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EVALUATION OF FOUR PIGEONPEA (*CAJANUS CAJAN* (L.) MILLSPAUGH) CROSSES FOR INHERITANCE OF SELECTED AGRONOMIC CHARACTERS

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ABSTRACT

The potential of four diverse crosses of pigeonpea (*Cajanus cajan* (L.) Millspaugh) to yield superior transgressive segregants among their selfed descendants for a number of agronomic characters were investigated. Analysis of their F_3 families revealed that all characters including days to flowering, days to maturity, plant height at maturity, number of pods per plant, seed weight per plant, hundred seed weight, estimated seed yield per plant in these crosses were heritable. Predictions of the proportion of recombinant inbred lines whose means achieved the desired targets indicated that it should be possible to obtain one or more lines for most of these characters if 100 such lines were extracted by single seed descent from each cross. The observed proportions of F_4 or F_5 families whose means met these targets were close to the corresponding predicted proportions for the great majority of characters. The pattern of genetic correlations between the majority of characters varied considerably over crosses, suggesting that the linkage disequilibrium of genes linked in their inheritance rather than pleiotropy, was the chief cause of these correlations. It was found that 13% of the F_4 families in one of the crosses investigated had a mean seed yield better than that of its F_1, the commercially released hybrid variety, ICPH-8. This indicates that the heterosis of the latter is due to dispersed dominant genes, rather than to overdominance.

KEY WORDS: *Cajanus cajan*, Genetic correlations, Pigeonpea, Plant breeding, Quantitative genetics, Recombinant inbred lines.

INTRODUCTION

Pigeonpea is one of the grain legumes grown in the tropical and sub-tropical areas of the world and its dry seed provide a valuable source of protein (21%). It can also be used as fodder for animals and as fuel wood. Once established, pigeonpea can withstand drought and is, therefore, a useful crop in the semi-arid tropics. It is often grown as an inter-crop with cereals, cotton or other legumes and harvested after the companion crop has been harvested (ICRISAT, 1990). Impressive gains have been achieved by breeders with the yields of the chief staples, wheat, rice and maize, in the last 30 years. Grain legumes, however, have received less attention. Most crops of pigeonpea raised by farmers are land races or selections from land races (Tunwar and Singh, 1985) whose yields are rarely more than 0.8 t/ha, though improved varieties have given yields of about 3 t/ha in research stations (Saxena et al., 1992). In addition, pigeonpea is susceptible to more than 100 pathogens (Nene et al., 1989) and 200 insect species (Reed and Latif, 1990), damage from which can cause total crop failure.

In 1987 the Department of Agriculture in Sri Lanka and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) initiated a collaborative programme of research with the aim of developing high yielding varieties of pigeonpea which are adaptable to local conditions. The objective of the investigation reported here, carried out as part of this programme, was to assess the potential of four crosses to produce inbred lines whose performance was superior to that of the better parent (or their F_1, where this displayed significant better parent heterosis) for a number of characters of agronomic interest, considered both singly and simultaneously, within one cycle of inbreeding.

MATERIALS AND METHODS

The crosses investigated were ICPL85059 x ICPL87111 (Cross 1), a soybean type x a single culm type (Cross 2), ms1 Prabhat (DT) x ICPL161 (Cross 3) and ICPL89020 x ICPL90033 (Cross 4). The parents of these crosses were newly developed inbred lines or recent selections from landraces of pigeonpea of short duration (110-140 days) type. ICPL85059 is a genetic dwarf homozygous for a single recessive gene, d_1 (ICRISAT, 1979); the single culm character of the male parent of Cross 2 is determined by two dominant and a single recessive gene (Gupta et al., 1989); and the female parent of Cross 3 is homozygous for a recessive male-sterility gene, *ms*1, which, when crossed with ICPL161 yields the F_1 hybrid variety, ICPH-8 (Gupta et al., 1983). ICPL85059, ms1 Prabhat (DT) and ICPL89020 are of determinate flowering type; the remaining parents are of non-determinate type. Four of these parents, ICPL85059, ms1 Prabhat (DT), ICPL161 and ICPL90033, are semi-spreading in habit; the others are of compact type. These crosses were made with the intention of extracting inbred lines from them that were shorter with fewer branches bearing a higher number of pods than their parents (Crosses 1, 3 and 4) or of soybean type (Cross 2), these being the desired type for mechanical harvesting.

The crosses were investigated in two experiments, namely the F_3 and single seed descent (SSD) trials. Each F_3 trial contained 10 plants of each of 40 F_3 families, 40 F_2 plants, and 20 plants of each parent and their F_1, giving a total of 500 plants in all, which were raised in a completely randomised design in four adjoining blocks, one for each cross. The SSD trials contained independently randomized duplicate plots of 5 plants of each of either 93 F_5 (Crosses 1 and 4) or 93 F_4 (Crosses 2 and 3) families, and also of each parent and their F_1 (included as checks), giving a total of 192 plots in each of four adjoining blocks, one for each cross. The blocks of the SSD trial were located next to those of the F_3 trial. Both trials were sown in the rainy season of 1993 in late June at ICRISAT, at a spacing of 60cm between plants both between and within rows, with fresh seed of the same age that had been produced earlier in that year from plants raised in the glasshouse. Agronomic practices recommended for pigeonpea were followed to raise these experiments.

The following characters were scored on the plants in these trials.

1. DF = days to flowering; the number of days from sowing until the first open flower;
2. DM = days to maturity; the number of days from sowing and 75% harvestable pods;
3. PH = plant height (cm) at maturity, measured from ground level to the tip of the main stem;
4. TB = total number of primary branches on the main stem at maturity;

5. FB = number of pod-bearing branches on the main stem at maturity;
6. TN = total number of nodes per plant at maturity;
7. TP = number of pods per plant at harvest;
8. SP = number of seeds per ten randomly chosen pods;
9. PW = total weight (g) of pods per plant;
10. SW = seed weight (g) per plant;
11. HSW = hundred seed weight (g);
12. EY = estimated seed yield per plant (g), calculated as [TP x (SP - PDS) x HSW]/100 where TP, SP and HSW are as above and PDS = number of seeds damaged by insects in the ten pods scored for SP;
13. HFB = height to first pod-bearing branch (cm) from ground level to the junction of the branch from the main stem measured at maturity;
14. PBL = pod bearing length (cm); the length between the uppermost and lower most pod at maturity;
15. IL = inflorescence length (cm), measured from the base to the tip on the inflorescence of the main stem at full flowering.

According to the parental characteristics, each plant in Cross 1 was scored for characters 1-3 and 5-12 (eleven characters); those of cross 2 for characters 1-5 and 7-15 (fourteen characters); and those of Crosses 3 and 4 for characters 1-5 and 7-12 (eleven characters).

RESULTS AND DISCUSSION

1. Parents and F_1's

The parents differed significantly for all characters scored in crosses 1 and 2, for nine in Cross 4 and for only six in Cross 3 (Table 1). None of the characters showed significant heterosis in Cross 1, only DM and PBL did so in Cross 2, and only one (TP) in Cross 4. Five characters, including PW, SW and EY, displayed positive heterosis in Cross 3.

2. Analysis of variance of F_3 families

Analysis of variance of the data from the F_3 families (results not shown here) showed that the Between Family mean square was significantly greater ($P<0.01$) than its corresponding Within Family mean square for every character in each of the four crosses. This indicates that every character was heritable, including those in crosses 3 and 4 for which the parents did not differ significantly. Estimates of narrow-sense heritability of these characters, obtained from the variance components of these analyses (Jinks and Pooni, 1980; van Ooijen, 1989), are shown in Table 2. Majority of these estimates are moderate to high. The very high estimate for PH in Cross 1 is expected because, as mentioned earlier, this cross was segregating for a single dwarfing gene.

3. Predicted and actual proportions of superior recombinant inbred lines that can be extracted from the crosses

These estimates of heritability are encouraging. They do not indicate, however, whether these crosses are capable of yielding useful transgressive segregants for all characters of interest. It is possible that although a character is highly heritable, all of the increasing genes for which the parents differ occur in the higher scoring parent, in which case further improvement is not possible. This possibility has to be taken seriously because differences between the parental means were large for some characters in each of the crosses (Table 1). To assess the potential of a cross, it is necessary therefore, to predict the extent of the transgressive variation expected from the cross in the later generations of selfing for each character in turn.

Table 1. Means of the parents and their F_1 progeny for each of the characters scored in the four crosses.

Cross 1

Family	DF	DM	PH	FB	TN	TP	SP	PW	SW	HSW	EY
ICPL 87111	60.3	**99.2**	**120.4**	11.25	**40.8**	176.8	**37.6**	**49.6**	**35.28**	**6.90**	**44.31**
ICPL 85059	**65.0**	97.0	52.9	**14.75**	28.7	**217.4**	30.1	23.3	14.70	4.12	22.49
F_1	62.1	97.3	112.1	12.75	42.3	208.9	37.7	49.6	34.70	6.24	44.16

Cross 2

Family	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY	HFB	PBL	IL
Single culm	**70.7**	108.2	**135.2**	6.94	4.95	**195.8**	**39.5**	**61.2**	**42.11**	**6.83**	**51.40**	**48.3**	**61.3**	**42.5**
Soybean type	63.4	**119.7**	65.5	**11.74**	**8.32**	93.0	31.4	18.5	12.97	6.10	18.16	11.3	46.0	28.2
F_1	65.5	**101.4**	118.7	8.94	6.95	148.9	37.4	42.5	30.43	6.57	35.81	20.3	**73.1**	48.1

Table 1 (continued).

Cross 3

Family	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY
Prahbat (DT)	65.5	105.4	118.2	**15.70**	13.20	**210.8**	38.8	57.8	39.46	6.62	50.10
ICPL 161	**72.2**	**115.0**	**133.3**	12.90	12.15	162.9	38.6	62.5	41.97	**9.39**	50.02
F_1	**73.7**	114.4	147.4	14.26	12.63	**269.4**	40.0	**87.1**	**60.35**	7.32	**72.58**

Cross 4

Family	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY
ICPL 90033	**64.8**	**102.3**	**108.9**	10.80	8.55	**101.5**	37.80	**44.19**	**29.44**	**9.34**	**34.72**
ICPL 89020	54.2	95.2	69.0	10.55	8.35	71.5	**44.00**	29.39	21.42	8.48	24.65
F_1	61.3	98.4	106.6	12.16	9.21	**128.0**	42.84	50.55	34.46	7.56	40.24

(The mean of the higher scoring parent is shown in bold where this differs from that of the lower scoring parent. Similarly, F_1 means which are significantly greater than that of their higher scoring [positive heterosis] or less than that of their lower scoring parent [negative heterosis] are also shown in bold.)

In the absence of epistasis, the expected mean and variance of the distribution of recombinant inbred lines (F_∞) for a character that can be extracted by single seed descent from a cross are m and D, respectively (Mather and Jinks 1982). Estimates of these statistics can be obtained from the early generations of the cross. Assuming that their means are normally distributed, the proportion of F_∞ lines whose means equal or exceed any desired standard, St, for a character can be predicted by calculating a one-tailed normal deviate, z, where $z = (St - m)/ (D)^{1/2}$ (Jinks and Pooni, 1976). Estimates of m and D were obtained from F_3 families (Jinks and Pooni, 1980). It has been assumed that pigeonpea breeders would prefer lower values than higher values of DF, DM, PH, TB, FB and HFB, and the standard used for each of these characters was the mean of the character of the lowest scoring parent or that of the F1 when the latter was significantly lower than the former. Further, it has been assumed that breeders would want to increase the expression of each of the remaining characters, and the standard used for each of them was the mean of the higher scoring parent of or that of the F_1, when the latteer were significantly greater than the former.

The predictions shown in Table 3 suggest that, with one exception, it should be possible to extract one or more inbred lines that achieve the desired target for every character if 100 such lines were raised from each cross by single seed descent. There appears, however, to be little prospect of being able to improve HSW in Cross 3. The proportion of F_5 families of crosses 1 and 4, and of F_4 families of crosses 2 and 3 whose means achieve the desired targets are, allowing for sampling variation, consistent with the predictions of these proportions for the great majority of characters. This is a particularly satisfactory outcome. Thus, whereas all of the additive genetical variation for a character is expected to have segregated out as differences between the F_∞ line means, only 3/4 and 7/8 of this variation is expected to have done so between the means of the F_4 and F_5 families, respectively. There is a tendency (but no more than this), however, for the observed proportion of superior of F_4 or F_5 families to be less than that predicted for a number of characters for which the difference between the parental means was particularly large. It is possible, therefore, that some of the increasing genes for these characters are linked in the coupling phase. Nevertheless, the means of these families displayed transgressive segregation for every one of these characters.

Table 2. Estimates of the heritability (%) of characters derived from the variance components of the analysis of variance of F_3 families.

Cross	DF	DM	PH	TB	FB	TN	TP	SP	PW	SW	HSW	EY	HFB	PBL	IL
1	37	37	95	-	18	71	27	39	42	41	44	27	-	-	-
2	62	58	53	49	52	-	52	35	54	55	28	63	35	47	40
3	57	46	60	23	22	-	34	35	39	38	54	32	-	-	-
4	67	69	100	25	21	-	52	19	50	45	54	47	-	-	-

Table 3. Targets for improvement, estimates of the mean (m) and variance (D), of the expected distribution of recombinant inbred lines that can be extracted by single seed descent from crosses, predictions (P), of the proportion of such lines that are expected to achieve the desired target and the observed proportion of F_5 or F_4 families, (P_{F5} and P_{F4}) whose means achieved the target for each character.

Cross 1

	DF	DM	PH	FB	TN	TP	SP	PW	SW	HSW	EY
Target	≤60.3	≤97.0	≤52.9	≤11.3	≥40.8	≥217.4	≥37.6	≥49.6	≥35.3	≥6.90	≥44.3
m	65.1	102.1	89.0	13.3	34.2	216.2	34.5	43.4	29.4	6.21	41.3
D	15.59	40.58	900.12	3.31	39.30	4711.41	12.90	278.88	131.10	0.70	191.92
P	11%	21%	12%	13%	15%	49%	19%	36%	31%	21%	41%
P_{F5}	17%	22%	5%	9%	20%	42%	18%	23%	16%	22%	29%

Table 3 (continued)

Cross 2

	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY	HFB	PBL	IL
Target	≤63.4	≤101.4	≤65.5	≤6.94	≥4.95	≥195.8	≥39.5	≥61.2	≥42.1	≥6.83	≥51.4	≤11.3	≥73.1	42.5
m	67.4	111.9	93.2	10.63	7.64	131.7	36.2	38.1	26.7	6.87	35.8	21.7	53.5	34.2
D	38.64	183.88	1238.9	11.62	7.57	8182.9	15.48	764.23	403.07	0.41	609.03	94.52	326.57	172.64
P	26%	22%	21%	14%	16%	24%	20%	20%	22%	52%	26%	14%	14%	26%
P_{F4}	37%	23%	23%	20%	10%	17%	20%	13%	14%	52%	16%	3%	9%	40%

Cross 3

	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY
Target	≤65.5	≤105.4	≤118.2	≤12.9	≤12.2	≥269.4	≥38.8	≥87.1	≥60.4	≥9.39	≥72.6
m	74.7	115	137.1	14.4	12.9	205.33	38.8	64.1	43.9	7.19	52.5
D	40.11	44.90	475.75	4.48	3.97	4779.98	10.21	638.31	297.57	0.72	350.02
P	7%	7%	19%	24%	36%	18%	50%	18%	17%	1%	14%
P_{F4}	5%	14%	27%	10%	43%	18%	56%	16%	13%	0%	13%

Table 3 (continued)

Cross 4

	DF	**DM**	**PH**	**TB**	**FB**	**TP**	**SP**	**PW**	**SW**	**HSW**	**EY**
Target	≤54.2	≤95.2	≤69.0	≤10.6	≤8.35	≥128.0	≥44.0	≥44.2	≥29.4	≥9.34	≥34.7
m	59.3	97.6	95.8	11.1	8.67	95.3	40.7	40.1	27.8	8.49	31.5
D	21.38	18.26	392.02	3.87	2.50	969.45	4.12	158.45	65.44	1.14	93.66
P	14%	29%	9%	40%	42%	15%	5%	37%	42%	21%	36%
P_{F5}	3%	26%	4%	47%	62%	7%	9%	10%	11%	5%	10%

(The scores of the better parent or F_1 raised in the F_3 trial shown in Table 1 provided the targets used for the predictions and calculation of the observed proportions of superior F_5 or F_4 families).

4. Genetic correlations between characters

It is also important to consider the interrelationships between these characters in order to determine the probability of being able to obtain inbred lines that achieve the desired targets for two or more characters simultaneously. Approximate estimates of genetic correlations were obtained from the components of the analysis of covariance of F_3 families that were carried out for all pairs of characters in each cross. Since the proportion of variation of one character due to its relationship with another is the square of the correlation between them, attention is confined to those pairs of characters where the absolute value of the estimate is greater than 0.5. Figure 1 shows the genetic correlations between the ten characters scored in all four crosses that meet this criterion. Some of these correlations are as expected; PW and SW are highly and positively correlated in all four crosses because the former is a component of the latter. The same argument holds for the relationship between TP, on the one hand, and PW and SW, on the other. It follows, therefore, that EY is expected to be highly and positively correlated with TP, PW and SW in every cross. DF and DM are also expected to be positively correlated in each cross. The most striking feature of the correlations between other pairs of characters, however, is the extent to which they vary over crosses. The chief cause of genetic correlations between most of the characters in these crosses appears, therefore, to be the linkage disequilibrium of genes which are linked in their inheritance, rather than to pleiotropy.

5. The best F_4 or F_5 families extracted from the crosses

It has been observed that, with the exception of HSW in Cross 3, one or more of the F_4 or F_5 families of these crosses met the target for each character considered on its own. In view of the results presented in the previous section, none of these families could be expected to achieve the targets for all the characters scored in these crosses simultaneously and none, in fact, did so. Several families of each cross, however, achieved the desired target, or came closer to achieving this for nearly half or more of these characters. The mean scores of these are shown in Table 4.

Table 4. The performance of the best F_5 or F_4 families extracted by single seed descent from each of the four crosses.

Cross 1

Family	DF	DM	PH	FB	TN	TP	SP	PW	SW	HSW	EY
11	*65.3*	*102.0*	128.3	14.9	**46.7**	**258.0**	**38.9**	**65.5**	**42.3**	6.2	**57.7**
42	*65.6*	107.1	102.3	17.7	*40.2*	**298.8**	*36.1*	**79.8**	**58.7**	**7.9**	**80.8**
55	*66.0*	*102.0*	116.1	15.6	**43.5**	**264.8**	**43.1**	**51.8**	*32.4*	5.0	**50.3**
71	68.6	*103.0*	125.9	19.5	**51.7**	**355.1**	33.5	**82.6**	**57.9**	6.3	**67.5**
84	*64.1*	*102.2*	120.4	14.4	**41.2**	**217.6**	*37.0*	**55.9**	**40.1**	6.1	**46.2**

Cross 2

Family	DF	DM	PH	TB	FB	TP	SP	PW	SW	HSW	EY	HFB	PBL	IL
3	*66.2*	**100.5**	125.0	11.5	8.9	**228.0**	**42.0**	*59.8*	**42.7**	5.5	**52.1**	26.4	64.1	**47.4**
4	72.0	*110.2*	138.2	11.1	10.5	**231.8**	*37.7*	**75.3**	**53.0**	**7.5**	**63.6**	23.1	*73.0*	**50.5**
10	71.8	*109.7*	155.2	*8.1*	6.6	**271.1**	**40.5**	**84.6**	**60.5**	**6.9**	**72.0**	36.4	**89.4**	**63.4**
11	76.9	113.8	156.6	9.2	8.2	**228.6**	**41.7**	**69.6**	**49.1**	**6.9**	**68.4**	34.3	**81.8**	**60.5**
14	74.9	119.3	114.4	14.1	11.4	**358.9**	34.6	**90.2**	**63.1**	*6.4*	90.0	21.2	58.3	*41.3*
15	74.1	112.5	119.7	12.9	10.6	**351.9**	**40.2**	**101.6**	70.7	**6.9**	**92.0**	24.3	56.7	*40.4*
68	*70.6*	*109.6*	147.6	10.2	8.5	**275.3**	*37.7*	**83.5**	**58.2**	**7.1**	70.6	31.9	**81.7**	**53.5**

Table 4 (continued)

Cross 3

Family	**DF**	**DM**	**PH**	**TB**	**FB**	**TP**	**SP**	**PW**	**SW**	**HSW**	**EY**
28	85.5	124.7	163.1	16.7	15.5	**362.3**	*36.7*	**106.3**	**69.6**	7.4	**85.5**
33	87.7	125.7	166.3	18.7	18.5	**373.3**	**39.3**	**131.1**	**84.7**	8.2	**108.0**
35	82.8	119.6	157.6	17.2	15.7	**336.6**	**40.0**	**93.9**	**65.4**	6.5	**84.0**
44	86.0	126.8	160.7	15.8	13.8	**381.6**	*37.2*	**108.4**	**67.7**	6.7	**88.3**
54	*68.4*	*109.3*	**110.0**	*13.2*	**11.8**	**291.3**	**41.1**	77.1	52.6	7.1	**74.5**
58	83.1	122.5	156.3	16.7	15.1	**294.2**	**39.8**	**102.1**	**70.3**	7.4	**81.0**
80	78.1	123.8	174.5	*14.1*	*13.0*	**329.4**	*37.0*	**117.8**	**75.6**	8.1	**88.0**
83	74.7	*113.7*	145.3	14.8	13.7	**327.0**	*37.3*	**99.6**	**72.0**	7.2	**81.7**

Cross 4

Family	**DF**	**DM**	**PH**	**TB**	**FB**	**TP**	**SP**	**PW**	**SW**	**HSW**	**EY**
33	64.4	*100.3*	101.7	14.3	12.2	**158.7**	36.3	**54.8**	**35.5**	7.8	**44.0**
34	*61.4*	*100.1*	100.2	14.2	9.6	**144.1**	*43.9*	**56.5**	**38.9**	7.2	**44.6**
56	66.9	106.7	114.7	11.9	10.5	**148.3**	*40.3*	**49.5**	**32.0**	6.6	**39.0**
93	65.0	*101.9*	105.2	12.2	10.6	**160.0**	38.5	**51.5**	**33.3**	7.2	**41.7**

(The entries shown in bold indicate mean scores which achieve the desired target and those in italic, mean scores which come close to doing so [see previous table]).

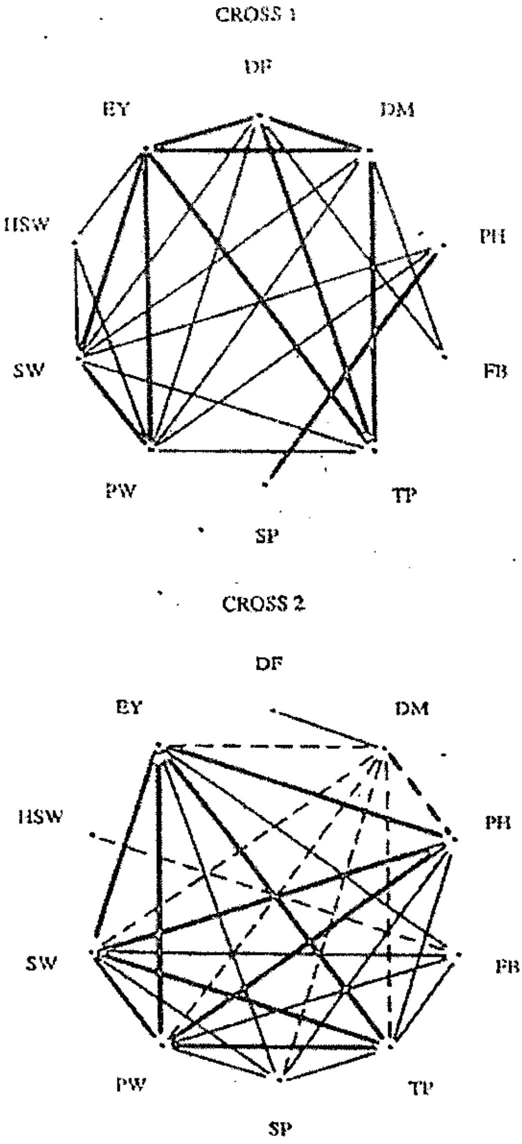
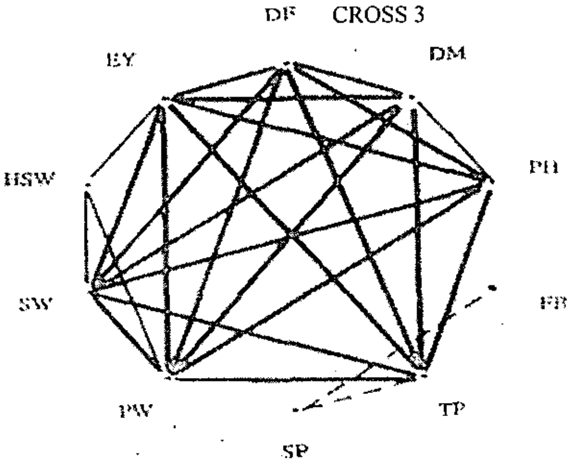
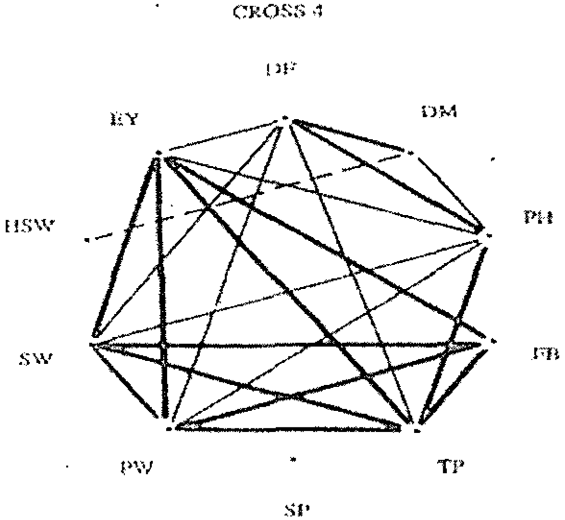


Figure 1. Genetic correlations between the ten characters scored in all four crosses (continued in next page).





(Heavy continuous lines connect characters for which r ≥ 0.75; light continuous lines those where 0.75 > r ≥0.5; heavy broken lines those where r ≤-0.75; and light broken lines, characters for which -0.75 < r ≤-0.5).

All of these families achieved the targets for EY and TP, and the majority did so for the other correlated characters, PW and SW. None of these families, however, achieved the targets for DF, and only one (No. 3, Cross 2) did for DM and another (No. 54, Cross 3) for PH. On the other hand, the means of several of these families were within seven days of the targets for DF and/or within ten days of the targets for DM (entries shown in italic); this suggests that one or more of the single seed descendants of these high yielding families might achieve the targets for these characters as well. Apart from the single exception mentioned above, it is unlikely that the descendants of any of these families would simultaneously achieve the desired targets for yield and plant height, since the means of all, but one of these families are well above the targets for the latter.

The results indicate that it should be possible to extract superior inbred lines from each of the four crosses for virtually every character considered on its own. Furthermore, because the means of a number of F_4 or F_5 families either met the targets or came close to doing so for half or more of the these characters simultaneously, it should be possible to extract one or more lines from each cross that also achieve this. It would be difficult, however, to extract high yielding lines from these crosses that are of required short stature with only one cycle of inbreeding. The chief cause of this difficulty in the case of crosses 2 and 3 is that, although more than 20% of their F_4 families achieved the target for stature, all but one had estimated yields which were well below the target for this character, because of a strong, positive genetic correlation between PH and EY ($r = 0.76$ and 0.81, respectively). In crosses 1 and 4, on the other hand, though PH was highly heritable (Table 2), only 4-5% of F_5 families met the target for this character. This suggests that, in contrast to crosses 2 and 3, the majority of decreasing alleles occur in the lower scoring parent. This difficulty is exacerbated in Cross 4 by a strong positive genetic correlation between PH and EY ($r = 0.74$). Hence, while it should be possible to decouple height and yield in crosses 2 and 3, by providing further opportunities for recombination between the genes controlling these characters with a second cycle of hybridisation and inbreeding, this is less likely to be successful with crosses 1 and 4.

There are three further points worth making about these results. First, 12 of the 93 F_4 families of Cross 3 had an estimated yield that was greater than that of their F_1, the hybrid variety, ICPH-8. The heterosis of this variety appears, therefore, to be due to the dispersion of genes between the parents whose dominance is in the increasing direction, rather than to overdominance. This suggests that it should be possible to "fix" this heterosis in an inbred line, thus avoiding the considerable inconvenience and cost of having to maintain and utilise the genetic male sterility of the female parent of this F_1 variety. However, while in principle it should be easier to produce and maintain new varieties of pigeonpea as inbred lines than as F_1 hybrid varieties, in practice this is difficult than cereals, such as wheat, rice and barley. Thus, although seed can be set by natural self-pollination, this is not, as with the cereals, virtually automatic, natural outcrossing ranging from 5% to 94% (Faris, personal communication). To produce inbred lines by single seed descent, it would be necessary to ensure self-pollination by protecting flowers a day or so before they open (as was done in the present investigation). Again, in order to multiply the seed of a new variety, it would be necessary to ensure that the seed crop was isolated from other crops. Bhatia **et al.** (1983) found that a distance of 100m between blocks of two cultivars reduced outcrossing between them from 15% to 3%. A distance of not less than 200m between seed crops should be sufficient to maintain their purity.

Second, pigeonpea is well known to be a rather plastic species. The results obtained from trials of the same material repeated in different seasons or locations are, therefore, expected to differ. The results reported here come from a trial carried out in a single season at a single location. The parents of each cross, together with their F_1 and F_2 progeny were, however, also raised in a preliminary, completely randomized trial at ICRISAT in the previous rainy season. Although the seed yield of the parents and their F_1 progeny of Crosses 1, 2 and 4 in this season were generally lower (Chithral, 1995) than in the following one, the higher scoring parent in 1992 was the same as that in 1993 for the great majority of characters. Again, all of the characters that displayed heterosis in 1993, also did so in 1992. More characters, however, displayed heterosis in the 1992 trial than in the following season; and this can be expected when plants are raised in a poorer environment. In Cross 3, however, the scores for every character except PH were very similar over seasons. It is likely that the greater stability of characters over seasons in this cross is a consequence of breeders selecting for this when developing the F_1 hybrid of this cross. The 1992 trial also contained forty F_3 families of Cross 4. The estimates of the heritability of DF and DM were lower in the 1992 trial than those of the following season. For all of the other characters these estimates were very similar in both seasons. Taken overall, therefore, these results show that the performance of the families of these crosses was reasonably consistent over seasons.

Third, both the F_3 and the SSD trials were sown at a spacing of 60 cm x 60 cm, a wider than the usual spacing used for the crop, in order to allow access to plants, for taking individual measurements. This wider spacing also allows plants of different genotype to express their full potential. In addition, because plants were assigned at random to the trial area (individually in the case of the F_3 trials and as duplicate plots containing five plants each in the SSD trials), it was possible to obtain unbiased estimates of family means of characters, and their heritability and additive genetical variance, D. Trials of this design are capable, therefore, of yielding more information about the potential of crosses than those of conventional type. This suggests that breeders could recognise and, hence, exploit the genetical variation in their crosses more efficiently if they were to use a procedure which incorporates the key features of the present trials. We have described elsewhere a biometrical breeding method which has this property (Lawrence and Senadhira, 1998). Although this new method was proposed with rice in mind, it is applicable to any crop, including pigeonpea, where the end products of breeding programmes are inbred lines.

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