction were significant in all cases (Table 2). For all characters, general combining ability variance for females or males was generally higher than specific combining ability variance (females × males interaction), showing the importance of general combining ability. The relative magnitude of the components of general combining ability ($\hat{\sigma}^2_g$) was higher than of specific combining ability components ($\hat{\sigma}^2_s$) for all traits. A linear relationship between general combining ability effects and *per se* performance of the parents was evident from the correlation coefficients, which were 0.57 ($P < .05$), 0.76 ($P < .01$) and 0.94 ($P < .01$) for tiller number, days to flower and ear thickness respectively. These results further emphasized the importance of general combining ability and the predominance of additive gene effects for all the characters.

Male sterile *L103A* was a good combiner for high tillering and earliness, while *L67A* had high general combining ability effects for ear thickness (Table 3). *BIL*-1, *Ghana 73* and *D55*-2 were high, while *Georgia 37*, *L107B* and *Georgia* 48 were poor in general combining ability effects for tillering capacity, earliness and ear thickness respectively (Table 3). Generally the

Table 2. *Combining ability analyses of variance for different characters*

Source of variation	d. f.	Tiller number	Days to flower	Ear thickness
Among F_1's	33	1.636**	39.55**	1.272**
Females	1	25.860**	318.00**	17.813**
Males	16	0.851**	44.13**	1.441**
Females × Males	16	0.908**	17.56**	0.069**
Error	99	0.118	2.02	0.013
$\hat{\sigma}^2_g$		0.328	4.30	0.252
$\hat{\sigma}^2_s$		0.195	3.91	0.011
$\hat{\sigma}^2_g/\hat{\sigma}^2_s$		1.682	1.10	22.909

** $P < .01$

Table 3. *General combining ability effects of parents for different characters*

Parent	Tiller number	Days to flower	Ear thickness
Females			
L103A	0.44	−1.53	−0.36
L67A	−0.44	1.53	0.36
S. E.	0.08	0.34	0.03
Males			
Ghana 73	0.14	−3.99	0.21
Droa 20	−0.17	−0.99	0.56
IP 139−75	−0.03	2.63	0.21
Georgia 37	−0.54	3.13	−0.33
Georgia 48	0.09	−1.49	−0.43
Georgia 485	0.09	0.63	−0.42
Georgia 507	0.20	−1.62	−0.13
D3	−0.06	−0.24	−0.39
BIL −1	0.59	−0.49	−0.42
T 55−33	0.15	−2.99	0.10
T 55−56	0.26	−1.62	−0.27
*S*350−122	0.54	1.26	−0.18
(*D54*^{4} × *S530*)−20	0.05	−2.49	0.41
D55−2	−0.53	2.51	1.08
L107B	−0.32	3.88	0.21
L103B	−0.03	−0.87	−0.38
L67B	−0.43	2.75	0.17
S. E.	0.24	1.00	0.08

Table 4. *Analyses of variance for epistasis for different characters*

Source of variation	d. f.	Tiller number	Days to flower	Ear thickness
Epistasis	16	0.670**	12.19**	0.127**
Error	153	0.228	3.91	0.025

** $P < .01$

Table 5. *Analyses of variance for sums and differences, and estimates of variances due to inbred parents ($\hat{\sigma}^2_m$) and inbred parents × testers ($\hat{\sigma}^2_{ml}$) for different characters*

Source of variation	Tiller number[1]		Days to flower		Ear thickness	
	I	II	I	II	I	II
Sums	0.425* (16)	0.365 (14)	22.07** (16)	20.48** (14)	0.717** (16)	0.396** (13)
Differences	0.454* (16)	0.410 (14)	8.75** (16)	9.97** (14)	0.034 (16)	0.032 (13)
Error	0.228 (153)	0.237 (135)	3.91 (153)	4.31 (135)	0.025 (153)	0.026 (126)
$\hat{\sigma}^2_m$	0.025	0.016	2.27	2.02	0.087	0.046
$\hat{\sigma}^2_{ml}$	0.028	0.022	0.61	0.71	0.001	0.001
$\hat{\sigma}^2$	0.228	0.237	3.91	4.31	0.025	0.026

* $P < .05$ ** $P < .01$
I = Inadequate additive-dominance model
II = Adequate additive-dominance model
[1] The values in parentheses are the respective degrees of freedom.

mean for all values of i. These inbred parents were then excluded from the analysis and the additive-dominance model was fitted after ensuring the absence of epistasis. The analyses of variance for sums and differences, and estimates for genetic and environmental parameters on an inadequate as well as adequate additive-dominance model are presented in Tables 5 and 6 respectively.

For tiller number, both the components $\hat{\sigma}^2_m$ and $\hat{\sigma}^2_{ml}$ were significant in the presence of epistasis, but were not significant on the additive-dominance model. This indicated a preponderance of epistatic variation with an insignificant contribution of additive and dominance components of genetic variance to the total variation for this character. $\hat{F}$ was significantly different from zero only when an additive-dominance model was adequate, which is trivial as $\hat{\sigma}^2_{ml}$ was not significant and could arise only from sampling error (Jinks *et al.*, 1969). The non-significant $\hat{F}$, therefore, showed an absence of directional dominance on an additive-dominance model, whereas an ambidirectional trend of dominance

Table 6. *Genetic and environmental parameters for different characters*

Parameter	Tiller number		Days to flower		Ear thickness	
	I	II	I	II	I	II
$\hat{D}$	0.100*	0.064	9.08**	8.08**	0.348**	0.184**
$\hat{H}_1$	0.112*	0.088	2.42**	2.83**	0.004	0.004
$\hat{F}$	0.399	1.106**	−34.28*	−39.64**	−0.136	−0.267*
$\hat{E}_2$	0.228	0.237	3.91	4.31	0.025	0.026
$\hat{r}_{\text{sum/diff}}$	−0.227	−0.715**	0.617*	0.694**	0.219	0.602*
$\sqrt{\hat{H}_1/\hat{D}}$	1.060	1.172	0.516	0.591	0.257	0.147

* $P < .05$ ** $P < .01$
I = Inadequate additive-dominance model
II = Adequate additive-dominance model

per se performance of the crosses was in agreement with the combining ability of their parents (Table 1).

The analyses of variance for epistasis (Table 4) show that variance due to epistasis was significant for all the characters, suggesting the prevalence of significant epistatic variation in each character. Although the additive-dominance model as such was inadequate for any character, the estimates for $\hat{D}$, $\hat{H}_1$ and $\hat{F}$ were obtained in order to see the effect of epistasis on these estimates.

Fitting an Additive-Dominance Model

The inbred parents showing epistasis had larger deviations in the value of $\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i$ from its

(that is, increasing and decreasing alleles were dominant and recessive to the same extent) was operative on an inadequate additive-dominance model. Complete dominance was, however, operative for this character.

In the case of days taken to flower, the components $\hat{\sigma}^2_m$ and $\hat{\sigma}^2_{ml}$ were significant in the presence of epistasis as well as when an additive-dominance model was adequate. Additive and dominance components of genetic variance were, therefore, significantly contributing towards the total variation for days to flower. However, the proportionate contribution of additive genetic variance was higher than that of the dominance component. $\hat{F}$ was significant

on both the models, with a higher value for $\hat{r}_{sum/diff}$ (0.694, $P < .05$) when parental arrays showing epistasis were excluded than otherwise (0.617, $P < .05$). These results suggested directional dominance, with slightly more directional element on the additive-dominance model. For days to flower, partial dominance was operative, which might be caused by a preponderance of dominant decreasing genes (due to negative sign of $\hat{F}$), indicating partial dominance for the early flowering genes.

For ear thickness, only the component $\hat{\sigma}^2_m$ was significant on both the models indicating the predominance of additive genetic variation for this character. Further, $\hat{D}$ was almost halved on the additive-dominance model, suggesting the presence of an additive × additive type of genic interaction. This genic interaction might be responsible for the inflated value of $\hat{D}$ on an inadequate additive-dominance model. $\hat{F}$ was significant only on an additive-dominance model and was trivial in the absence of significant $\hat{H}_1$ (Jinks *et al.*, 1969).

These studies have revealed the importance of general combining ability and the predominance of additive gene effects for various traits. Male sterile *L103A* shows promise for developing high-tillering, early-maturing hybrids in pearl millet.

Epistatic variation was prevalent for all the characters under study. Ahluwalia *et al.* (1962), Singh and Lal (1969), and Phul and Singh (1970) also reported epistatic variation for most of these characters in pearl millet. The conspicuous effect of epistasis on the additive and dominance components of genetic variance could be seen in the case of tiller number, where the upward bias in their estimates in an inadequate additive-dominance model seemed to be due to additive × additive, additive × dominance and dominance × dominance effects if digenic interactions were considered. This suggests the importance of partitioning the total genetic variance into additive and dominance components after accounting for the genic interactions. The biased information due to epistasis might lead to wrong breeding procedures for the improvement of quantitative traits.

A considerable amount of additive genetic variability prevailed for early flowering and ear thickness, which could be exploited by simple breeding procedures for the improvement of these characters. Alternatively, desirable genes could be accumulated from diverse sources by a simple recurrent selection procedure. However, epistatic variation in tiller number may be exploited either by selection among the families in segregating generations or by developing F_1 hybrids.

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