Theoretical and Applied Genetics 43, 18–22 (1973)

A Comparative Analysis of Biparental Mating and Selfing in Pearl Millet (*Pennisetum typhoides*) S & H

I. Nature of Variation and Changes in Association

B. B. SINGH and B. R. MURTY

Indian Agricultural Research Institute, New Delhi (India)

Summary. A study was made of the nature of variation and changes in association for characters related to yield, development and disease resistance in two sets of progenies one set derived through biparental mating (A-series) and the other by traditional inbreeding (selfing) from the F_2 onwards (T-series), in a 22×22 diallel of dwarf derivatives of *Pennisetum typhoides* S & H. Comparison of means and variances within and between the two groups of progenies (A and T-series) and with those of released hybrids (HB-1, HB-2, HB-3, HB-4) for seventeen characters (six related to development, six to productivity, three to vegetative growth and one each to earliness and disease incidence) showed significant variation among the lines of the two series for synchrony of tillering, earliness, disease incidence, chlorophyll depth, grain hairiness, tiller number, plant height, length of earhead, grain yield and grain weight. The A-series selections were significantly superior to the T-series for most of the characters, indicating the effectiveness of selection in biparental matings compared with selection in selfed progenies for these traits. Many of the A-series (220 out of 800) selections were also superior to the existing released hybrids.

Changes in the magnitude and nature of association among twelve important characters in the two populations were more favourable in the biparental matings: of 66 possible correlation coefficients examined, 25 cases were found with changes in favour of selections from biparental matings (A-series). These changes were probably due to the breakage of unfavourable linkages and changes in phase of linkage, and indicate the usefulness of biparental matings in the simultaneous improvement of the population for several attributes.

Introduction

The effectiveness of selection in any biological population depends on the nature of diversity in the base population and the parents from which it is derived, the past history of selection, the magnitude and phase of linkage, the correlated response for one or more traits not directly selected for and the pattern of genetic variation in the material (Moll *et al.*, 1964; Moll and Robinson, 1967; Murty *et al.* 1967). The association of some desirable agronomic features with some unfavourable traits in the same material limits the advance realised under selection. Inter-crossing in early segregating generations is expected to break such unfavourable linkages (Moll *et al.*, 1964; Ahmed 1970). The usefulness of biparental mating for breaking tight but unfavourable repulsion-phase linkages can be examined by comparing the mean performances and changes in the variation and association of the same attributes among F_3 lines and BIPs of the same crosses. The results of such a direct comparison in pearl millet are presented in this paper.

Materials and Methods

The material for the present study comprised 800 selections from biparental progenies (A-series) and 700 selections from the corresponding F_3 progenies (T-series) of a 22×22 diallel involving dwarf derivatives of *Pennisetum typhoides* S & H. The material was grown with four controls, which were released high-yielding hybrids (HB_1, HB_2, HB_3, HB_4), in an augmented randomized complete block design consisting of fifteen blocks, during July–October, 1969. Each of the fifteen blocks had 104 entries comprising 100 selections and four controls. The plot size was a single row of 210 cm length with a spacing of 75×10 cm between and within rows after thinning. The 1500 selections and four controls were compared for seventeen characters, ten related to growth and development, six to productivity and one to disease resistance, following the method of Federer (1956).

The nature and degree of associations between twelve developmental and productivity traits was examined in the two sets of populations. The correlation coefficients between all possible pairs of characters were worked out for the two groups of selections separately based on treatment means adjusted for block effects (Federer, 1956).

Observations were recorded on seven of the seventeen characters on the basis of plot population performance. Visual scores ranging from 1 to 10 were given for these characters, namely, early vigour, synchrony of tillering, leafiness, chlorophyll depth, leaf drying, grain hairiness and disease incidence. A higher score was considered desirable for all these characters, except disease incidence where a higher score represented a higher degree of susceptibility to diseases.

Early growth vigour of seedlings was recorded three weeks after sowing. Synchrony of tillering was recorded 45 days after sowing, a higher score being given to the lines exhibiting a high degree of synchrony in tiller production.

In order to consider the total photosynthetic area of the plants (leafiness), scores were given 50 days after sowing. Higher scores were given to the lines with greater photosynthetic area.

Chlorophyll depth was recorded 45 days after sowing. The lowest score (unity) was given to pale green plots and a maximum of ten to the plots which were dark green.

Leaf drying was considered to be an indication of active photosynthetic surface at maturity. Scoring was done 85 days after sowing. Scores ranging from 1 to 4 were given to those lines which were still green, and from 6 to 10 for those which were completely dry, a lower score being desirable.

Bristling on the panicle was scored on the basis of the length of bristles. A higher score for this trait represented the presence of strong, long bristles. This character is of advantage against bird damage.

Days from sowing to 50 percent heading were recorded as a criterion of earliness.

The number of effective tillers/metre and grain yield/metre plot length were recorded by counting the ear-bearing tillers, and by weighing the grains obtained by threshing the ears harvested from one-metre plot length, respectively.

The other characters, such as plant height, ear length, circumference of the earhead, length of longest leaf in main tiller and its width in the middle, were recorded on five plants sampled at random in each plot.

A random sample of 250 seeds was drawn from the bulk seed of each plot and their weight was recorded in grams. The weight of 1000 grains was computed from this.

Results

Analysis of Means

The analysis of variance of the entries, comprising four controls (released hybrids) and 1500 selections, revealed highly significant variation among the entries for all the characters except early growth vigour, synchrony of tillering, leaf drying, ear circumference, leaf length and leaf breadth (Table 1). The variation among controls was not significant for different developmental traits except for early vigour, synchrony of tillering, days to 50 percent heading and chlorophyll depth. Significant variability existed among the controls with respect to yield and its components, such as productive tillers per metre, length and circumference of ear-head and 1000-grain weight. This ensured the effectiveness of the controls in comparing the selections in this experimental design.

Significant variation was observed among the selections for synchrony of tiller production, earliness, disease resistance, chlorophyll depth, bristle length, tillers per metre, plant height, length of ear head, tillers per plant, grain yield and grain weight. More than 50 per cent variation among selections was accounted for by the A-series for all these traits, except for early vigour, synchrony of tillering and disease incidence, where the T-series accounted for more variation than the A-series. The contribution of A and T-series to the total observed variation among selections was of equal order for chlorophyll depth, length of ear and breadth of leaves.

Significant differences existed between selections and controls for all the characters except early vigour and days to 50 percent heading. The differences between the two sets of selections (A vs T) were large for all the characters examined in the present study except for plant height. The contribution of the A vs T component with a single degree of freedom to the total observed variation among selections was highest for disease resistance (33 per cent). It was also pronounced for early vigour, synchrony of tillering, leafiness, tiller number, length of leaves and grain yield.

When the mean performance of the A series was compared with that of the T-series, the A-series was significantly superior or equal to the T-series in desirable mean performance for almost all the characters, except for ear circumference for which the T-series was superior. The selections from biparental progenies were relatively more vigorous, synchronous in tillering, earlier by one day, and relatively free from diseases compared with those from selfed progenies, (T-series). They were also superior to the T-series in their higher number of tillers per plant and per unit area. On average, they yielded about 20 per cent more than the T-series of selections. Thus, biparental mating was found to be superior to conventional inbreeding (selfing) both for the release of new variation and improvement of the means.

The comparison of mean performance of the selections and controls (Table 1) indicated that the selections (A+T) were equal to the controls or better in their mean performance for early vigour, leafiness, chlorophyll depth, leaf senescence, bristling, length and circumference of ear head, length and breadth of leaves and grain weight. They had lower means than the controls for the other characters. However, the performance of the selections versus the elite hybrids which were used as controls indicates the high potential of the entire group of selections compared with the best hybrids. A large number of selections were superior to the hybrids (220 from the biparental matings and 116 from selfed progenies). This was interesting because no selection was practised for yield or its components. Thus, new hybrids involving these selections would offer a substantial advantage over the existing hybrids.

Changes in Association

The coefficients of correlation for each of the possible pairs of 12 characters related to development and productivity were worked out separately for the two groups of progenies on the basis of plot means adjusted for block effects. The results are presented in Table 2.

Among the selections from the progenies derived from selfing (T-series), yield was positively associated with synchrony of tillering, effective tillers per unit of plot length and leaf length. The correlation between grain yield and grain weight was positive but not significant.

The number of effective tillers was significantly correlated with chlorophyll depth, leaf length, tiller number per plant and grain yield, although association of this trait was positive with all other characters except leafiness.

Table 1. *Anova for plot means of Bi-parental progenies (A-series) and corresponding selfed progenies*

Source	D.F.	Early vigour	Synchrony of tillering	Days to 50 per cent heading	Leafiness	Disease incidence	Chlorophyll depth	Leaf drying
		1	2	3	4	5	6	7
				Mean sum of squares				
Blocks (Eliminating treatments)	14	3.25	1.18	12.04	5.67	1.90	1.95	5.46
Treatments (Controls + selections, ignoring blocks)	1503	1.85	2.27**	19.68**	1.18**	2.87**	1.99**	3.34**
Controls	3	4.15**	4.59**	230.06**	0.42	0.85	3.66	2.91
Entries (Selections)	1499	1.84	2.21**	19.28**	1.18**	2.84**	1.98**	3.29**
T-series	699	1.99	2.26**	17.49**	0.98	2.68**	1.92**	2.87**
A-series	799	1.37	2.62**	20.32**	1.33**	2.24**	1.99**	3.65**
A vs T-series	1	227.61**	33.30**	432.50**	10.82**	583.20**	27.40**	7.34**
Selections vs controls	1	1.44	84.63**	9.92	67.38**	67.88**	22.28**	55.15**
Intra block error	42	1.43	1.13	10.68	0.35	0.62	0.73	3.72
				Comparison of means				
Selections (A+T-series)	(1500)	6.02	5.65	53.31	6.60	2.75	6.87	3.92
A-series	(800)	6.41	6.15	52.73	6.67	1.85	6.98	3.86
T-series	(700)	5.55	5.07	53.81	6.49	3.77	6.71	3.99
Controls	(4)	5.77	6.45	50.39	6.43	1.64	6.96	4.99
Selections vs controls	–	N S	S < C	S < C	S > C	S < C	S < C	S > C
A vs T-series	–	A > T	A > T	A > T	A > T	A > T	A > T	A > T

** Significant at p = 0.01. — * Significant at p = 0.05; N.S. — Not significant.

When the degree of association between different traits related to yield and development were examined among selections from biparental progenies (A-series), yield was found to be significantly positively correlated with synchrony of tillering, tillers per unit of plot length, plant height and tiller number/plant. Significant correlations were also observed between synchrony of tillering and all other traits except length of leaves and grain weight. Synchrony of tillering was negatively associated with disease incidence and plant height, which is encouraging. The interesting feature which emerged from examining these correlations was that there were significant favourable associations between several developmental traits and yield and its components in both series.

Comparison of the nature and degree of interrelationships in the two series revealed significant differences in the magnitude and direction of correlations between several character pairs in the two populations Of a total of 66 possible correlation coefficients examined, changes of degree and nature of association were found in favour of selections from bi-parental progenies in 25 cases. Yield was involved in six of these associations. The other characters frequently involved in such favourable associations were synchrony of tillering, total photosynthetic area (leafiness), disease incidence and tiller number per unit area (in five comparisons for each of these characters). Chlorophyll depth, bristle length and effective tillers per plant exhibited desirable changes in favour of the A-series in four cases, while plant height and ear length were involved in three such associations. These changes in the nature and magnitude of inter-relationships in favour of selections from biparental matings might be caused by breakage of unfavourable and tight linkages and changes in the phase of linkage due to intermating at the F_2 level.

Discussion

The information gathered in this investigation on the pattern of genetic variation for yield, its components, developmental traits and grain quality in the selected populations developed through two systems of mating from the crosses of dwarf derivatives has permitted direct comparison of the efficiency of the two systems of mating (biparental mating and selfing) for the magnitude of variation and correlated changes in different traits and has produced many interesting results.

Moll and Robinson (1967) and Miller and Rawlings (1967) considered that the estimates of additive genetic component from advanced generations would be more reliable than those from the corresponding F_2 generation. They suggested that estimates from the F_2 might be biased in the presence of repulsion-phase linkages which over-estimate non-additive variance and may, therefore, conceal additive variation. These effects could be dissipated in biparental matings. If this proposition holds true, superior recombinants should be expected in the progenies of biparental matings compared with selfed progenies. The present findings, based on a comparison of selections from biparental matings and F_3's, supports this hypothesis. The selections from biparental matings were signifi-

(T-series) for some characters in pearl millet in an augmented randomized complete block design

Bristling	Tillers/metre	Plant height	Ear length	Ear circumference	Length of leaves	Breadth of leaves	Tillers per plant	Grain yield/metre	1000 grain weight
8	9	10	11	12	13	14	15	16	17
				Mean sum of squares					
0.20	19.03	480.13	12.04	0.46	46.87	0.11	3.60	62.85	0.71
2.61**	35.55**	442.18**	19.42**	0.41	51.23	0.27	2.26**	16386.05	1.38**
0.46	45.04**	2508.33**	20.77**	1.02**	49.88	0.17	0.05	35213.67**	1.42**
2.60**	34.85**	437.45**	18.88**	0.60	50.75	0.26	2.24**	15867.44**	1.34**
3.13**	28.58**	395.19**	18.57**	0.56	50.53	0.27	2.31**	14377.64**	1.23**
2.09**	37.18**	474.71**	18.38**	0.61	48.38	0.26	2.13**	16120.34**	1.44**
43.70**	2647.60**	214.00	620.80**	21.45**	2102.40**	0.66**	46.93**	855170.00**	5.91**
17.23**	1051.27**	1315.00**	824.18**	7.49**	772.26**	12.76**	32.65**	737290.00**	54.14**
0.42	6.20	200.41	4.59	0.68	38.96	0.18	1.16	3096.59	0.52
				Comparison of means					
2.49	27.27	158.76	26.68	6.45	67.22	3.31	4.63	296.13	8.76
2.27	28.42	156.90	26.69	5.78	68.24	3.83	4.96	316.11	8.80
2.61	26.74	158.14	25.96	6.31	65.87	3.78	4.82	268.17	8.68
1.79	29.31	154.17	21.68	5.78	60.12	3.17	4.98	378.69	7.42
S > C	S < C	S < C	S > C	S > C	S > C	S > C	S < C	S < C	S > C
A < T	A > T	N.S.	A > T	A < T	A > T	A > T	A > T	A > T	A > T

cantly superior to those from selfing for all the economic characters. Selections from biparental matings (A-series) were, in general, more vigorous, more synchronous in tiller production, slightly earlier in maturity, comparatively free from diseases, had more photosynthetic area with high chlorophyll depth, were slow in leaf senescence, produced on average three tillers more and yielded 50 gms more per unit area than the corresponding selections from selfed progenies (T-series). In the A-series, 220 progenies (27.5% of the selections in the A-series) were superior in yield to the hybrids, whereas only 116 lines (16.57% of the selections) in the T-series were better than the hybrids. The mean yield of superior selections of the A-series was nearly 30 per cent more than that of the hybrids, while in the T-series only 19 per cent superiority was observed in grain yield. Therefore, both in yield potential and frequency of superior progenies, selections from biparental matings were better than those from selfing. The A-series accounted for more than 50 percent of the total observed variation among selections (A + T-series), indicating the role of biparental mating in releasing concealed genetic variability, particularly when repulsion-phase linkages predominate in the parental material.

The present study confirms the expectations of earlier workers that biparental mating is an effective way of creating populations of high-yielding potentiality, by breaking undesirable and repulsion-phase linkages. This was also confirmed by the changes in the nature of association between important characters in the two populations and the favourable changes in association in biparental mating. Such a mating system could be effective in the simultaneous improvement of the performance in several attributes of base populations.

Association of Developmental Traits with other Characters

The importance of developmental traits in increasing yield potential and conferring wide adaptation of crop plants has been realized only recently (Allan *et al.*, 1968; Roy and Murty, 1970). Of all developmental traits, dwarfing was paid great attention and its significant contribution to producing potential phenotypes in cereals has been clearly established during the past decade (Borlaug, 1968). Direct evidence of the role of various developmental traits in productivity was examined mostly with reference to the concept of ideal plant type, particularly by plant physiologists (Beachell and Jennings, 1965; Asana, 1968). During the present investigation, the role of various developmental traits in general improvement of lines with reference to yield and yield components was examined separately for the two populations (A and T-series) developed through different mating systems. No adverse association was observed between early growth vigour, synchrony of tillering, days to heading and tiller number. These findings accord with those of Allan *et al.* (1968) in wheat. These characters were positively correlated with yield.

A favourable association between total photosynthetic area (leafiness) and chlorophyll depth was found with tiller number, plant height and yield, among both the A and T-series' selections. Therefore, the significant influence of developmental traits on

Table 2. *Coefficients of correlation between twelve yield and developmental characters based on adjusted means in A and T-series of selections*

Character		X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12} (Grain weight)
Synchrony of tillering	A	**0.57***	−0.63*	0.08**	−0.45*	**0.19***	**−0.12***	**0.19***	0.03	0.16*	0.21*	−0.01
	T	−0.63*	0.64*	0.09**	**−0.12***	0.04	0.03	0.14*	−0.80*	0.19*	0.13*	0.06
X_1	D	*	*	NS	*	*	*	NS	*	NS	NS	NS
Leafiness	A		−0.45	**−0.13**	**+0.44**	0.04	0.06	0.01	0.02	**0.08****	**0.22**	−0.03
	T		−0.48	−0.04	+0.10	0.01	−0.04	0.04	9.13	−0.07	−0.08**	−0.06
X_2	D		NS	NS	*	NS	NS	NS	*	*	*	*
Disease incidence	A			**0.01**	**−0.32***	0.03	0.02	0.22*	0.09**	0.25*	**−0.06**	**−0.01**
	T			0.17*	0.09*	0.05	0.09**	0.14*	−0.05	0.23*	0.11*	0.13*
X_3	D			*	*	NS	NS	NS	*	NS	*	*
Chlorophyll depth	A				−0.03	−0.08*	**0.09**	0.04	**0.14**	0.01	0.13*	−0.01
	T				−0.05	0.16*	−0.02	0.05	−0.06*	0.08	0.10*	0.00
X_4	D				NS	*	*	NS	*	NS	NS	NS
Bristling	A					**−0.07**	0.19	0.01	0.08	−0.06	**0.27***	0.00
	T					0.09**	−0.02	0.05	0.03	0.02	−0.09**	0.10*
X_5	D					NS	*	NS	NS	NS	*	*
Tillers/metre	A						**−0.04**	−0.02	**0.10***	0.00	**0.48**	−0.02
	T						0.01	0.02	−0.07	0.12*	0.15*	0.03
X_5	D						NS	NS	*	*	*	*
Plant height	A							−0.01	0.08**	0.02	0.23	−0.07
	T							0.05	−0.04	0.01	0.10	0.05
X_7	D							NS	NS	NS	*	NS
Length of ear head	A								**0.23**	**0.18***	−0.03	0.07
	T								0.10	0.02	0.01	−0.07
X_8	D								*	*	NS	*
Length of leaves	A									**0.15**	**0.48**	−0.05
	T									0.11	0.09	−0.02
X_9	D									NS	*	NS
Tillers/plant	A										**0.29***	0.01
	T										0.06	−0.06
X_{10}	D										*	NS
Yield/metre	A											−0.04
	T											0.06
X_{11}	D											NS

A — Coefficient of correlation for A-series; T — Coefficient of correlation for T-series; D — Difference between correlation of A and T-series. — * Significant at p = 0.01. — ** Significant at p = 0.05; NS = Not Significant; — Change in favour of A series.

yield and its attributes was supported by the present study. The relationship between early developmental traits and adult plant performance was probably due to developmental canalization which has a genetic basis. Waddington and Robertson (1966) and Roy and Murty (1970) have pointed out that selection for developmental traits confers wide adaptation by accumulating alleles with superior buffering capacity, and thus is of considerable importance from the breeder's point-of-view.

Literature

1. Ahmed, Z.: Fractional diallel analysis and biparental study on some metric traits in *Pennisetum typhoides* S & H Unpublished Ph.D. Thesis, Division of Genetics, I.A.R.I., New Delhi (1970). — 2. Allan, R. E., Pritchett, J. A., Patterson, A.: Juvenile and adult plant growth relationships in wheat. Crop Sci. **8**, 176—178 (1968). — 3. Asana, R. D.: In quest of yield. Indian J. Plant Physiol. **XI**, 1—10 (1968). — 4. Beachell, H. M., Jennings, P. R.: Need for modification of plant type. In: The mineral nutrition of rice plant. Proc. Symp. Int. Rice Res. Inst. 1964, 29—35 (1965). — 5. Borlaug, N. E.: Wheat breeding and its impact on world's food supply .3rd Intern. Wheat Genet. Symp. Canberra, Australia, pp. 1—36 (1968). — 6. Federer, W. T.: Augmented (or Hoonuiaku) design. Hawaiian Planter's Record **55**, 191—207 (1956). — 7. Miller, P. A., Rawlings, J. O.: Break up of initial linkage blocks through intermating in cotton population. Crop Sci. **7**, 199—204 (1967). — 8. Moll, R. H., Robinson, H. F.: Quantitative genetic investigations of yield of maize. Der Züchter **37**, 192—199 (1967). — 9. Moll, R. H., Lindsey, M. F., Robinson, H. F.: Estimates of genetic variances and level of dominance in maize. Genetics **49**, 411—423 (1964). — 10. Murty, B. R., Arunachalam, V., Anand, I. J.: Diallel and partial diallel analysis of some yield factors in *Linum usitatissimum* L. Heredity **22**, 35—42 (1967). — 11. Roy, N. N., Murty, B. R.: A selection procedure in wheat for stress environment. Euphytica **19**, 509—521 (1970). — 12. Waddington, C. H., Robertson, E.: Selection for developmental canalization. Genet. Res. Camb. **7**, 303—312 (1966).

Received April 1, 1972
Communicated by M. S. Swaminathan

B. B. Singh
B. R. Murty
Indian Agricultural Research Institute
New Delhi-12 (India)