INHERITANCE OF SEED SIZE IN COWPEA (*VIGNA UNGUICULATA* (L.) WALP.)

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SUMMARY

The inheritance of seed weight in cowpea was examined in a field planting of the parents, reciprocal F_1s, F_2s and backcrosses to both parents of a cross between TVu 1977-OD (small seeded) and ACC 70002 (large).

Seed weight was inherited quantitatively and small seed was partially domimminant to large seed size. Gene action was predominantly additive but dominance and additive × additive epistatic effects were also significant.

Broad and narrow sense heritabilities were 85.1 ± 5.3% and 75.4 ± 18.6% respectively. The minimum number of loci involved in the inheritance of seed size was eight, and each gene pair contributed up to 1.02 g increase to seed weight. The estimate of genetic advance from F_2 to F_3 generations with 5% selection intensity was 3.58 g.

INTRODUCTION

Seed size is an important characteristic of cowpea in West Africa where seeds of most of the cultivars preferred and grown by farmers are large and white or brown with a rough testa.

Genetic investigations of seed size have given contradictory results with regard to the relative importance of additive and dominance effects in its inheritance and the number of genes controlling the character. BRITTINGHAM (1950) reported heterosis for seed size and transgressive segregation for large seed. Heterosis for seed size was also reported by AGBLE (1972) who concluded that gene action determining seed size may not be additive. SENE (1968) found that seed weight was controlled by six pairs of genes acting additively and that each gene corresponded to a weight increase of 1.1 g. ARYEETEY & LAING (1973) concluded that this character was controlled by ten pairs of genes. DRABO et al. (unpublished) found that additive, dominance and epistasics effects were present in the inheritance of seed size and that additive gene effects

Table 1. Mean seed weights (g/100 seeds) of reciprocal F_1, F_2, and BC generations of a cross of TVu 1977-OD (P_S) and ACC 70002 (P_L).

Generation	Female parent of first cross	Number of plants	Mean	S.E. ($\pm$)
F_1	P_S	40	16.9	0.20
F_1	P_L	40	16.3	0.11
F_2	P_S	128	14.6	0.23
F_2	P_L	128	14.7	0.23
BC_S	P_S	80	12.0	0.18
BC_S	P_L	80	12.1	0.17
BC_L	P_S	80	20.0	0.22
BC_L	P_L	80	19.8	0.22

were greater in magnitude than other gene actions. The authors also concluded that large was dominant to small seed size. Conversely, ARYEETEY & LAING (1973) and LELEJI (1976) observed dominance of small over large seed size.

Broad and narrow sense heritability estimates of 80% and 71% respectively were reported by SENE (1968) for seed size. Corresponding values by ARYEETEY & LAING (1973) were 63% and 37.4%. LELEJI (1976) found broad sense heritability for seed size to range from 49% to 82%. Corresponding values by DRABO et al. (unpublished) were 48% to 90.2%.

This paper reports studies of the inheritance of seed size in a cross made to incorporate the large seed of a photosensitive and low yielding cowpea cultivar, typical of the landraces grown throughout the West African savannas, into a high yielding background.

MATERIALS AND METHODS

The parents were two accessions from the world cowpea germplasm maintained by the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria: TVu 1977-OD, which originated in Zimbabwe and was described by IITA as VITA-4 and designated P_S (9 to 10 g per 100 seeds); and ACC 70002 collected in the Niger Republic and designated P_L (around 26 g per 100 seed).

Reciprocal crosses were made in 1978 and seed of the F_2s and backcrosses to small (BC_S) and large (BC_L) seeded parents obtained in 1979. The parents and the reciprocal

Table 2. Genetic variances for seed weight (g/100 seeds) in different generations of a cross between TVu 1977-OD and ACC 70002.

Generation	d.f.	Variance
P_S	36	0.598
P_L	36	1.204
F_1	72	0.573
F_2	248	5.302
BC_S	152	2.373
BC_L	152	4.233

F_1 and F_2 and backcross populations were sown in the field on the research farm at IITA in September 1980 in a randomised complete block design with four replicates. The plot sizes were two rows for the parents and F_1s, four rows for the F_2s and three rows for the BC generations, each of 3 m length. The planting density was 1 m between and 30 cm within rows. The seed weights were recorded for ten random plants from each plot for parents and F_1s, 32 for F_2s and 20 for the backcross generations, and expressed as weight of 100 seeds in grams (all sampled plants had at least 100 seeds).

Generation means were obtained from the averages of plot means. The variances and standard errors of the means for each generation were obtained from the within plot sums of squares (LAWRENCE & JINKS, 1973). A simple analysis of variance was performed to compare reciprocal F_1, F_2 and backcross generations. A generation means analysis was performed according to MATHER & JINKS (1971).

MATHER's (1949) ABC scaling test and CAVALLI's (1952) joint scaling test were used to test for the significance of additive and dominance gene effects in the inheritance of seed weight. Generation means were also analysed using the six parameter model of JINKS & JONES (1958). Narrow and broad sense heritability estimates, and the number of effective factors differentiating the parents were evaluated according to LAWRENCE & JINKS (1973). Genetic advance under selection was calculated by the method of ALLARD (1960).

RESULTS AND DISCUSSION

The differences between the means of the reciprocal crosses were small and non-significant so the reciprocals were pooled for subsequent computations (Table 1). The F_1 mean was less than the midparent value and the mean of the F_2 lay between the means of the F_1 and the small seeded parent. The mean of the backcross to the large seeded parent lay between the F_1 and its recurrent parent, ACC 70002, and was closer to the F_1 value than that of the backcross to the small seeded parent, which lay between the means of the F_1 and TVu 1977-OD. These data conform with the conclusions of ARYEETEY & LAING (1973) and LELEJI (1976) that small seed is partially dominant.

There was no transgressive segregation for large seed in the F_2 since no F_2 plant exceeded the large seeded parent (Fig. 1). From a population of 256 F_2 plants no parental types were recovered suggesting that the inheritance of seed weight is controlled by more than 3 genes.

The variance of the F_2 population (Table 2) was much greater than the variances of the parents and the F_1 generations in which variation is attributed to environmental effects. The variance of BC_L was larger than the variance of BC_S. Since twice the variance of the F_2 was greater than the sum of the variances of the backcross generations ($2\,VF_2 - VBC_S - VBC_L = 3.998$), nonadditive gene action is indicated.

MATHER's (1949) scaling test and CAVALLI's (1952) joint scaling test were significantly different from zero (Table 3) also suggesting the occurrence of epistasis in the inheritance of seed size. Analysis according to JINKS & JONES (1958) (Table 3) indicated that the additive (d) and dominance (h) gene effects were significantly different from zero, the magnitude of the additive gene effect being nearly double that of the dominance gene effect. Among the epistatic effects only (i) was significantly different from zero indicating additive × additive gene action. Therefore it appears that additive
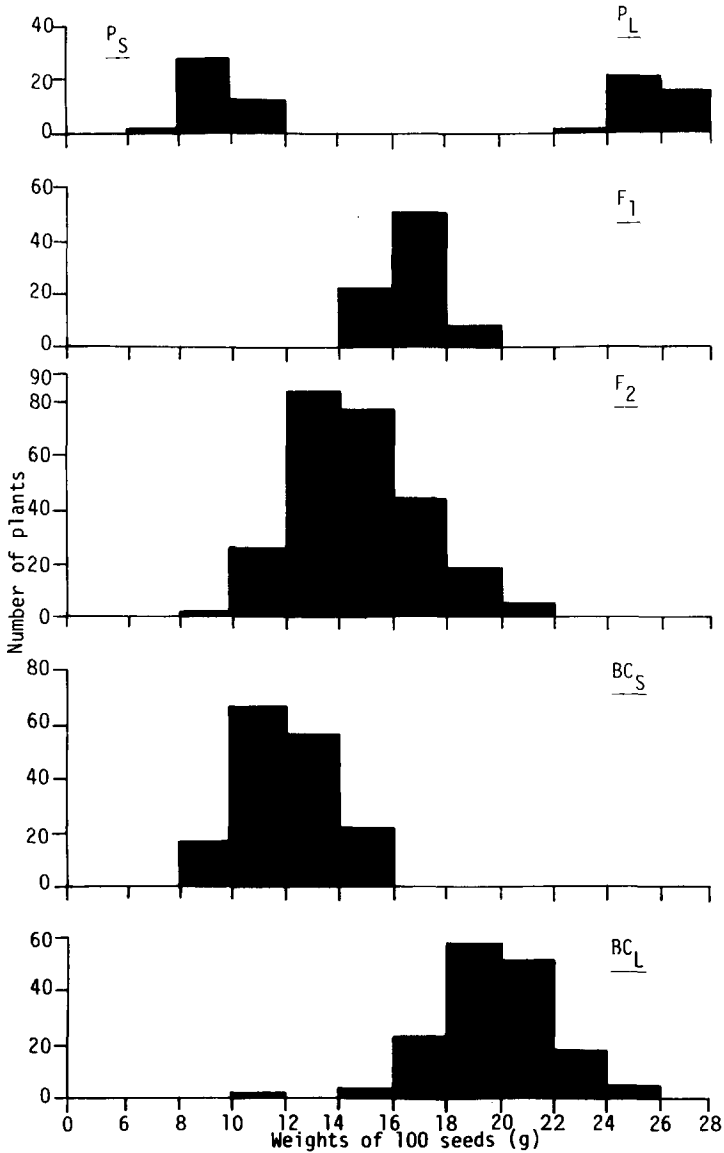
Fig. 1. Frequencies of seed weights of parental (P_S and P_L), F_1, F_2 and backcross (BC_S and BC_L) generations of the cross of TVu 1977-OD (P_S) and ACC 70002 (P_L).

and additive × additive gene actions played a major role in the inheritance of seed size although dominance gene action was also significant. This result is in agreement with SENE (1968) and DRABO et al. (unpublished).

Broad and narrow sense heritability estimates were 85.1% ± 5.3 and 75.4% ± 18.6 respectively. This estimate of narrow sense heritability includes both additive and additive × additive epistatic effects and is therefore an upper limit. Similar results with

Table 3. Scaling test and gene effects estimated using 3 and 6-parameter models from generation means of a cross between TVu 1977-OD and ACC 70002.

Model and effect	Estimates
Scaling test (MATHER, *1949*)	
A	$- 2.71^{**} \pm 0.286$
B	$- 2.20^{**} \pm 0.379$
C	$-10.21^{**} \pm 0.636$
Joint scaling test (CAVALLI, *1952*)	
m	$17.00^{**} \pm 0.092$
(d)	$7.94^{**} \pm 0.093$
(h)	$- 0.92 \quad \pm 0.134$
Six-parameter model (JINKS & JONES, *1959*)	
m	$12.51^{**} \pm 0.736$
(d)	$8.14^{**} \pm 0.212$
(h)	$4.49^{**} \pm 1.393$
(i)	$5.30^{**} \pm 0.705$
(j)	$- 0.51 \quad \pm 0.459$
(k)	$- 0.40 \quad \pm 1.034$

** = Significantly different from zero at 0.01 level of probability.

regard to broad sense heritability were published earlier by SENE (1968), LELEJI (1976) and DRABO et al. (1982).

Assuming that the 5 per cent of F_2 plants with the largest seeds (18–22 g) are selected for further propagation, the expected genetic advance was 3.58 g.

The estimate of K suggested that a large number of genes (at least eight pairs) control seed size. Although this estimate may be biased by epistasis (WARNER & HONMA, 1980), it is in agreement with the average number of genes found by SENE (1968) and ARYEETEY & LAING (1973) who found that seed size was controlled by six and ten pairs of genes respectively. Also each of the proposed eight gene pairs contributed to a 1.02 g weight increase, which compared well with the 1.1 g estimated by SENE (1968). However, the qualifying assumptions of equal additive effects at all loci, and complete association of all (+) and (−) genes in the respective large and small seed parents and either absence of linkage or redefinition of a gene as an effective factor of linked genes (LAWRENCE & JINKS, 1973), indicate that estimates of K are at best only a useful guide to the genetic basis of seed weight.

The study indicated that seed weight is governed by several genes acting mainly additively. The high narrow sense heritability estimate indicates that progress would be expected with early generation selection for large seed size.

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