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# Breeding Implications from a Diallel Analysis in two Environments of Yield and Component Characters in Upland Cotton *(Gossypium hirsutum)*

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Summary. In a full diallel set of crosses involving nine Albar 51 lines the genetic control of yield and yield components were largely accounted for by additive effects, although non-additive effects were evident. Significant differences in correlation coefficients between sites and the interaction of genetic effects indicate the effect of the environment on development and gene action. The failure to achieve yield improvements appears to stem from a combination of testing at the early selection stage in a single environment and of a narrow genetic base. The implications for future breeding programmes are discussed.

## 1. Introduction

BPA is the present commercial variety of African Upland cotton in southern Uganda (Arnold, Costelloe and Church, 1968). Pedigree selection has produced lines that differ from the first BPA seed issue in some characters, but no line has been obtained that is superior to it in yield. Recent attempts to improve the yield and other characteristics of successive BPA seed issues have, therefore, been based on the use of multiline seed issues (Arnold, Innes and Gridley 1970, 1971; Innes, Gridley and Busuulwa, 1973).

In an attempt to increase genetic variability within BPA stocks and obtain information on the genetic control of yield and its component characters, a full diallele set of crosses was made in 1969 between nine pedigree selected lines. Environmental conditions in the equatorial regions of Africa are extremely variable, and to assess the effect of the environment on estimates of the genetic parameters, parents and $F_1$ hybrids of the diallel set were included in a rain fed trial at Namulonge, Buganda, and in an irrigated one at Mubuku, Western Region.

## 2. Materials and Methods

The nine parents used in the crossing programme, which included reciprocals, were the pedigree selections BPA 68, A(66)22, 29, 36, 102, 131, 134 and A(67)8, 12 from Albar 51; all nine selections stemmed from A(57)5 (Innes and Jones, 1972). The derivation of these lines is shown in Fig.1 where A(57)5 is the sixth generation inbred from A474, with single plant selection in each generation. The parents were therefore highly inbred and closely related.

In 1970-71 parents, hybrids and reciprocals were grown in a 9 × 9 balanced lattice square with five replicates at Namulonge and Mubuku. Plot size was 4.3 m$^2$ in the Namulonge trial and 3.2 m$^2$ in the one at Mubuku with two plants per stand in two row plots at a spacing of 0.9 m × 0.3m.

The yield components, seed cotton per boll, loculi per boll, seeds per loculus, seeds per boll, seed weight and lint per seed were determined from fifteen boll samples at Namulonge and ten boll samples at Mubuku taken at the time of second pick. Ginning percentage and lint yield were estimated from the produce of whole plots.

### Genetic Analysis

In the Hayman (1954) analysis, variation is divided into components which measure additive and non-additive genetic effects and reciprocal differences. Item 'a' refers to additive parental effects and 'b' to non-additive effects. Where an additive-dominance model is adequate the latter can be partitioned into terms providing tests of mean dominance ($b_1$), of variation of dominance from array to array ($b_2$) and of dominance deviation that is unique to each $F_1$ ($b_3$). If tests of the value of Wr (covariance) and Vr(variance) do not show the expected relationship, then non-additive effects can not be interpreted in terms of simple dominance. Item 'c' de-

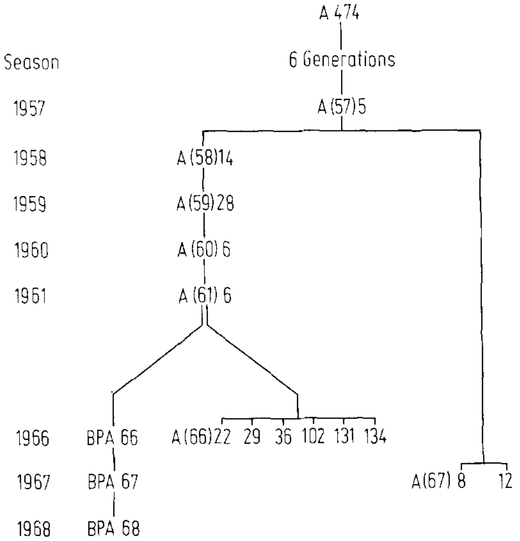

Fig. 1. Pedigree of Albar 51 selections used in the 9 × 9 full diallel set of crosses

Table 1. Parent and hybrid performance for the eight yield components at Namulonge (N) and Mubuku (M)

| Character | Site | Parental mean | $F_1$ mean | % increase $F_1$ mean over parental mean |
|---|---|---|---|---|
| Seed cotton per boll (g) | N | 4.8 ± 0.08 | 4.9 ± 0.02 | 2.8* |
| | M | 5.3 ± 0.05 | 5.4 ± 0.02 | 1.9 |
| Loculi per boll | N | 4.2 ± 0.02 | 4.2 ± 0.01 | 0.5 |
| | M | 4.3 ± 0.02 | 4.3 ± 0.01 | -0.3 |
| Seeds per loculus | N | 6.8 ± 0.08 | 6.8 ± 0.02 | 0.3 |
| | M | 7.9 ± 0.04 | 7.9 ± 0.02 | 0.4 |
| Seeds per boll | N | 28.7 ± 0.37 | 29.0 ± 0.12 | 0.9 |
| | M | 33.7 ± 0.34 | 33.7 ± 0.09 | 0.1 |
| Seed weight (mg/seed) | N | 119 ± 1.1 | 119 ± 0.30 | 0.5 |
| | M | 108 ± 1.0 | 109 ± 0.40 | 1.2 |
| Lint per seed (mg) | N | 4.8 ± 0.05 | 4.9 ± 0.02 | 1.2 |
| | M | 5.2 ± 0.05 | 5.3 ± 0.02 | 1.7 |
| Lint yield (kg/ha) | N | 651.0 ± 12.17 | 710.6 ± 4.50 | 9.1*** |
| | M | 531.0 ± 14.00 | 560.4 ± 5.74 | 5.5 |
| Ginning percentage | N | 31.2 ± 0.15 | 31.3 ± 0.05 | 0.2 |
| | M | 32.2 ± 0.09 | 32.2 ± 0.05 | 0.3 |

*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

tects average maternal effects and item 'd' the reciprocal differences not ascribable to c. If there are differences between reciprocal crosses, then the mean squares for items c and d become the appropriate error terms for the a and b items, respectively (Wearden, 1964).

A joint Hayman (1954) analysis of the data from the two sites was also carried out. The presence of an interaction of genetic effects with sites was then tested by comparing the item x sites with the item x blocks mean square.

Adjusted data from the lattice square analysis were used to calculate the phenotypic correlation coefficients but for the Hayman (1954) analysis rows and columns of the lattice square were ignored.

All statistical analyses were carried out at Rothamsted Experimental Station on an I.C.L. System 490 Computer using Genstat.

## 3. Results

### Heterosis

Data in Table 1 indicate that significant heterosis, expressed as the percentage increase of the $F_1$ hybrids above the average of the parents, is shown only by seed cotton per boll and lint yield at Namulonge.

### Correlations

Phenotypic correlation coefficients among the eight yield components for parents and hybrids at the two sites are given in Tables 2a and 2b. The greater number statistically significant in the hybrid populations reflects differences in sample size which was 72 for the hybrids but only 9 in the case of parents. The correlations in the two populations at both sites of seed cotton per boll with loculi per boll, seeds per loculus and seeds per boll were generally significant or high. This suggests that total seed number contributes more to boll size than seed weight and lint per seed, although the latter are highly correlated with boll size in the hybrid population at Mubuku. The hybrid populations show a positive effect of increasing boll size on lint yield.

Correlations significantly different between sites are indicated by a bracket in Tables 2a and 2b and range from differences in degree of relationship to a switch from a positive to a negative relationship. Examples from the hybrid populations are seed cotton per boll and lint per seed for the former and seed weight and ginning percentage for the latter.

### Diallel Analysis

Analyses of variance of lint yield, using Hayman's (1954) model, are shown in Table 3. The variance ratios (VR) were calculated using the associated block interaction terms. The relevant mean squares and variance ratios for interaction of additive or non-additive effects between sites for lint yield are shown in Table 4. Results for the other components were calculated similarly and are in-

Table 2a. Phenotypic correlation coefficients between the eight yield components for parents at Namulonge (upper value) and Mubuku (lower value)

| *Character* | Seed cotton per boll | Loculi per boll | Seeds per loculus | Seeds per boll | Seed weight | *Lint per seed* | *Lint yield* |
|---|---|---|---|---|---|---|---|
| Loculi per boll | 0.56<br>0.75* | | | | | | |
| Seeds per loculus | 0.62<br>0.19 | -0.07<br>0.53 | | | | | |
| Seeds per boll | 0.85**<br>0.53 | 0.47<br>0.86** | 0.85**<br>0.88** | | | | |
| Seed weight | 0.44<br>0.35 | 0.40<br>-0.17 | -0.30<br>-0.70* | -0.06<br>-0.52 | | | |
| Lint per seed | 0.37<br>0.09 | 0.06<br>-0.23 | -0.13 ]*<br>-0.86 ] | -0.07<br>-0.65 | 0.74*<br>0.73* | | |
| Lint yield | 0.11<br>0.18 | 0.11<br>-0.33 | 0.32<br>-0.53 | 0.32<br>-0.50 | -0.31<br>0.43 | -0.50 ]*<br>0.59 ] | |
| Ginning percentage | -0.60<br>0.10 | -0.24<br>-0.23 | -0.29<br>-0.57 | -0.41<br>-0.47 | -0.27<br>0.57 | -0.35<br>0.64 | 0.34<br>0.59 |

*Note:* Bracketing of two correlation coefficients indicates they are significantly different with the level of significance shown at the top right hand corner

Table 2b. Phenotypic correlation coefficients between the eight yield components for hybrids at Namulonge (upper value) and Mubuku (lower value)

| *Character* | Seed cotton per boll | Loculi per boll | Seeds per loculus | Seeds per boll | Seed weight | *Lint per seed* | *Lint yield* |
|---|---|---|---|---|---|---|---|
| Loculi per boll | 0.43**<br>0.36** | | | | | | |
| Seeds per loculus | 0.71*** ]**<br>0.30* ] | 0.10<br>-0.02 | | | | | |
| Seeds per boll | 0.80*** ]**<br>0.48*** ] | 0.58***<br>0.70*** | 0.87*** ]**<br>0.69*** ] | | | | |
| Seed weight | -0.02 ]***<br>0.74*** ] | -0.20<br>-0.05 | -0.50*** ]*<br>-0.12 ] | -0.50*** ]*<br>-0.13 ] | | | |
| Lint per seed | 0.30* ]**<br>0.69*** ] | -0.33<br>-0.10 | -0.08<br>-0.18 | -0.23*<br>-0.20 | 0.50*** ]**<br>0.81*** ] | | |
| Lint yield | 0.29*<br>0.48*** | 0.19<br>-0.02 | 0.25*<br>0.05 | 0.30<br>0.00 | -0.11 ]***<br>0.53*** ] | -0.01 ]***<br>0.56*** ] | |
| Ginning percentage | -0.02 ]*<br>0.33** ] | 0.24<br>-0.09 | 0.08<br>-0.17 | 0.19 ]*<br>-0.20 ] | -0.28* ]***<br>0.39*** ] | -0.25* ]***<br>0.58*** ] | 0.47***<br>0.48*** |

cluded in a summarised form, with lint yield, in Table 5.

Additive effects were highly significant at both sites for all characters except seed weight at Namulonge. Non-additive effects were evident for seed cotton per boll at Namulonge and for lint per seed and lint yield at both sites. As the parents were inbred, statistical tests described by Mather and Jinks (1971) using Wr and Vr were performed to investigate whether an additive-dominance model was appropriate. None of the three characters satisfied all three tests, involving (a) the consistency of Wr-Vr over arrays, (b) agreement between the regression of Wr on Vr for individual blocks and (c) the agreement of the joint regression slope with unity. This suggests that simple dominance is not an adequate explanation of the non-additivity and does not allow the estimation of the components of variation D1, H1, H2, F and E. However, the statistically significant $b_1$ item is associated with significant heterosis for two out of three components.

Differences between arrays of reciprocal crosses were evident for seed weight and ginning percentage at Namulonge. For both characters differences between reciprocals were small. For the former there were indications that hybrids involving BPA 68 as the female

Table 3. Hayman analysis of variance for lint yield in the 9 × 9 full diallel set of crosses at Namulonge and Mubuku

| Site | | Namulonge | | Mubuku | |
|---|---|---|---|---|---|
| Item | DF | MS | VR | MS | VR |
| a | 8 | 30451.20 | $8.72^{***}$ | 44844.80 | $4.30^{**}$ |
| b | 36 | 8732.29 | $2.87^{***}$ | 9670.71 | 1.37 ns |
| $b_1$ | 1 | 154814.00 | $90.54^{***}$ | 18112.11 | $16.13^{*}$ |
| $b_2$ | 8 | 4016.80 | 1.74 ns | 11725.20 | 1.30 ns |
| $b_3$ | 27 | 4719.04 | 1.42 ns | 8749.33 | 1.31 ns |
| c | 8 | 4297.32 | 2.19 ns | 10729.99 | 1.60 ns |
| d | 28 | 4201.41 | 1.13 ns | 5218.23 | 0.60 ns |
| a × blocks | 32 | 3491.70 | | 10439.30 | |
| b × blocks | 144 | 3046.55 | | 7061.76 | |
| $b_1$ × blocks | 4 | 1709.97 | | 1123.09 | |
| $b_2$ × blocks | 32 | 2303.27 | | 9036.86 | |
| $b_3$ × blocks | 108 | 3316.29 | | 6696.50 | |
| c × blocks | 32 | 1961.61 | | 6699.00 | |
| d × blocks | 112 | 3709.00 | | 8701.30 | |

ns non-significant

Table 4. Analysis of item × site interactions for lint yield in the 9 × 9 full diallel set of crosses

| Item | Item × Sites | | | Item × Blocks | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Namulonge | | Mubuku | Pooled | |
| | DF | MS | VR | DF | MS | MS | DF | MS |
| a | 8 | 8165.00 | 0.78 ns | 32 | 3491.70 | 10439.30 | 64 | 6965.50 |
| b | 36 | 6723.65 | 0.95 ns | 144 | 3046.55 | 7061.76 | 288 | 5054.16 |
| $b_1$ | 1 | 33779.51 | $23.85^{**}$ | 4 | 1709.97 | 1123.09 | 8 | 1416.53 |
| $b_2$ | 8 | 8010.63 | 0.89 ns | 32 | 2303.27 | 9036.86 | 64 | 5670.07 |
| $b_3$ | 27 | 5340.26 | 0.80 ns | 108 | 3316.29 | 6696.50 | 216 | 5006.40 |
| c | 8 | 8864.50 | 1.32 ns | 32 | 1961.62 | 6699.00 | 64 | 4330.31 |
| d | 28 | 3314.04 | 0.38 ns | 112 | 3709.00 | 8701.30 | 224 | 6205.15 |

Note: The variance ratios for all items except $b_1$ are based conservatively on the greater mean square as tests showed them to be heterogeneous

Table 5. Summary of Hayman analysis of variance for eight yield characters in a 9 × 9 full diallel set of crosses at Namulonge and Mubuku

| Site | Namulonge | | | | | Mubuku | | | | Interaction | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Character | | | | | | | | | | | | | | | |
| Seed cotton per boll | $a^{***}$ | | $b_1^{*}$ | | $d^{*}$ | $a^{***}$ | | | | $a^{***}$ | | | | | |
| Loculi per boll | $a^{***}$ | | | | | $a^{**}$ | | | | $a^{***}$ | | | | | |
| Seeds per loculus | $a^{***}$ | | | | | $a^{**}$ | | | $d^{*}$ | | | | | | |
| Seeds per boll | $a^{***}$ | | | | $d^{*}$ | $a^{***}$ | | | | $a^{***}$ | | | | | |
| Seed weight | | | | $c^{**}$ | $d^{**}$ | $a^{***}$ | | | | $a^{***}$ | | | | | |
| Lint per seed | $a^{***}$ | | $b_1^{*}$ | | | $a^{***}$ | $b_1^{*}$ | $b_3^{*}$ | | $a^{***}$ | | | | | |
| Lint yield | $a^{***}$ | $b^{***}$ | $b_1^{***}$ | | | $a^{***}$ | $b_1^{*}$ | | | | $b_1^{*}$ | | | | |
| Ginning percentage | $a^{***}$ | | | $c^{**}$ | $d^{***}$ | $a^{***}$ | | | $d^{***}$ | $a^{***}$ | | $b_2^{*}$ | $b_3^{*}$ | $c^{***}$ | $d^{***}$ |

parent were contributing, in that six out of eight had marginally heavier seeds than their reciprocals, while all hybrids involving A(66)36 as the female parent had slightly lower ginning percentages.

Differences between arrays of reciprocal crosses, other than that measured by c, were evident for seed cotton per boll, seed weight and ginning percentage at Namulonge and seeds per loculus and ginning percentage at Mubuku. Differences were small and for all components appeared to be due to the behaviour of a number of crosses involving different parents.

For practical purposes it is doubtful if either of the above sets of differences is important.

Interactions of additive or non-additive effects between sites were evident for all characters except seeds per loculus. Where there was evidence of heterogeneity of variance between the two sites the variance ratio was calculated using the larger mean square only. Parts or all of these interactions may have been due to scale differences, but only for seed cotton per boll and ginning percentage was a significant proportion of the variance accounted for by a linear regression of Wr - Vr on parental or array means, in neither case for both at the same site.

## 4. Discussion

An understanding of the genetic control of agronomically desirable characters is necessary in crop improvement where genetic variability is exploited through selection. The control of the eight yield components is largely determined by genes of additive effect at both sites although non-additive effects are also evident. The interaction of genetic effects for all characters except seeds per loculus shows that parental differences vary between sites. A similar pattern emerged in the analysis of three fibre quality characters in this material (Innes, Wimble and Gridley, in press).

Knight (1973) has shown that parents and hybrids having a similar shaped response surface reach optima at different levels of one environmental factor and relations between $F_1$'s and parents will vary in different environments, resulting in changes in dominance relations. In East Africa cultivated cotton is subject not only to large climatic variation from place to place and season to season (Arnold 1971) but also to a wide range of soils and management, resulting in many environmental combinations. Arnold and Innes (1975) have shown that under such conditions striking interactions occur between genotypes and environment for yield.

The yield of a crop plant depends on the coordinated action of many genes but the differences in correlation coefficients between sites, particularly those switching from positive to negative, reflect a change in development pattern. This may stem purely from the interplay of the genotype and environment and be non-transmissible, or it may be caused by a change in expression of genes or by the expression of previously masked or silent genes. The diallel analysis indicates one or both of the latter two alternatives as the cause but can not distinguish between them. Arnold (1971) found genes determining resistance to bacterial blight in Tanzanian cotton stocks that are only expressed in certain environments; Walker (1969), in his review, quoted authors who had found unexpected variation in phenotypically nonvariable material after transfer to a new environment. The present data serve further to illustrate the dynamic interplay of genotype and environment and emphasise the care which must be taken in interpreting results from a single environment.

In a breeding programme, testing at the early selection stages, owing to limited seed supplies, is often restricted to a single environment employing advanced agricultural practices. Selection for improved yield may produce lines adapted to these conditions but lacking the stability required for commercial cultivation. For example, reselection in the parents of the diallel cross has produced lines which exhibit yield advantage in trials sampling a few environments, but fail to maintain this in wide ranging district trials (Arnold, Innes and Gridley, 1970, 1971). The selection of barleys with wide adaptation was achieved in Canada by alternating each year the environment in which the segregating material was grown (St. Pierre, Klinck and Gauthier, 1967). Such use of the environment as a practical aid is worthy of further evaluation and might prove beneficial if applied to the hybrid populations, although advances may be limited as the parents stem from a programme of pedigree selection and intensive inbreeding, which is characteristically accompanied by a rapid decrease in variability (Arnold, 1971).

Short term inprovements might stem from the use of multiline seed issues comprising a number of closely related lines. In district trials they have shown small yield advantages over the mean of their component lines in Uganda (Arnold, Innes and Gridley, 1970) and in Tanzania (Lee, Walton and Jackson, 1973). Theoretically such mixtures of genotypes will be better buffered against the environment than a single genotype. Although conclusive evidence is lacking, the large amount of additive genetic variation detected suggests the feasibility of such an approach where a seed issue is grown commercially for several years.

The yield advantage of the $F_1$ hybrids at both sites is not sufficient for the economic production of hybrid seed, as crossing has to be achieved by time consuming methods of emasculation and hand pollination. Several genes causing male sterility have been found (Weaver and Ashley, 1971) but no satisfactory system of restoring fertility has yet been discovered.

Long term improvements in yield will have to stem from selection in genetically wide-based populations synthesised from the crossing of exotic material to locally adapted stocks. These results, and those on lint quality (Innes et al., in press), emphasise the need to test early generation selections over as wide a range of ecological conditions as is practicable. The synthesis of a random mating pool of the best lines in the early stages of a programme might preserve genetic variability to which a breeder could later return.

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