THE THEORY AND APPLICATION OF THE BACKCROSS TECHNIQUE IN COTTON BREEDING

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Introduction

The essential value of backcrossing is that it provides a means of limiting the heterogeneity which would result from 'straight' crosses between two types, making it possible to produce a hybrid similar to whichever of the two varieties has the more valuable genetic constitution, yet containing desirable characters transferred from the other parent. Backcrossing obviates the necessity for rigid selection generation after generation, in F_2, F_3, F_4, etc., by progressively and automatically rendering the hybrid more and more homogeneous. In many ways it is, to the plant breeder, the equivalent of line breeding to the stock breeder, with the added advantage that many plants are not harmed even by the closest inbreeding.

Harland (1934) gives a list of some of the gene transferences which have been effected in interspecific crosses in cotton. He was the first to realize the value of backcrossing as a tool for the cotton breeder, and his work remains a milestone in the development of the genetical approach to cotton breeding. The classical example (in cotton) of backcrossing with a commercial aim is probably the transference, by Harland and Evelyn, of red plant body-weak spot from Trinidad Red Kidney to the Sea Island strain, V135, and, on the genetical side, the transference, by Harland (1935), of the gene R_2^{RS} from the diploid cotton *Gossypium arboreum* L. to the allotetraploid American Upland (*G. hirsutum* L.) U4. The fact that these, and all other, attempts at gene transference failed to produce commercially successful types, indicates faults in the technique employed, since it is unlikely that, in every case, the genes which it was desired to transfer had unbreakable deleterious linkages. This lack of success had made cotton breeders sceptical as to the value of backcrossing although the technique has been successful in other crops, and, in consequence, its possibilities have not been adequately exploited.

The following notes record the writer's experience of inter- and intraspecific backcrossing over a number of years, during which period four distinct genes from three different species of cotton* have been successfully transferred to two commercial strains of *G. barbadense* L., whilst several intraspecific transferences have been made in *G. hirsutum* L.

Theory of backcrossing

The usual object in backcrossing is gene transference, but the technique has also been employed to add genetic variability to existing cotton types in the hope that it might be possible, later, to isolate entirely new varieties of commercial value. Notable examples of this latter use are the assortment of crosses sent out to the African cotton experiment stations in 1932 by Harland and Evelyn (Evelyn & Harland, 1934). These hybrids were very heterogeneous and were derived from early backcrosses of accepted American Upland varieties and Jamaica Xerophytic, Gambia Native, or Galapagos Native, the backcross parent† being the American Upland type. The object, in this case, was to 'increase the genetic variability of U4 so that selection for any particular environment would be facilitated' (Evelyn & Harland, 1934), but, at the same time, to avoid the complete heterogeneity which would have resulted from straight crosses between these widely divergent types. Some of this material did not involve interspecific hybridization, and Ducker & Miller (1942) appear to be breeding successful varieties from (U4 × Cambodia) × U4 hybrids sent out by Harland and Evelyn at the same time as their interspecific crosses. Hutchinson (1938) suggests that 'an important reason for the lack of success of Harland's U4 hybrids' is that 'U4 itself was improved by selection so rapidly that the products of selection in the hybrid material usually failed to compete' This use of interspecific backcrossing to increase variability has yet to prove its value in cotton breeding and it is not proposed to deal with it in greater detail here.

In gene transference, the object is to move a single, dominant, or partially dominant, gene‡ (or a small number of such genes) from one cotton type to another, without deleteriously affecting the other qualitative or quantitative characters of the backcross parent variety. A general example would be the transference of a gene **A** from a donor parent§ variety Y to a backcross parent variety Z. The procedure would be to cross $Y \times Z$ and cross the F_1 back to Z, to produce a backcross progeny of **Aa** and **aa** plants. An **Aa** plant selected from this first backcross progeny would again be crossed with Z, giving the second backcross. This process should be repeated until the **Aa** plants in the backcross progeny

* Transference of the blackarm resistance genes $\mathbf{B}_1$ and $\mathbf{B}_2$ from *G. hirsutum* L., of the blackarm resistance gene $\mathbf{B}_3$ from *G. punctatum* Sch. & Thon. and of the *G. arboreum* L. gene R_2^{RS} from Harland's RU4 (*hirsutum* × (*barbadense* × *arboreum*)). In addition, other gene transferences are nearly completed. It is, perhaps, premature to call the R_2^{RS} transference successful, since spinning tests on the final backcross material are not yet available.

† *Backcross parent* (or recurrent parent): that parent of a hybrid with which it is again crossed or with which it is repeatedly crossed.

‡ It is also possible to transfer recessive genes by backcrossing but the procedure is laborious, since it is necessary to self after the first backcross in order to obtain homozygotes for further backcrossing. Third and fifth backcross selections would similarly be selfed. An alternative method is to select several plants in each backcross progeny for further backcrossing and to obtain self-bred seed from each. The selfed progenies would demonstrate whether or not any particular parent possessed the required recessive gene. Backcross progenies of those lacking this gene would be discarded.

§ Donor parent: that parent from which, by backcrossing, one or more genes are transferred to the backcross parent.

are indistinguishable qualitatively and quantitatively from their backcross parent, except for the presence of **A**. This process of elimination is shown in Table 1 (below).

Table 1. *Rate of elimination of donor genotype by backcrossing (neglecting the effects of selection and linkage)*

	Donor parent %	Backcross parent %		Donor parent %	Backcross parent %
F_1	50·0	50·0	6th backcross	0·8	99·2
1st backcross	25·0	75·0	7th backcross	0·4	99·6
2nd backcross	12·5	87·5	8th backcross	0·2	99·8
3rd backcross	6·3	93·7	9th backcross	0·1	99·9
4th backcross	3·1	96·9	10th backcross	0·05	99·95
5th backcross	1·6	98·4			

In the end-product of this hybridization a number of **Aa** plants would be selfed and the bulk self-bred seed sown. This would give a progeny consisting of 25 % **AA** : 50 % **Aa**: 25 % **aa** plants. Assuming the gene **A** to show only partial dominance, then the three genotypes would be phenotypically distinct.

The **Aa** and **aa** plants would be pulled up before flowering and the remaining plants (**AA**) would be bulked together to form the new strain. Had the gene **A** been fully dominant, instead of only partially dominant, the **Aa** and **AA** plants would have been phenotypically identical and a short progeny row from each plant of the **A** phenotype would have to be grown. All progenies producing a proportion of **aa** plants would be eliminated and the remaining rows would be bulked as the new strain.

The foregoing account gives the broad basis of the theory of backcrossing, but success or failure is largely a matter of attention to the finer points of technique dealt with below.

Application of backcrossing in cotton breeding

(1) *Pollen parent*

If possible, the hybrid should be the male parent and the strain to which it is being backcrossed, the female. The objects of this are threefold:

(*a*) Any pollen from the backcross parent accidentally left on the stigma would produce self-bred plants which would automatically be eliminated from the backcross progeny since they would not contain the gene being transferred. Their only effect would be to bias the genetic ratio.

(*b*) Each flower from the hybrid can be used to pollinate about ten prepared flowers on a pure-line family of the backcross parent.

(*c*) It is possible to grow at least two generations per year because the hybrid plants need only produce pollen which can be used on well-established 'mother' plants.

(2) *Female parent*

Hybridization cannot replace selection and, during the time taken to carry out a backcrossing programme, the plant selectionist will probably have improved the original variety used as the backcross parent. It is, therefore, essential to keep the backcrossing up-to-date. This is done by using, each season, the latest substrain of the parent variety for backcrossing.

The parentage of one of the blackarm resistant Sakel strains synthesized by the writer illustrates this point. The original objective was the production of a blackarm resistant

X1530 strain,* the resistance being derived from the American Upland type, Uganda B31, which contains the blackarm resistance factors $\mathbf{B}_1$ and $\mathbf{B}_2$ (Knight & Clouston, 1939). At the time this crossing was started, the substrain X1530A was replacing X1530 in the Gezira† area of the Sudan, and X1530B, the latest substrain, seemed a likely successor to X1530A. B31 was, accordingly, crossed with X1530B, but as this substrain failed, on test, to show superiority over X1530A, the first backcross was made to the latter strain. At this stage X1530E showed definite promise as a type for replacing X1530A, and the next two backcrosses were, accordingly, made to X1530E. During this time X1730 and its substrains had come to the fore in the Gezira, and X1530E, though the equal of X1730, did not go into commercial cultivation. (The X1730 type derives from the same "blood" as X1530 and the two strains are very similar in all characters (Lambert, 1938).) The next two crosses were made to the latest substrain of X1730. viz. X1730G, and subsequent crosses were made to X1730H. Thus the parentage of the first blackarm-resistant X1730 strain to go into commercial bulk was as follows:

$$\{[((B31 \times X1530B) \times X1530A) \times X1530E^2] \times X1730G^2\} \times X1730H^2.$$

(The superscripts denote the number of times each strain was used as a parent. For the sake of clarity, the practice of writing the female parent first has not been followed.)

Commerical bulk propagation was started from the seventh backcross progeny, and this is being replaced by ninth backcross material of the following parentage:

$$\{[((B31 \times X1530B) \times X1530A) \times X1530E^2] \times X1730G^2\} \times X1730H^4.$$

Omitting selection and linkage effects the percentage composition of these two commercial bulks should be as follows:

Strain	7th backcross	9th backcross	Strain	7th backcross	9th backcross
B31	0·39	0·10	X1530E	4·69	1·17
X1530B	0·39	0·10	X1730G	18·75	4·69
X1530A	0·78	0·20	X1730H	75·00	93·75

The value of the two final backcrosses lay, not so much in the elimination of B31 genotype (which was reduced from 0·39 to 0·10 %), as in bringing the type up-to-date by increasing the percentage of X1730H blood from 75·00 to 93·75.

A second example of keeping the backcross parent up-to-date is given by the blackarm-resistant NT2 strains bred at Shambat.‡ Bulk propagation was started from the fifth Sakel (fourth NT2) backcross. This fifth backcross material was completely satisfactory in its lint quality but was still heterogeneous for seed size and had too low a ginning outturn. Seventh backcross material replaced the fifth backcross in bulk propagation and this, in turn, will be succeeded by a final wave of ninth backcross origin, of the following composition:

$$[((B31 \times X1530B) \times NT2/36^2) \times NT2/37] \times NT2/38^6.$$

* X1530 is a strain of Sakel origin which was bred in the Sudan. Subselections from it were distinguished alphabetically; thus X1530A was the first advance on X1530, X1530B was a still later selection, and so on, the later the letter of the alphabet added to the strain number, the more modern the substrain.

† The Gezira is a tract of land lying between the Blue Nile and the White Nile. In this area about 200,000 acres of Sakel cotton are grown annually, irrigation being carried out by gravity flow from the Sennar Dam.

‡ Shambat is in the Northern Sudan in the immediate vicinity of Khartoum.

Omitting selection and linkage effects, the percentage composition of these three bulks should be:

Strain	5th backcross	7th backcross	9th backcross
B31	1·6	0·4	0·1
X 1530 B	1·6	0·4	0·1
NT2/36	9·4	2·3	0·6
NT2/37	12·5	3·1	0·8
NT2/38	75·0	93·8	98·4

(The NT2/38 parent of these crosses was reselected for leaf-curl resistance each year but was not given a new number.)

This question of using, each year, the latest selection of the backcross parent strain may seem to have been unduly stressed. The point, however, is of paramount importance, and it has not received the attention it merits in hybridization programmes.

To sum up, the final backcrosses are relatively unimportant in eliminating the genotype of the donor parent but are essential in bringing the strain up-to-date. Thus, though the eighth, ninth and tenth backcrosses together remove only 0·35 % of the donor parent genotype, they put in 87·5 % of the 'blood' of the latest subselections.

(3) *Progeny size*

Where single gene transference is the object, the question whether to use small or large progenies arises. Each system has its advantages in certain circumstances, but the small progeny method is of more universal application.

(*a*) *Small progenies*. Where a single, easily distinguished gene is being transferred, only one selection, for further backcrossing, need be made in each backcross progeny, and it is therefore only necessary to grow a family sufficiently large to guarantee the presence of one such plant, with a margin of safety to allow for possible poor germination and insect damage. For determination of family size Mather's (1938) Table 3 is excellent and the following figures for 1 : 1 and 3 : 1 expectations are taken from it.

Table 2. *Size of family requisite to give at least one plant containing the transferred gene*

Ratio expected	Level of probability						
	0·900	0·950	0·980	0·990	0·995	0·998	0·999
1 : 1	3·3	4·3	5·6	6·6	7·6	9·0	10·0
3 : 1	8·1	10·4	13·6	16·0	18·4	21·6	24·0

The numbers in the body of Table 2 show, for various levels of probability, the size of progeny which should be grown in order to produce at least one plant containing the gene or genes being transferred. It will be seen that a family of ten plants is adequate ($p = 0{\cdot}999$) to ensure the presence of the required type in a backcross where a single gene is being transferred; in a backcross involving a two-factor transference, a progeny of twenty-four plants would be desirable. These figures refer to *plants*, and suitable allowance must be made at sowing time to cover risks of poor germination and pest damage.

(*b*) *Large progenies*. Where research and breeding must be concurrent, through a lack of genetical knowledge of the character to be transferred, large progenies are essential. Wide basis backcrossing is also suited to interspecific crosses where the differences in appearance are great (e.g. in most *hirsutum* × *barbadense* crosses), since it is possible, by using large progenies, to speed up the elimination of the donor genotype. For the first two or three backcrosses very large progenies are grown—a thousand plants, if possible. All plants not possessing the factor, or factors, being transferred, are pulled up. The remaining plants are then rogued severely on their vegetative similarity to the backcross parent type. The most off-type plants are removed first, the process being repeated till only a few plants are left. If a single factor is being transferred, these remaining plants can be rogued down to some four or five, one of which is chosen for crossing and the remainder kept as spares. This process of severe roguing (or selection) is of great importance in eliminating the genom of the donor parent, since the culling of plants showing donor parent characters automatically removes not only the genes concerned but also, presumably, a relatively large segment of chromosome in the immediate vicinity, since cotton averages only 1·7–1·8 chiasmata per bivalent.

After the second or third backcross, the material is usually so near the backcross parent in appearance that large progenies possess little or no advantage. Small progenies become just as effective in eliminating any of the donor genotype which may remain, and much time and unnecessary labour are saved.

This system is valueless in intraspecific crosses because such hybrids, by the first backcross, are normally very similar vegetatively to the backcross parent. This is one of the dangers of hybridization—the hybrid may look like the backcross parent but it still contains a large proportion of the donor genotype and is unlikely to breed true for the various qualitative and quantitative characters desired.

To sum up: the most profitable size of backcross progeny to grow depends on the number of visible character differences between the original parents. Where a large number of differences exist these give a valuable basis for selection for the elimination of the donor genotype. Hence with many such visible differences the best policy is to grow large early backcross progenies and to concentrate on selection as a means of rapidly removing the donor genotype. Large progenies are best obtained by treating a pure line of some fifty plants of the backcross parent type as one female parent. With few visible differences between the parents it is advisable to grow small backcross progenies and to concentrate on the elimination of the donor genotype by making as many backcrosses per year as possible.

(4) *Basis of selection in hybrids*

Selection in backcross progenies should be limited to vegetative characters *not* lint, except where the object is lint improvement and lint genes are being transferred intentionally. The aim should be complete similarity to the backcross parent and the avoidance of all forms of hybrid vigour, such as increased yield or longer lint. Frequently F_1 types have excellent lint, and a too early use of lint as a basis for selection might merely mean that the more heterozygous plants were being selected. On the other hand, differences in plant appearance are, presumably, due to numerous genes, and their elimination would involve the removal of numerous unwanted chromosome segments. Lint examination can be made when vegetative similarity is attained but, even then, lint length and quality should be used more as a measure of success than as a basis for selection. Bulk seed from unselected plants in the later backcrosses is used to sow trial plots from which lint samples can be obtained for spinning and grading (see next section).

(5) *The end-point*

A major difficulty in backcrossing is to know when to cease crossing and start bulking; several promising hybridization programmes have failed for lack of a method of determining the correct end-point. Usually an arbitrary point, such as the fourth backcross, seems to be chosen for bulking, and the failure of the bulked product attributed to a deleterious linkage. Such a linkage might exist, but it would be desirable to prove its presence more conclusively before discarding one's breeding material.

An arbitrarily chosen end-point would probably be completely satisfactory in flower breeding or in hybridization work on many food crops. The cotton breeder, however, has a much more complicated problem: not only must he watch such 'agricultural qualities' as vigour, yield and ginning out-turn, but also lint quality—spinning quality, strength, staple, lustre, colour, fineness and 'feel'; even the percentage of oil in the seed is of commercial importance. In the better quality cottons (Sea Island and Sakel) the market will only permit variation of lint quality within very narrow limits. It is for this reason that no arbitrary end-point for backcrossing can be fixed—the breeder of long stapled cottons must obtain as his product a strain entirely unaltered as to its quality, etc., except for the effect of the gene, or genes, intentionally transferred.

No question of bulking should arise until the backcross progeny is vegetatively homogeneous, except for the presence or absence of the transferred gene. When homogeneity is attained *backcrossing should be continued*, but at the same time bulk seed of all **aa** plants in the progeny should be collected. A second bulk should be made consisting of seed of all the **Aa** plants. These two bulk seed lots should be put into a yield trial (or, if the seed is inadequate, into a replicated trial for lint test) with the backcross parent type as control. The seed from the **Aa** plants would, of course, produce a mixture, but this should contain enough **AA** and **Aa** plants to show any major faults due to linkage or to pleiotropic effects. If the lint (or other characters) of this **AA**, **Aa**, **aa** mixture is below the backcross parent standard, the failure may either be due to linkage or to the portion of the donor parent genotype still remaining in the hybrid. The comparison between the **aa** plots and the backcross parent strain will show whether or not the failure is due to linkage (and/or pleiotropy). A scheme of backcrossing should not be abandoned unless the homozygous recessive material (the **aa** bulk) is qualitatively and quantitatively indistinguishable from the parent type and the heterozygous (**Aa**) bulk a failure. Even then one more test on a later backcross would definitely be desirable before finally discarding the material. If both types fail (as will most likely happen), the test should be repeated on successive backcrosses until either the presence of deleterious linkage is proved or the heterozygous bulk is found to be the equal of the backcross parent strain. At this stage bulking should be started, and, since backcrossing will have gone on whilst the foregoing tests were being made, the type bulked will be one backcross ahead of the type which succeeded.

Where it is proposed to use the product of this backcrossing as a female parent in integrating a still newer strain, it is advisable to take the backcrossing one or more stages further. Thus a Sakel strain to which **A** has been transferred by five backcrosses may prove to be a commercial success and be propagated in bulk. Later it may be decided to add, say, a Tanguis gene for jassid resistance and a *punctatum* gene to increase blackarm resistance using the **AA** Sakel as backcross parent. These additional crosses may well fail if the fifth Sakel backcross **AA** material is used as backcross parent because the percentage of donor blood left in this successful fifth Sakel backcross may be fatal when there is added to it the residual percentages from the Tanguis and *punctatum*. For this reason it is advisable to carry out two or more apparently unnecessary additional backcrosses in order to remove as much as possible of the donor blood from the **AA** Sakel before using this as a backcross parent.

(6) *Additive factors*

In transferring two or more factors with additive effect, it may be necessary, or at least desirable, to separate them and deal with each individually to avoid the danger of the accidental loss of one of them. Where the additive effect is marked, so that there is no possibility of confusing the **AaBb** phenotype with either the **Aabb** or the **aaBb**, then obviously, separation of the two genes would merely entail extra labour. Where, however, the **AaBb** phenotype merges into either, or both, of the others, separation is likely to save considerable labour, since the plant breeder will only need to deal with two families per generation—a backcross progeny containing **Aa** and **aa** plants and a progeny consisting of **Bb** and **bb** plants. In each of these families he will only require one selection for further backcrossing—an **Aa** plant and a **Bb** plant. Had the genes not been separated, far more selections would have had to be backcrossed to avoid the danger of losing a factor (Table 2).

When the end-point is reached the two factors are recombined by crossing the **A** and **B** strains together, backcrossing to the strain containing the weaker factor, selfing, selecting and reselecting. Thus suppose **A** and **B** are dominant genes showing weak additive effect with **A** the weaker factor of the two. Then **AA** and **BB** strains are crossed and the F_1 backcrossed to the **AA** strain. This should give:

(i) 1**AABb** : 1**AaBb** : 1**AAbb** : 1**Aabb**

The last two genotypes in (i) will have the same appearance and, since they contain only the weak factor **A**, plants belonging to this group can be discarded.

Plants of **AB** phenotype should be selfed and their progenies grown in rows. All rows containing a proportion of bottom recessive (**aabb**) plants should be discarded. The remaining rows should show a 3 : 1 ratio of **AB** plants to **A** plants as follows:

(ii) 1**AABB** : 2**AABb** : 1**AAbb**

This ratio will be clear-cut and easily seen because, although **B** plants and **AB** plants might overlap in phenotypic appearance, the **AB** phenotype will be distinct from the group containing only the weak factor **A**.

All **AAbb** plants in (ii) should be discarded and a number of the remaining plants selfed for sowing in progeny rows. All *rows* containing the **A** phenotype should be pulled up; the remainder would be of **AABB** composition and would constitute the first bulk plot of the new variety.

This problem of additive factors is best illustrated by a concrete example. The blackarm resistance factors B_1 and B_2 (both dominant) are a case in point. Factor B_1 imparts weak resistance to Sakel whilst B_2, alone, confers considerable resistance. Although B_2 resistance is slightly increased by the further addition of B_1, it is impossible, in material derived from late backcrosses, to distinguish with certainty between B_1B_2 and b_1B_2 plants or to identify the progeny of a $B_1B_1B_2B_2$ plant as distinct from that of a $B_1b_1B_2B_2$ plant. Yet, the slight extra degree of resistance conferred by the addition of B_1 should be of economic importance when the cotton is grown on a commercial scale.

The method of solving this problem has been to backcross B_1 and B_2 separately to Sakel, to cross the end-products and backcross to the B_1B_1 type. The progeny of this cross consisted of $B_1B_1B_2b_2$, $B_1b_1B_2b_2$, $B_1B_1b_2b_2$ and $B_1b_1b_2b_2$ plants in equal numbers. The last two genotypes, being only weakly resistant, were uprooted. A number of plants showing strong resistance ($B_1B_1B_2b_2$ and $B_1b_1B_2b_2$) were selfed and sown in progeny rows. All rows containing a porportion of fully susceptible plants were pulled up. The remaining progenies displayed a ratio of three very resistant plants to one with weak resistance. The weakly resistant plants were removed and a number of the markedly resistant plants selfed. Progeny rows were sown from these plants. All progenies containing a proportion of weakly resistant plants were uprooted and the remaining progenies bulked as the new resistant strain, all the plants in them being of $B_1B_1B_2B_2$ composition.

(7) *Linked factors*

Where two linked factors are to be transferred from one variety of cotton to another, it is advisable to select cross-overs in the first backcross progeny as parents for further backcrossing. This enables the plant breeder to handle each gene separately and the separation of the two genes facilitates the elimination of the segment of donor parent chromosome between them.

(8) *Blending inheritance*

Blending inheritance is common in hybridization work with cotton. Its presence is apt to suggest that inheritance of the character concerned is based on a complex of cumulative genes with small individual effect. It may be, however, that the character is, in the main, governed by one or two major genes and that the genetic ratios are masked by numerous minor genes and modifying factors. Such minor genes may have a stronger effect on the bottom recessive in a cross than on plants containing the major genes governing the character, and, for this reason, although they are strong enough to mask the scheme of inheritance, such genes are often of slight economic value. As there is no known technique whereby a host of minor genes can be transferred from variety to variety, such genes are best eliminated since their presence will only confuse the issue.

Blending inheritance may mean that, on our present state of knowledge, the character concerned is not transferable from one variety to another. The point is that, because no clear-cut segregation appears in the early stages of a hybridization programme, it does not *necessarily* follow that the character cannot be transferred. It may prove impossible to transfer it in the full strength which it displayed in the donor parent, but at least some portion, possibly the major portion, of it can probably be transferred. A plant breeder, faced with blending inheritance in a first backcross, should select, for further backcrossing, plants showing the maximal effect of the character required, in the hope that, in later backcrosses, clear-cut ratios will be obtained.

(9) *Bulk propagation*

(*a*) *Full dominance.* The first decision to be made is the size of propagation plot to be sown. Under irrigation conditions, an acre plot, sown at a spacing of 90 × 90 cm. at one seed per hole, requires about 4200 seeds. At Shambat, an average Sakel plant sown at normal crop time should yield upwards of 250 self-bred seeds and, winter sown, it should give about 200 such seeds provided suitable precautions are taken. To produce 4200 seeds of **AA** composition from a winter sown backcross F_2 therefore needs a family containing at least 21 **AA** plants, so that the total F_2 population must not be less than 80–90 plants. The F_2 is grown out-of-season (winter) and recessive (aa) plants are eliminated. All plants belonging to the **A** phenotype are selfed and given serial numbers. As soon as two or more bolls have opened on all plants, progeny rows are sown, each progeny consisting of ten holes sown with three seeds per hole. These rows are examined and all numbers containing any recessive (**aa**) plants are noted. The parents of these particular rows are then pulled up from the F_2, leaving only plants homozygous for **A**. Seed from these plants sows the bulk propagation plot. In this plot the individual progenies are kept separate as an additional safeguard.

Using this technique, it is possible to produce, from a small backcross progeny in one season, seed for several acres propagation area of homozygous material in the next season. Seed from the heterozygotes in the F_2 can be usefully employed in a small yield or lint trial (see § (5), 'The end-point'). Where only small plots are required, the F_3 progeny rows can, themselves, be used as the propagation area after removing 'splitting' progenies.

(*b*) *Partial dominance.* Where the transferred gene though not recessive, lacks full dominance, bulk propagation is simplified. To avoid selfing, the backcross F_2 should be sown in an isolated position. **Aa** and **aa** plants should be pulled up and the **AA** plants left to produce bulk seed of the new strain for further propagation.

(10) *Purity of backcross parent*

The foregoing account of backcross technique suited to cotton breeding is based throughout on the assumption that a pure breeding, homogeneous variety is being used as the backcross parent. Backcrossing is only one of the tools of the plant breeder, it is not a complete system of plant breeding in itself and the plant selectionist must first have produced pure strains before backcrossing can be used at all. A strain showing marked heterogeneity would be useless as a backcross parent but it should be possible, by suitable modifications of technique, to transfer genes to a variety showing a certain amount of heterogeneity. The technique would be to start with several F_1 families, each arising from a cross between the donor parent and a different plant in the backcross strain. These F_1 families would then each be backcrossed separately, on the 'small progeny' system previously described, and the end-products bulked. For a strain showing only slight heterogeneity, probably three or four separate lines of backcrossing would be sufficient; obviously the number required would increase with the degree of variation shown by the backcross parent strain. In backcrossing each 'line' it would be preferable to use 'bulk backcrossing' rather than to select a single **Aa** plant in each line. The **aa** plants in each progeny would be eliminated and the **Aa** plants treated as a single male parent for use in pollinating the recurrent parent.

SUMMARY

Backcrossing, though successful in other crops, has, in the main, failed to produce economic results in cotton. The use of the technique discussed in this paper has produced several commercially successful interspecific gene transferences. The following suggestions are made:

1. The hybrid should be the male parent.

2. The latest substrain of the backcross parent variety should be used each season as female parent to keep the crossing programme up-to-date.

3. Where a large number of visible differences exist between the original parents, these provide a valuable basis for selection. In such a case large early backcross progenies should be grown and severe selection in the field utilized to accelerate the removal of the

donor parent genotype. With few visible differences between the parents it is advisable to grow small backcross progenies and to concentrate on the elimination of the donor genotype by making as many backcrosses per year as possible.

4. Selection of hybrid plants for further backcrossing should be made solely on (*a*) presence of transferred gene and (*b*) vegetative similarity to the backcross parent. All characters likely to be due to heterosis should be avoided, e.g. longer lint or higher yield than the backcross parent.

5. An arbitrary end-point in backcrossing should be avoided. The criterion should be a replicated test of bulk seed from heterozygotes from the backcross, against bottom recessives from the backcross, against the backcross parent as control. When the heterozygous bulk is qualitatively and quantitatively equal to the backcross parent, bulk propagation and large scale testing should be started.

6. Cumulative factors with only slight additive effect should be separated in backcrossing and recombined later.

7. Linked factors are best separated to facilitate the elimination of the donor parent chromosomal segment between them.

8. The appearance of blending inheritance in a first backcross need not discourage a plant breeder since inheritance of the character may still be mainly due to one or two major genes and clear-cut ratios may appear in later backcrosses.

9. A method of bulk propagation from a backcross progeny via an out-of-season backcross F_2 to an F_3 homozygous propagation plot in the following season, is discussed.

10. A technique is suggested for transferring genes to a strain showing moderate heterogeneity.

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