BACK CROSSING

The Theory and Practice of the Backcross method in the breeding of some non-cereal crops

by

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TECHNICAL COMMUNICATION 16

Commonwealth Plant Breeding

Bureau of and Genetics

Cambridge

1952
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CHAPTER I

THE THEORY OF BACKCROSSING

In straight hybridization, that is the production of \(F_1\), \(F_2\), \(F_3\), \(F_4\) generations and so on by selfing or open pollination, the hybrids in each generation contain equal or approximately equal numbers of genes from each of the original parents. If however the \(F_1\)'s are crossed with one of the parents instead of being selfed or crossed among themselves, the plants of the next generation will have three times as many genes from one parent as from the other. In other words \(\frac{3}{4}\) of the genes of the first backcross hybrids will be from the recurrent or backcross parent and \(\frac{1}{4}\) from the non-recurrent or donor parent. If another backcross to the recurrent parent is carried out, the resulting hybrids will have \(\frac{7}{8}\) of their genes from the recurrent parent and \(\frac{1}{8}\) from the donor parent, in the third backcross only \(\frac{1}{16}\) of the genes will be from the non-recurrent parent, in the fourth backcross only \(\frac{1}{32}\) and so on. Thus each successive generation is more like the recurrent parent and less like the non-recurrent parent than the previous one. The backcross method is therefore specially suitable for obtaining a new variety which differs from an existing variety by only a small number of genes determining some desirable character which is lacking in that variety but present in some other which can be used as the donor parent. In a programme of repeated backcrossing designed to transfer a character from one variety to another, this character must be preserved in successive generations by selection.

The ease with which such selection can be carried out depends of course on whether the character is dominant or recessive. The simplest case is that of a character dependent on a single dominant gene. If this gene is designated \(A\), the hybrids in the backcross to the \(aa\) parent will consist of plants with the constitutions \(Aa\) and \(aa\). The former can easily be picked out and used as parents for the next generation.

When the character to be transferred is recessive the heterozygotes cannot be distinguished by their appearance from the double dominants. If the hybrids are selfed however the heterozygotes can be recognized by the fact that their progeny segregate with respect to the required character. Alternatively the hybrids may be crossed with the non-recurrent (double recessive) parent to find out which are the heterozygotes. If
Backcrosses are not made until the constitution of the hybrids has been determined they can be made only in alternate seasons, but time can be saved by carrying out backcrosses and test crosses simultaneously and afterwards discarding those backcrosses involving hybrids not carrying the required gene.

Ideally backcrossing might be continued until the genetic constitution of the hybrids was identical with that of the recurrent parent except for the one gene transferred from the non-recurrent parent. But it is possible that other genes possibly undesirable may be so closely linked with the gene it is intended to transfer that they cannot be eliminated without losing also the gene which is required. This situation may defeat the programme.

When several genes are to be transferred from one variety to another it is usually advisable, when they have recognizable individual effects, to transfer them separately and then bring them together by intercrossing the hybrids. When minor or modifying genes are to be transferred it is necessary to grow large progenies and to avoid intensive selection for the characters of the recurrent parent during the early generations since this may lead to the loss of some of the genes required.

When the original cross is interspecific it is usually necessary to make a relatively large number of backcrosses so as to eliminate practically all the genes of the donor parent except those to be transferred. In crosses between closely related varieties however the parents will have many genes in common and less of those contributed by the donor parent need be eliminated. Sometimes only one or two backcrosses are made, the aim being to introduce genetic variability into a variety rather than to transfer one particular character to it.

Backcross hybrids are, of course, heterozygous for the gene or genes from the donor parent. In crops propagated by seed it is necessary to attain homozygosity. This is done by selfing in the case of self-fertilized crops and if the character is dominant, selecting those lines which breed true when selfed again. If the character is recessive the homozygotes are recognizable without selfing a second time. In cross-fertilized crops the heterozygous backcross hybrids are crossed among themselves. The homozygous offspring may then be recognized, if the character is dominant, by the fact that they do not segregate in crosses with the double recessive.

The backcross method has the great advantage that it makes possible the introduction into commercial varieties of desirable characters from species and varieties which are otherwise undesirable and could not be made use of in straight hybridization.
This is especially valuable when economically important characters such as resistance to various diseases are not present in cultivated varieties but can be found in related wild species. Harlan and Pope (7) who used the backcross method for transferring the smooth awned character to Manchuria barley from the variety Lion are generally regarded as the first to suggest and use this technique. But J. O. Ware (14) refers to its having been employed by John Griffin of Greenville, Mississippi, in breeding work leading to the production of the cotton variety Griffin as early as 1867, long before the genetical implications of backcrossing were realized.

As soon as Harlan and Pope had pointed out the possible value of the backcross method, F. N. Briggs began to apply it to wheat breeding. Among other things he transferred the bunt resistance of Martin, which is governed by a single dominant gene, to other wheat varieties grown in California (2, 4). He has published several papers on the backcross method (2–6) in which he is particularly concerned with the rate at which successive generations become homozygous. This has also been discussed by Miles (9) and by Ayachit (I).

Sapehin (12), Roemer (11) and Patel (10) have pointed out the advantages of the backcross method, and Temovskii (13) and Knight (8) have discussed the method with special reference to the breeding of tobacco and cotton respectively. Wellensiek (15, 16) has discussed the application of the backcross technique in different sets of circumstances.

The work of Briggs and others on the use of backcrossing in cereals is fairly generally familiar and in this publication we are concerned with the application of the method to the more important non-cereal crops in which it has been extensively used, namely cotton, tobacco, tomatoes and potatoes.

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CHAPTER II

THE BACKCROSS METHOD IN COTTON BREEDING

I. INTRODUCTION

The species of *Gossypium* are divided into two groups on the basis of their chromosome numbers: the tetraploids with \(2n = 52\) chromosomes and the diploids with \(2n = 26\). Within the first of these groups are the New World cultivated species *G. hirsutum* (the Upland, *punctatum* and *Marie-galante* types), *G. barbadense* (the Peruvian type) and the wild Hawaiian species *G. tomentosum*. The second includes the Old World cultivated cottons *G. arboreum* and *G. herbaceum* and four groups of wild species. By means of the backcross method the transference of genes has been effected not only between varieties and between species with the same chromosome number but also between diploids and allotetraploids.

It is of interest to consider hybridization between New and Old World cottons in terms of the genomes involved. There is evidence, part of which is mentioned in this chapter, that cultivated Asiatic diploids and wild American diploids have taken part in the evolution of New World cultivated cottons in the way indicated by applying the genome formulae \(AA\), \(DD\) and \(2(AD)\) respectively to these three groups. Patel, Thakar and Deodikar (152) have suggested that since \(F_1\) hybrids between New World cultivated tetraploids and cultivated Asiatic diploids can be backcrossed to New World cottons the \(F_1\) allotriploids, having the constitution \(A(AD)\), probably produce gametes with the constitution \(AD\), but Skovsted has shown that the chromosome numbers of the viable gametes approach that of the triploid \(A(AD)\).

In using the backcross method the breeder is working in the dark unless he knows the genetics of the characters he wishes to transfer. The magnitude of his task depends, as we have said, on the number of genes involved and on their linkage relations.

Realizing the need for such information, several investigators, among which S. C. Harland and R. L. Knight may be specially mentioned, have, over the past 25 years, studied the inheritance of various characters in cotton, with the result that we now
have a much better theoretical basis for practical cotton breeding experiments.

In view of the large number of backcross projects which have been and are being carried out it may seem surprising at first sight that so few have resulted in the production of commercially useful strains. J. B. Hutchinson points out the following reasons for this. Most of the early projects either were studies in pure genetics or were undertaken to explore the genetic implications of the technique and from the nature of the material used were unlikely ever to be of anything but genetic interest. S. C. Harland's gene transfersences tabulated on page 9 fall into this category. Many of the backcross transfersences undertaken for purely practical reasons have also failed to produce anything of commercial value, and in this class of experiment the main reason for failure has been the fact that the backcross lines have been surpassed by other breeding stocks which developed more quickly. The fate of Harland's early U4 x Cambodia material (cf. p. 22) illustrates an important lesson in the use of the technique. Straight selection in U4 led to greater improvement than was to be realized in the hybrid material and nothing that could compete with the newer issues of U4 seed was ever bred from Harland's original crosses. Nevertheless Harland's crosses were of real value in pointing the way to later improvements, as the variability of U4 was eventually almost exhausted and fresh crosses were then made with Cambodia. Improvement in backcrosses of this parentage was more rapid than in U4 and gave rise to the very successful strain A2106 (cf. p. 25). In R. L. Knight's recent work in the Sudan, the risk that the hybrid stocks would be left behind by straight selection in other stocks of the recurrent parent has been obviated by insisting on the use of the most recent selection of the recurrent parent in each backcross generation.

II. EARLY EXPERIMENTS CONCERNING MARKERS AND OTHER CHARACTERS

S. C. Harland is generally recognized as the pioneer in applying the technique of repeated backcrossing to cotton breeding. Part of his work at the St. Vincent Experiment Station has been concerned with the introduction of marker characters into lines of cotton so as to facilitate the maintenance of purity. If a strain is "tagged" with a particular combination of recessives, natural crosses and most of their progeny can easily be distinguished. In order to "tag" Sea Island cotton (G. barbadense) he introduced into it the red plant body and spotless or weakly
spotted corolla of a Peruvian cotton (also *G. barbadense*) (99, 92, 93, 86). Segregation in crosses between Sea Island or Egyptian and Red Tree cotton of the Peruvian type was as shown below:

<table>
<thead>
<tr>
<th></th>
<th>Sea Island</th>
<th>Red Tree Cotton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green plant body</td>
<td>Strong petal spot</td>
<td>Red plant body</td>
</tr>
<tr>
<td>Strong petal spot</td>
<td></td>
<td>Weak petal spot</td>
</tr>
</tbody>
</table>

\[ F_1 - \text{Red plant body} \]
\[ \text{Strong petal spot} \]

\[ F_2 - 1 \text{ Red plant body} \]
\[ 2 \text{ Red plant body} \]
\[ 1 \text{ Green plant body} \]
\[ \text{Weak petal spot} \]
\[ \text{Strong petal spot} \]
\[ \text{Strong petal spot} \]

Thus, crosses of a Sea Island strain having red plant body and weak petal spot with the normal Sea Island type could easily be eliminated in the field. After four backcrosses to Sea Island the hybrids had the red plant body and weak petal spot character but were otherwise similar to pure Sea Island. Presumably several desirable genes had been introduced from the Red Tree cotton, for some of the red Sea Island strains obtained exceeded normal V 135, the parental Sea Island type, in lint weight per seed and per boll and in ginning percentage, although they were somewhat inferior in respect of number of bolls per tree and spinning quality (85, 88, 90). It was also observed that, compared with V 135, they showed quicker germination and more vigorous early growth and a better root system, enabling them to resist high winds (87, 92). Selections were made for a combination of superfine lint, high lint index and high ginning percentage, for very long lint and for the highest number of bolls. A detailed analysis of the best selections was made in the 1936–37 season (89). A plant with a lint length of 57 mm. selected in the first season of the trials in St. Vincent formed the original parent of all the subsequent selections in this programme. Later backcrosses of its progeny proved inferior to selections from the selfed progeny of the second backcross and were therefore discarded. Unlike previous tests, trials conducted in 1938 showed that the hair weight and spinning value of the material were typical of "ordinary" and not superfine Sea Island. Though superior to V 135 in germination and certain yield characters it was still inferior as regards bolling (91). The following year it proved significantly inferior as regards yield of seed cotton per plot and could not be considered as a possible substitute for Superfine V 135 in spite of its higher ginning percentage and lint index (135). Although none of the Red Sea Island strains was introduced into commercial cultivation,
the production of them was nevertheless a significant step in the progress of cotton breeding in that it showed to some extent the possibilities and limitations of the backcross method as applied to this crop and gave results which encouraged the use of the technique in other breeding projects.

The gene transference just described was carried out within the species *G. barbadense*. We turn now to the interspecific transference of marker genes. Prior to the use of the backcross technique all attempts to combine the desirable characters of two species had failed. For instance, in experiments to produce strains with the large bolls of Upland cotton and the lint quality of Egyptian or Sea Island a promising $F_1$ was obtained, but the $F_2$ gave very unsatisfactory types, and even after selection for three or four generations the desired combination of characters could not be obtained (97).

In 1929 Harland obtained a partially fertile hybrid between a Sea Island–Egyptian $F_1$ with $n = 26$ chromosomes and a red flowered strain of the Old World $n = 13$ species, *G. arboresum* (98). In successive backcrosses to New World cotton the fertility of the hybrids increased until a fully fertile New World type carrying the $R$ gene from *G. arboresum* was obtained (101). The first backcross had to be made to a *G. barbadense* x (*G. barbadense* x *G. hirsutum*) hybrid since attempted crosses of the $F_1$ to pure *G. hirsutum* or *G. barbadense* were not successful. In the *G. arboresum* genotype $R$ was responsible for red plant body, red flower and intense petal spot; when transferred to *G. hirsutum* it caused less intense red coloration of the plant body and flower and no petal spot. It was concluded from the results that this gene, which was already known to be a member of the multiple alleomorphic series of genes governing anthocyanin pigmentation in Asiatic cottons had become an allelomorph in a similar series in New World cotton. The different phenotypic expression in the two types of cotton was attributed at the time to the influence of modifiers but Silow showed later that loss of the red spot was due to $R$ becoming mutable when transferred to *G. hirsutum*.

Again other useful genes in addition to the $R$ gene were also transferred, for according to Evelyn (85, 86, 88, 91) backcrosses to U4 carrying the marker character were outstanding for early maturity, almost complete immunity from angular leaf spot (blackarm caused by *Xanthomonas malvacearum*), the presence in some cases of clean seeds, and, in many of them, of higher yields and lint of better quality and staple length than that of U4. One plant matured in $3^{1/4}$ months as compared with the normal
6 months for New World cottons in that area. Selfed seed of the best strains was distributed for trial in India and Africa. As reports from stations to which material had been sent indicated that it was susceptible to jassid (Empoasca spp.) attack because not sufficiently hairy, selection in 1936–37 was carried out on the basis of hairiness and early maturity. The best strains were intercrossed and many of them were again backcrossed to U4 (90).

Early maturity was also exhibited by selfed selections of a fifth backcross of Asiatic × New World cotton to the Upland variety Triumph, from which they inherited high yield of lint per boll and per seed (85, 88).

The following are some other transferences of genes reported by Harland (100). It will be seen from the remarks that some deterioration in the economic qualities of the cotton is often involved.

<table>
<thead>
<tr>
<th>Character</th>
<th>Transferred from</th>
<th>Remarks on new type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hairiness</td>
<td>G. tomentosum to G. barbadense</td>
<td>Intensely hairy (longish hairs)</td>
</tr>
<tr>
<td>Hairiness</td>
<td>G. tomentosum to G. hirsutum</td>
<td>Very hairy (short hairs)</td>
</tr>
<tr>
<td>White lint</td>
<td>Sea Island to Egyptian</td>
<td>Pale brown with longer lint than Egyptian</td>
</tr>
<tr>
<td>Brown lint</td>
<td>Egyptian to G. hirsutum</td>
<td>Very pale brown lint</td>
</tr>
<tr>
<td>Laciniated leaf</td>
<td>Upland to Sea Island</td>
<td>More laciniated and weak</td>
</tr>
<tr>
<td>Long lint</td>
<td>Sea Island to Upland</td>
<td>Lint length reduced to about 41 mm.</td>
</tr>
<tr>
<td>Naked seed</td>
<td>Upland to Sea Island</td>
<td>Practically lintless</td>
</tr>
<tr>
<td>Red leaf</td>
<td>Upland to Sea Island</td>
<td>Red, much weakened</td>
</tr>
<tr>
<td>Crinkled</td>
<td>Sea Island to Upland</td>
<td>Less vigorous and productive</td>
</tr>
<tr>
<td>Red leaf</td>
<td>Kidney tree cotton to Sea Island</td>
<td>Little change</td>
</tr>
</tbody>
</table>

These transferences are all within the New World, $n = 26$, group of cottons. The following, like that of the $R$ gene from G. arboreum to G. hirsutum to which reference has already been
made, are from $n = 13$ to $n = 26$ chromosome types, the diploids in these cases being wild American species (103, 104).

<table>
<thead>
<tr>
<th>Character</th>
<th>Transferred from</th>
</tr>
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<tr>
<td>Normal (Cr)</td>
<td><em>G. aridum</em>, <em>G. Armourianum</em> and <em>G. trilobum</em> to <em>G. barbadense</em> having the gene $c^t$ for crinkled.</td>
</tr>
<tr>
<td>Petal spot</td>
<td><em>G. aridum</em> to <em>G. barbadense</em> and <em>G. hirsutum</em>.</td>
</tr>
<tr>
<td>Petal spot</td>
<td><em>G. Armourianum</em> to <em>G. barbadense</em>.</td>
</tr>
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</table>

The $F_1$ hybrids between the cultivated and wild species were partially fertile on the male side. Complete fertility was obtained after two backcrosses to *G. barbadense* or *G. hirsutum*.

An interesting theoretical aspect of these intergroup transfers of genes is the support they give to the viewpoint referred to above that both Asiatic and wild American diploids have been involved in the evolution of the New World amphidiploids. It will be seen that each of the three diploid species was found to carry a normal allele of crinkled. The different expression of genes in different genetic backgrounds is another point of interest. In the third and subsequent backcrosses to *G. hirsutum* the *G. aridum* petal spot gene became mutable (104). This differential effect of genomes on gene stability has also been observed in backcross hybrids within the New World amphidiploid group. Harland found for example that the somatic mutability of the *G. purpurascens* petal spot gene $S^p$ increased when it was transferred to *G. hirsutum* (102). This increase in mutability was observed in the second and third backcrosses, whereas the stability of the gene was little affected in the first backcross. The *G. hirsutum* petal spot gene, $S^H$ proved slightly mutable in both *G. hirsutum* and *G. barbadense*.

Other work by Harland will be referred to further on in this chapter.

III. BREEDING FOR GOOD FIBRE CHARACTERS

Some of the early experiments on backcrossing were carried out at the Cotton Experiment Station, Sigatoka, Fiji, where, in the 1928–29 season, natural hybrids between Sea Island and Kidney cotton introduced from New Guinea and subjected to selection in Fiji (53, 54) were backcrossed to Sea Island, the object being to improve the length and texture of their lint (55, 61, 80).
One backcross yielded remarkably well in the following year and two new first backcrosses were made (56). The promising results were maintained in 1930–31 when more than twice the yield of Sea Island was secured from the progeny of selfed backcross hybrids (57). Samples sent to England for testing were classed, in the preliminary examination, as good grade, creamy colour, 13/4 inch staple, strong, moderately fine and lustrous, and nominally valued at 11/2d. below Extra Fine Sakel. Subsequent spinning tests at the Shirley Institute showed that the fibre of the hybrids was appreciably longer than the best Sakel but considerably weaker.

Selection was continued (58), and in the 1932–33 season more samples were sent to the Shirley Institute. Of these Type 172 showed the most promise.

In the 1933–34 varietal tests, the New Guinea x Sea Island backcrosses yielded more than twice as much as the control, Sea Island, in every case, the highest yield obtained from the backcross types being 1219 lbs. of seed cotton per acre, while the control averaged 443 lbs. per acre (60). Spinning tests showed that two of the backcross types were slightly superior in some respects to the control, a White Egyptian cotton. The better of these two was multiplied up to commercial proportions. In this season tests of second backcrosses were carried out.

When the 1934–35 cotton planting season was well advanced government permission was obtained to distribute seed for planting. The weather was very unfavourable and only about 230 acres were planted of which about half was Sea Island. Presumably the other half consisted of the backcross material. Single plant selections were made from the F₁ of the second backcross (81).

Selection within Type 172 was continued in 1936–37. The second backcross selections proved disappointing and it was decided to discard them (82).

In February 1938 a storm severely damaged the cotton crop on the north western side of the island, and it was noticed that while many plots of Sea Island failed to recover, Type 172 proved much harder. Plants which had already set fruit and were stripped put on new growth and eventually produced quite heavy crops (83). Two selections were retained from the progeny rows of Type 172. Of these 172/23/1 had a lint length of 50 mm., a lint index of 5.00, a ginning percentage of 31.5 and a yield of 1354 lbs. of seed cotton per acre, and 172/23/5 gave a somewhat similar performance. To further the aim of securing a typical Sea Island lint while retaining the backcross plant
habit, two second backcross plants were again crossed with Sea Island. The resulting hybrids were robust, upright and uniform, resembling Type 172.

Type 172 was not grown commercially in 1938–39, because of a government decision to distribute only Sea Island, but the strain was maintained by ratooning. Increase plots of 172/23/1 and 172/23/5, each of which showed an improvement over Type 172 in regard to length and fineness of lint were grown in increase plots in 1939–40 (163). Selection of first and third backcrosses was continued.

In 1940–41, 172/23/1 and 172/23/5, after suffering hurricane damage, yielded respectively 318 and 605 lbs. of seed cotton per acre (84). Progeny rows of first and third backcrosses were selfed and single plant selections were made. A mean maximum lint length of up to 57 mm. was recorded for the third backcrosses. In most of these strains the lint was somewhat harsh.

The government's decision to withdraw its support from the cotton industry was announced in the 1940–41 report and no further reports have been published.

Crosses had been made in St. Vincent as early as 1919 with the object of combining the lint length and quality of the Sea Island strain V 135 with the high yielding capacity of Montserrat Sea Island. In 1930 the cross between the two strains was repeated, and the F₁ was backcrossed the following year to Montserrat Sea Island. In 1932 the backcross hybrids were selfed and two plants combining long lint and high lint index were selected for further study in progeny rows (92). Five plants were obtained from selfed derivatives of the first backcross, and two from selfed second backcrosses, combining the V 135 lint length of 57 mm. with lint indices ranging from 49 to 59 mg. as compared with 43 for V 135 and 60 for the Montserrat parent, H 39. They also had ginning percentages of 27·2 to 31·3 as compared with 26 for V 135 and 34 for H 39 (93). The mean loculi values of each of the progeny rows of the first backcross derivatives were identical with that of the Montserrat parent; those of the second backcross derivatives were intermediate between those of the two parents (86). Three of the first backcross derivatives bred true for the V 135 lint length. In the next season 57 selections were grown, of which 37 bred true for this character, but only 9 of them combined it with high weight of lint per seed. Strains with superfine, intermediate and short staple lengths were selected and grown in 1936–37. The results were seriously affected by unfavourable weather
conditions, but 37 strains were carried forward (90). In this project, the products of repeated backcrossing failed to compete with first backcross derivatives and were discarded (91). Of the 37 strains mentioned, only ten long stapled ones were retained. There was much variation in lint length among the long stapled strains, and though in agricultural characters they appeared inferior to the Red Sea Island strains, they had better spinning quality and soon proved their superiority over the latter. Three strains VH 8, 9 and 10, proved outstanding (135) and in 1939-40, when their progenies were included in the main breeding trial, they gave very satisfactory results (136). After several more years of testing and selection (106, 137-139) it became quite evident that the VH material was considerably better than V 135 as regards yield. VH 8 showed the most promise (142, 143). All its progenies were well within the superfine quality range although none equalled V 135 in fibre strength. Those progenies not closely resembling V 135 in spinning behaviour were eliminated in the 1946-47 season, when the number of families under test had been reduced to four (144). Spinning tests the next year again showed that the VH 8 fibre was of superfine quality, while the superiority of the VH progenies over V 135 in yield characters was well established (145). According to the most recent report (132) only five of the 24 VH 8 progenies tested were of lower yarn strength than the V 135 material. VH material was to be produced commercially in Antigua in 1951.

In India and Pakistan, backcross hybrids have been used in several schemes for the improvement of quality and disease resistance, including projects at various places in Bombay Province, at Indore and in Sind, the Punjab and Baroda State. Since in most cases only first backcrosses and their derivatives appear to have been involved, and we are chiefly concerned with repeated backcrossing, it is not proposed to give a full description of all these schemes, but short accounts follow of a few which are of particular interest or importance or serve as examples of the type of work in progress.

Work on the hybridization of Asiatic with American cottons was begun in Surat, Bombay Province, in 1932 (51, 52, 4, 11-13). The aim was to combine the superior fibre qualities of New World cottons with the hardness and adaptability to the Indian climate of G. herbaceum and G. arboreum varieties. All the F₁ hybrids were sterile, but when first backcrosses were made to the New World cottons as pollen parents, hybrids ranging in fertility from fully fertile to completely sterile were obtained.
In 1941-42, 41 F₁ plants and 46 backcross plants were under observation, 40 of the latter being more or less fertile and most of them having 52 chromosomes (I4). Advanced cultures from three of them, including (Co 2 x Red Arboreum) x Co 2 gave promising results the following year in replicated block tests against 1027 ALF (15). With a view to obtaining better combinations of characters some new first backcrosses were made with long stapled American cottons such as Meade and Coker-Wilds as recurrent parents.

Trials and selection were continued each year (16-19); several families equalled or exceeded 1027 ALF in yield and had better ginning percentages and staple lengths at Surat, receiving favourable reports also from other parts of India to which they had been sent for testing.

One might have expected more than a single backcross to be made in this project since the original crosses were interspecific, but backcrossing appears to have been used in this instance rather to overcome the sterility problem than as a special method for the interspecific transference of genes.

In another project at Surat F₂ hybrids between hexaploid 28-1 (Co 2 x 1027 ALF doubled) and G. Armourianum were backcrossed twice to cultivated American cotton and 47 plants were selected from the progeny in 1944-45 (17). These are not mentioned in subsequent annual reports and presumably did not give rise to any very promising strains.

A scheme for the production of long staple cottons for cultivation in Sind, was started in 1940 in order to develop a cotton variety of the 289 F type with a staple length of over 11/16 inches which would spin about 60 counts and yield not less than 6 maunds of seed cotton per acre. Four methods of tackling the problem were followed, one of them being the production of backcross hybrids between cottons of the 289 F type and long staple varieties (12). Reciprocal crosses were made in the 1940-41 season between long stapled G. hirsutum types and Sind Sudhar (also G. hirsutum), the established commercial variety of long stapled cotton grown in Sind. Crosses were made, also, with a new Sind-American strain, M4 (13). The F₁'s of the Sudhar and M4 crosses were similar with respect to staple length but the latter were superior as regards ginning outturn (14).

During the 1942-43 season some 6000 plants belonging to F₂ and first backcross progenies of crosses of Sind Sudhar and M4 with the following six long staple Upland types from the USA were studied in a replicated experiment; Express, Wilds, Delfos, Acala, Missdel and Delta Type Webber (15). All the
backcrosses gave higher yields and showed a lower incidence of "tirak," an important defoliating disease, than the F₄'s. Plants with high yield, a ginning outturn of 32% or over, staple at least 3 mm. longer than that of Sind Sudhar and M4, and only mild tirak attack were selected. Tests of F₄'s and backcrosses were conducted the following year, and some healthy, high yielding progenies similar to Sind Sudhar and M4 but with an extra staple length of 1/₄ inch were obtained (16). The backcross hybrids are not mentioned in the subsequent annual reports, however, and have apparently been discarded in favour of the promising F₄ selections.

Backcrossing has been employed also in a scheme for the improvement of Dharwar–American cotton (G. hirsutum), begun at Gadag in April 1942 with the objective of developing an early maturing type superior to Gadag 1 in respect of yield, staple length and ginning percentage and more resistant to red-leaf blight (15). Two strains, 9766 and 4411, derived from the backcross (Gadag 1 x Co 2) x Gadag 1 both proved superior to Gadag 1 in respect of ginning percentage; 9766 equalled Gadag 1 in yield in 1943–44 (16) and both significantly out-yielded it in 1944–45 and equalled it in 1945–46 as well as producing longer staple (17, 18). Their spinning capacity, however, was slightly inferior to that of Gadag 1. One segregate from the cross between Gadag 1 and Co 2, known as 9–3, showed particular promise and has recently been used in several crosses, including a backcross to Co 2 (19, 20).

At the Institute of Plant Industry, Indore, hybrids between G. arboreum and G. Thurberi and between G. hirsutum and G. Raimondii were made fertile by colchicine treatment. This was followed by repeated crossing with G. hirsutum and G. barbadense and with G. hirsutum respectively (5, 9, 10, 95). A large number of seeds were grown in 1946–47 and observations were recorded on the germination, fertility and other characters of the plants; 680 fertile plants were obtained from the G. Thurberi crosses and 10 from the G. Raimondii crosses. In the following year, 1915 fertile plants were obtained, showing a wide variation in economic characters, particularly halo length. Selection was carried out for earliness, good boll bearing and long staple.

Backcrosses of the hybrids between the desi (G. arboreum) varieties Jarila and Dhar 43 to Dhar 43 were also made and tested (6). The F₃ progenies of the backcrosses proved superior to Dhar 43 in yield and fibre length while equalling both parents in ginning outturn (7). In 1945–46 F₁'s, F₂'s and F₃'s of backcrosses to both parental varieties were tested in replicated
progeny rows, and several promising progenies were selected for further trial (8). Some of these again showed promise the following year (9).

Afzal, Sikka and Ahsan-ul-Rahman (50) have reported the improvement of Jubilee cotton by means of the backcross technique. Jubilee is the collective name for a number of strains of desi cotton, *G. arboreum* var. *neglectum* f. *bengalensis*, grown in the Punjab. The hybrid Jubilee x *G. anomalum* was highly sterile. By backcrossing it twice to Jubilee, however, and selecting for high boll number and seed setting in subsequent generations, strains were obtained which were not fully fertile but had completely white lint and were superior to Jubilee in yield of seed cotton, ginning outturn, staple length and lint fineness. Desi varieties have now been obtained from this material which have a spinning performance as good as Punjab–American 4 F. Details of their yield, technological properties and cash value per acre are given in a recent paper by Afzal (49).

An attempt was started in 1934–35 to transfer smoothness of lint to the *G. barbadense* variety Ishan A, which was the chief variety grown in Southern Nigeria. Ishan A was crossed with the smooth linded Sea Island cotton V 135 and the F$_1$ was backcrossed twice to Ishan A (160). It will be noticed that the two parental varieties belong to the same species; hence one would not expect many generations of backcrossing to be necessary.

At first part of the hybridization and selection was carried out by Harland in St. Vincent, but the hybrids selected there and sent to Nigeria proved unsuitable for Nigerian conditions, although they showed definite improvement over Ishan in St. Vincent, as regards both yield and quality. First and second backcrosses were tested in 1934–35 and selections were made. The rough lint character appeared to be very persistent, especially in the second backcrosses, indicating a probable association between roughness of lint and the vegetative characters producing a strong, vigorous, late flowering and hairy plant.

Tests were continued in the following four years of first and second backcrosses and their progeny (161, 162, 168, 69). It became apparent that the necessary vegetative characters were not likely to be found in any first backcross strain. Second backcrosses gave better results and in 1938–39 proved somewhat superior to Ishan A in smoothness of lint. But progress was very slow, and the project was abandoned the following year on the advice of J. B. Hutchinson of the Trinidad Cotton Research Station who suggested that the connexion between roughness of
lint and the hairiness necessary for jassid resistance might be so close that it either could not be broken down or would require the expenditure of too much time and money (2).

In experiments at Barberton, South Africa, to combine finer lint with the jassid resistance and other desirable characters of U4 and MU 8 these *G. hirsutum* varieties were crossed with several fine linted types including the Sea Island strain V 135 and the Egyptian strain X 1530, both of which belong to *G. barbadense*, and the *G. hirsutum* varieties Coker–Wilds USA and BP 52 Uganda. The crosses with V 135 and X 1530 were backcrossed to U4 8161 in the 1940–41 season (149) and a few selections were made the following year (150). Bulks were also carried forward for future selection. But after 1942–43 attention seems to have been confined to the straight crosses.

F₂’s and backcrosses of U4 x Coker–Wilds and MU 8 x Coker–Wilds were grown in 1942–43 season (151). The next year, however, these too were discarded since plants combining lint quality approaching that of Coker–Wilds with good fruiting and hairiness could not be found.

The hybrids involving BP 52 were more promising. This strain had the best combination of hairiness and lint quality of any parent so far used. The F₂’s of crosses of U4 and MU 8 with BP 52 were backcrossed to hairy BP 52 plants in the 1942–43 season (151).

Many plants in the MU 8 x BP 52 backcrosses had better lint than was found in the straight crosses but also showed a loss of hairiness which was important for jassid resistance. There was little difference in lint quality or hairiness between F₂ and backcross plants in the case of U4 5143 x BP 52 crosses (126).

In 1945–46, however, some of the backcross plants in the MU 8 group of hybrids had much better lint than the straight crosses and showed no corresponding deterioration in habit and hairiness. But in the U4 group, plants with the required combination of characters could be found more easily in the straight cross hybrids than in the backcross (123).

Backcross progenies of both groups, especially the crosses with MU 8 were better than the straight crosses in 1946–47 and it was easy to find prolifically fruiting plants having hairiness approaching that of MU 8 combined with lint equal to that of BP 52 in length and fineness as judged by feel and in many cases with a ginning outturn higher than that of either parent. Sixty plant selections were carried forward which had a ginning
outturn of 34–36% combined with lint lengths of 34–37 mm. (127).

Testing and selection were continued in 1947–48. In spinning tests of lint samples collected in the previous season, two MU 8 x BP 52 backcrosses, A 616 and A 618 gave “highest standard counts” of 63 and 54 respectively, that of the BP 52 control being 62 (128). Promising backcross strains of this type included in varietal tests the following year were remarkable for their good recovery from drought as compared with BP 52 and other strains (131). The best of them, A 7262, had a ginning percentage of 35.3, a seed weight of 10.5 and a lint length of 34.4 and yielded 479 lbs. of lint per acre. In the two seasons 1947–48 and 1948–49, under good and bad conditions, the best MU 8 x BP 52 backcrosses were outyielded only by A 2106, to which they were superior as regards lint quality. A 618 was superior also in earliness and hairiness. Arrangements have been made for large scale spinning tests to be carried out in Natal and in Lancashire on these promising hybrids. Their standard of jassid resistance was good. As a small proportion of the hybrids showed bunch or cluster type of fruiting associated with inferior boll opening, particular attention was paid to selection for good opening.

The transference of fibre characters from Sea Island (G. barbadense) to Upland cotton (G. hirsutum) has been effected at the Pee Dee Experiment Station in South Carolina. In 1935 when the first crosses were made the Sea Island industry in the southeastern United States had ceased with the advent of the boll weevil (Anthonomus grandis) to which this kind of cotton is susceptible. As there was still a demand for the long fibre produced by Sea Island, a variety combining the weevil resistance, found in Upland cotton, with the lint character of Sea Island was needed. Crosses were therefore made between desirable, long stapled Upland varieties and seven strains of Sea Island. The Upland varieties used were Coker–Wilds strains 7 and 8, Tidewater strains 12 and 29, J. C. Seabrook’s Tidewater strains 5 and 6, Meade strains A 54 and 71 and Meade Artesia (23). Several thousand crosses were made. The experiments were continued the following year, and a number of promising selections were obtained (24). First and second backcrosses to both parents were carried out in 1936 and 1937 (25). Outcresses to different Sea Island and Upland stocks were also made. The second backcrosses to Upland varieties greatly resembled the recurrent parents in plant type and showed hardly any Sea
Island characters. Similarly, second backcrosses to Sea Island were very much like the Sea Island parents. As weevil resistance depends on boll characters, and most of the bolls of these hybrids were like those of Sea Island it seemed that repeated backcrosses to Sea Island would ultimately lead back to the Sea Island type susceptible to weevil damage. Backcrossing to Upland types appeared more promising (26).

The fourth backcross stage was reached in 1939. Long stapled Upland varieties were found to be the best parents, since when short or medium stapled ones were used only one or two backcrosses could be made before the staple of the hybrids became too short to serve as a substitute for Sea Island (27).

Backcrossing of F₁'s was found to be as good as backcrossing of F₂'s and gave more uniform progenies.

In the 1940 season progeny rows of first, second, third and fourth backcrosses were grown, the populations being as large as was practicable in order to provide a good chance of selecting desirable types (28). Fortunately fibre characters appeared to be inherited independently of general plant characters (29).

In 1942 some of the backcross hybrids were becoming stabilized but their fibre was neither as long nor as fine as Sea Island fibre (30, 31).

Very promising results were given however by some of the hybrids in 1944 (32). Strains 391 and 394, two sister selections from a line obtained by repeatedly backcrossing Seabrook (Sea Island) x Wilds (Upland) to Wilds, possessed many desirable characters including fibre very similar to that of Sea Island cotton. Strain 542, the hybrid with the strongest fibre was from Bleak Hall x Wilds backcrossed to Wilds. Strains 394 and 400 showed resistance to Fusarium wilt, though this was not present in any of the pure Upland strains tested. In 1945, five hybrid strains had lost all signs of the Sea Island plant type but had longer, finer and generally stronger fibre than extra long staple Upland strains (33).

A large number of genes, having small effects individually, are involved in the inheritance of fibre qualities, and the procedure must therefore be somewhat different from that used in the transference of a character such as resistance to wilt or blackarm, dependent on a relatively small number of genes. In the early backcross generations at the Pee Dee Station very careful selection was carried out which tended to result in the elimination of all segregates except those largely Upland in nature and the retention of plants which had, in general, too few genes from the Sea Island parent. Experience showed that a larger range of
hybrid types should be used in a programme of this kind (33). It was also found that data on the physical properties of the early, unstable hybrids such as staple, yield, ginning outturn and boll structure were of little use in predicting the nature of the end product, whereas in transferring a single gene, selection for the character it determines is necessary from the very beginning.

The following is a detailed account of the breeding of Sealand 542, the most promising strain developed in the experiments in S. Carolina (34). As already stated it was derived from a cross between Bleak Hall and Wilds. The characters to be transferred from the Sea Island parent, Bleak Hall, to the Upland plant type were length, strength and fineness of the fibre, high bolling capacity and reduced susceptibility to fruit shedding. Coker-Wilds, the recurrent parent, was to contribute earliness, boll toughness, boll size, good boll opening and fluffing qualities and satisfactory productivity as well as plant characters of the Upland type. Bleak Hall is an extra long stapled Sea Island variety, and Wilds is a long stapled strain of Upland.

The original cross was made in 1936. All the F₁ plants had long, fine fibre and staple lengths of at least 1 \( {20/32} \) inches which is only \( 1/16 \) inch less than that of Bleak Hall. The F₁ was planted the following year and the first backcross was made on to Coker–Wilds strain 9 which had a staple length of \( 1^{3/6} \) inches. The progeny showed some undesirable characteristics such as crooked irregular fruiting branches and some fasciation. The second backcross was made between plant 1 of the first backcross progeny and a selection from Coker–Wilds strain 9. The former had a lint percentage of 27.3, a staple length of \( 1^{5/6} \) to \( 1^{11/16} \) inches and large bolls with good fluff. The Coker–Wilds parent had a staple length of \( 1^{5/16} \) to \( 1^{3/16} \) inches and a lint percentage of 35.9 but also showed some undesirable plant characters. The third backcross was made in 1939 between plant 4 of the second backcross progeny and a selection from Coker–Wilds strain 8 which had unusually long staple of \( 1^{1/2} \) to \( 1^{3/16} \) inches, large bolls, good fluff and satisfactory plant characters. The plants of the third backcross were 2\( 1/2 \) to 3\( 1/2 \) feet high, productive and with good bolls; the staple length ranged from \( 1^{3/8} \) to \( 1^{11/16} \) inches; and the lint percentage of the nine plants selected varied from 27 to 34.7. Plant 3, which was backcrossed to a selection from Coker–Wilds strain 11 had a staple length of just under \( 1^{1/2} \) to \( 1^{5/8} \) inches and a lint percentage of 31.3. The Coker–Wilds parent plant had a staple length of \( 1^{5/16} \) to \( 1^{1/2} \) inches and a lint percentage of 34.3.
Only two plants were selected from the progeny of this fourth and last backcross. Their staple length was $1\frac{7}{16}$ to $1\frac{9}{16}$ inches, their lint percentage 31 and their lint index 6.7. Segregation for staple length, lint percentage, lint index and other characters occurred in 1942 in the F₂ of the fourth backcross. Sealand 542 was selected from the F₃ in the following year. It consisted of small to medium large plants, two to three feet tall, mostly well shaped like Coker-Wilds, with some a little open in type. They fruited well and produced good bolls which opened and fluffed well. The fibre was generally fairly fine and of good character and had a staple length of $1\frac{1}{2}$ to $1\frac{9}{16}$ inches. The lint percentage of the 12 plants which were selected varied from 29.1 to 34.75.

There was some segregation with respect to plant type, bolls and fibre in the F₄ grown in 1944. The progenies of the best selections were grown in 44 progeny rows the next year. In this breeding block the plants were very uniform and productive, with good-boll opening and staple lengths generally of $1\frac{3}{8}$ to $1\frac{1}{2}$ inches. Only three or four plants showed a definite tendency towards shorter staple. Tests indicated very good fibre strength, exceeding that of Cicala 1517, Mesa Acala and Coker-Wilds, three Upland varieties with unusually strong fibre.

Sealand 542 has been used in crosses with other strains in order to obtain productive types with fluffier bolls (35).

In interspecific crosses and backcrosses made at the Texas Agricultural Experiment Station in order to transfer desirable characters from *G. barbadense*, *G. purpurascens* and related types to Upland varieties of cotton (76-79, 121) special attention has been paid to fibre strength. Some second backcrosses of a hybrid involving wild cotton from the southwestern United States had a fibre strength index equal to that of Sea Island cotton (78).

In Arizona, S x P, a *G. barbadense* variety originating from a cross made in 1918 between Sakel and Pima, was backcrossed on a selected strain of the Pima parent (III). The backcross hybrid was characterized by small plant size and very early maturity and had lint intermediate in length between that of S x P and that of Pima and with much of the fine silky character of S x P.

Other backcrosses involving Pima were also made in breeding for good fibre properties (36-40).

In another project in Arizona designed to combine the strength and fineness of the fibre and disease resistance of *G. barbadense*
cottons with Upland the cross (Hopi x Stoneville) x [(G. barbadense x Upland) x Stoneville] was backcrossed twice to Stoneville (36). Only a single hybrid plant was used as pollen parent in each backcross however, and the G. barbadense factors for length and strength of the fibre were found to be much reduced in the progeny.

Backcrosses have also been made in the Upland cotton breeding programme, in which two backcrosses of Santan on Santan x NM 1517 have proved particularly promising (32–43).

IV. BREEDING FOR JASSID RESISTANCE

In 1930 S. C. Harland visited the experiment stations of the Empire Cotton Growing Corporation in South Africa, and it was decided, as a result of his visit, to attempt to improve Parnell's jassid resistant U4 by introducing gene complexes from other strains known to possess either resistance to jassids (Empoasca spp.) or great powers of resistance to unfavourable conditions. U4 was a selection made at Barberton in 1925 from the variety Uganda and subsequently improved by several years' selection (148). For the purpose of introducing new gene complexes the following combinations were made (99, 92):

(Cambodia x Jamaica Xerophytic) x U4
(U4 x Jamaica Xerophytic) x U4
(U4 x Cambodia) x U4
(U4 x Gambia 14) x U4
(U4 x Gambia 14) x Cambodia
(Cambodia x Galapagos) x U4.

The hybrids were selfed twice and seed of over 1200 of the resulting plants was distributed for trial to stations in Africa.

Crosses of (U4 x Cambodia) x U4 sent by Harland to Southern Rhodesia gave promising results, and it was decided to make some more crosses of the same types. Accordingly U4 was crossed with Cambodia at Gatooma, Southern Rhodesia, in the season 1934–35 (154). It was hoped that the very hairy leaf character of Cambodia could be transferred to U4 strains so as to increase their jassid resistance. In other respects they were well adapted to commercial cultivation. In the 1935–36 season 132 hybrid bolls were obtained from 373 crosses, including backcrosses to the U4 parents which were of the 64/7/10 type (134). The similar series of (U4 x Cambodia) x U4 crosses obtained from Harland in 1933 were still showing promise. More backcrosses were made in the next two seasons (155, 156). In 1936–37 none of the hybrids performed as well as the best
U4/64 selections, and in 1938–39 Harland's backcrosses were discarded because they were inferior to those made locally. There were over 30 blocks of the crosses in the 1941–42 season (70). They grew vigorously from the start and developed into uniformly large, coarse, and generally very hairy plants. Most of them were highly resistant to jassids; but relatively few of them had good lint, and those which did were usually of the very bushy, vegetative, large leaved type. Their amount of leaf was perhaps their chief drawback as it afforded shade for staines (Dysdercus spp.). Similar tendencies were noted also the following season; the outstanding characteristic of the plants which were retained was their marked jassid resistance (71). The 1943–44 trials showed that the families derived from the crosses yielded significantly better than anything else tested (72) and they continued to give high yields in the following four seasons although their lint remained relatively short (74, 75, 146, 73). In 1947–48, two of the backcross strains, 12204 and 12405, were being considered for commercial cultivation, and according to the most recent report (133) seed stocks of these two strains were being held in reserve pending possible release to growers. Derivatives of the (U4 x Cambodia) x U4 crosses are described as, in general, heavier yielders with appreciably better ginning percentages than 9L34, the U4 strain in commercial cultivation. Some of the hybrids, including 12405, have a plant habit suitable for mechanical picking. Although bred originally for jassid resistance the hybrids apparently were not particularly outstanding in this respect; 12204 showed sufficient resistance for normal purposes, but so did 9L34. Their chief advantage lay in their superior yields.

A similar project was started in the season 1937–38 at Barberton, South Africa, with a similar objective, namely to increase the hairiness and therefore the jassid resistance of U4.

(U4 x Cambodia) x U4 backcrosses received from Harland had been tested in South Africa for several years but meanwhile U4 had been considerably improved, and the jassid resistance of the hybrids appeared very similar to that of the best U4 selections. Therefore, in the hope of getting better results than had been obtained with the two original U4 strains sent to Harland as parents for the crosses, new crosses were made between good Cambodia plants and the best strains of U4, lots 5143 and 5149 (122). The following season the F1 hybrids were backcrossed to their U4 parents (124). In 1939–40 the 5143 backcrosses proved definitely the better in plant characters.
generally and particularly in hairiness. Good plants selected for hairiness from each group were again backcrossed with their respective U4 parents (125). First backcrosses and $F_2$ generations were grown in large plots in 1940–41 along with small plots of the three parents, replicated four times over ten acres (149). They made good growth and formed the best block of cotton on the station. The hybrids of 5143 parentage had better plant development and much greater hairiness than those involving 5149. From all four groups of hybrids, plants combining good field characters with good hairiness were selected. Many plants in the 5143 lots were far more hairy than the Cambodia parent while in ginning percentage and lint length the backcrosses equaled U4. In both the 5143 and the 5149 lots, the backcross selections were superior to those from the $F_2$'s.

It was decided to carry forward only 30 of the best plants of 5149 parentage, and retain 100 from the 5143 backcrosses and 50 from the 5143 $F_2$.

Different correlations between characters were found in the two groups. Neither of the 5143 lots showed any correlation between lint length and degree of hairiness, and only a slight negative correlation between lint length and ginning percentage was observed; whereas in the 5149 lots there was no correlation between lint length and ginning percentage but there was a very slight negative correlation between lint length and amount of hairiness.

A few hairy plants in each of the first backcrosses were again backcrossed to the best reselections of their respective U4 parents. Observations made the following year, 1941–42, again showed the inferiority of the 5149 crosses, and these were entirely discarded (150). Both bulk and single plant selections were made from the 5143 hybrids, combining good field characters, a high degree of hairiness, and lint rather longer than that of U4.

A total of 143 single plant selections and 66 special bulks were carried forward into the next season and planted in 4 to 8 row plots, with the parental varieties, on a 10 acre block (129). It was found that a large majority of the lots combined greater hairiness than was possessed by the Cambodia parent with field characters as good as, or in some cases better than, those of the U4 parent. No single plant selections were made during this season as it was felt that further reselection might lead towards overspecialization. Large bulks were taken instead, covering a wide range of types all of which possessed the required combination of hairiness and economic characters. Apparently no further backcrossing was carried out.
Very good results were obtained in the 1943–44 season and the best 19 strains judged on all characters were carried forward as large selfed bulks (130). One of these strains was A.2106 which gave the highest yield in the variety trial. Whether it was a first or a second backcross is not indicated. It will be referred to again below.

Because of their longer lint, the hybrids had been expected to surpass U4 in spinning quality, but results of spinning tests on the 1943–44 hybrids showed that their spinning quality was only about the same as that of U4 (125). Fruiting was remarkably good in the following year, despite a short growing season, and the hybrids showed a desirable degree of earliness.

Little progress was made in 1945–46 because of bad hail damage (123). The following year plants were looked for having longer and finer lint than the average (127). Such characters proved to be normally associated with the lowering of other desirable characters such as ginning percentage, fruiting and hairiness, and it was decided that to effect even a small improvement in lint quality, without loss of other economic characters, would require much more time than was available. In a varietal test in the 1947–48 season, A.2106 not only outyielded all the other strains tested but set up an all-time yield record for Barberton (128). This strain had been distributed to farmers in the 1944–45 season, for multiplication, after giving the highest yields in varietal tests, under widely different conditions, in two successive years. It produced 707 lb. of lint per acre in 1947–48 and was regarded as beyond doubt the most satisfactory strain in general for the Barberton district. In the 1948–49 season it again outyielded all other strains, though it was inferior in other respects to A 618, an MU 8 x BP52 derivative (131).

This project shows the advantage of starting with more than just one pair of parental types. If 5149 had been the only strain of U4 to be crossed with Cambodia, comparatively poor results would have been obtained. But two sister strains of U4, 5143 and 5149 were used, and, as it happened, the crosses involving 5143 produced many excellent types including A.2106, whereas in those involving 5149 nothing really good was found. It was impossible to predict beforehand how the two kinds of progenies would differ.

In another attempt made at Barberton to increase the leaf hairiness of U4, a Malva Upland type from Indore was used. This strain, MU 8A, was by far the hairiest variety of G. hirsutum available. It was a compact, free fruiting type of plant but its ginning percentage was rather low and its lint shorter and
harsher than that of U4. In the 1940–41 season hybrids between this strain and U4 were backcrossed to U4 (149), and the backcrosses, F2's and parents occupied two acres of land the following season (150). Three U4 strains were used as parents: 8161, 8171 and 8202. There was a tendency for hairiness to be associated with the short harsh lint of the MU 8 parent in these crosses, and the MU 8 x 8171 and MU 8 x 8202 lots were discarded because of poor lint quality (129). It was possible to find individual plants combining the required amount of hairiness with long fine lint in the crosses involving 8161, however, and bulks from these crosses were still being maintained in the 1947–48 season (128).

A rather different project, also involving U4, was begun in Queensland in the same season, 1937–38, as the Barberton project, in which U4 and Cambodia were the parents but here U4 was the non-recurrent, not the recurrent parent, the reason being that small bolls and weak lint made the South African U4 unsuitable for growing commercially in Queensland. Only its jassid resistance was required. Whereas at Barberton, and also at Gatooma, the objective had been to increase the jassid resistance of U4, the aim in Queensland was to transfer the jassid resistance of U4 to a variety better adapted to local conditions.

Miller, a popular, big-bolted, American Upland type was chosen as the recurrent parent and was crossed with U4 at the Cotton Research Station, Biloela (169). Although it appeared to be the least susceptible to jassids of the varieties under cultivation in Queensland, Miller had only about 3% as much resistance as U4.

From a study of a small population of Miller x U4 hybrids and their parents (157) it appeared that the jassid resistance of the F1 was practically the same as that of the resistant parent, U4, while boll size was intermediate between the boll sizes of the two parents. The weight of seed cotton per boll was practically equal to that of Miller.

In the 1939–40 season the second generation hybrids included some good plant types again combining the better characteristics of each parent (170). Backcrosses were made to Miller, and these proved superior in boll and lint characters to the F3 and F4 hybrids (178). This was to be expected of course in view of their greater proportion of Miller chromosomes. Their jassid resistance was mostly satisfactory. Good results were again reported for the backcrosses in the following year when selections were tested in a simple demonstration plot (172). In the third
generation after backcrossing Miller x U4 to Miller three hybrid strains were isolated with high jassid resistance, staple lengths of 1 inch or more, full bodied, very strong lint and lint percentages promising to surpass that of commercial Miller, i.e. 33.5 to 34.5% (173). Moreover, they appeared sufficiently uniform in essential characters to warrant extensive testing. When F₂'s of second backcrosses, F₁'s of third backcrosses and new fourth backcrosses had been obtained, backcrossing was discontinued. These various types of hybrids all approached the general boll and lint characters of the recurrent parent, Miller, and a high degree of jassid resistance had been maintained by selection. In the following season, 1943–44, the breeding programme was hampered somewhat by the almost complete absence of jassids on the experimental plots, but a strain trial which included advanced hybrids indicated that, in many characters, the jassid resistant material was as uniform as the commercial stocks of Miller and New Mexico Acala (174). Rigid selection for large boll types, and the use of a large boll strain as recurrent parent had apparently resulted in the elimination of the small boll type of U4. On the other hand, the flowering rate of the hybrids was much closer to the prolific U4. Four hybrid strains significantly outyielded three of the commercial stocks. Again in the 1944–45 season there was no severe jassid attack and attention was largely given to characters other than resistance (1). The tests, which included Umil 12, the first Miller x U4 backcross hybrid released for commercial testing, indicated that this strain, while undoubtedly a very high yielding and quick fruiting type had its lint percentage substantially reduced by dry conditions. As reselections with lint percentages up to 40 were obtained in the bulk stock, which averaged only 32%, it was decided to discontinue further testing of the hybrid until a superior strain from one of the new selections was available. It was possible to test the jassid resistance of advanced hybrids by taking advantage of the fact that late planted cotton grown under frequent supplementary irrigation usually experiences sufficient attack by jassids to indicate its degree of resistance. The results showed that many hybrids were markedly resistant and much superior in this respect to commercial varieties. The following year, two out of eight fourth backcrosses had 100% of the population with dense or very dense long leaf hairs and another two had over 95% of the population with such hairs (175). Thus, leaf hairiness had been transferred from U4 to Miller and retained by selection through four generations of backcrossing to the non-hairy parent. In boll weight and fibre type the
hybrids closely resembled Miller. Good results were also obtained with selections from second backcrosses, which were very uniform with respect to high leaf hair density, plant type and ginning percentage. Highly resistant and prolific backcrosses, including Umil 12, which had low ginning percentages were crossed with the new Miller strain 43-9, developed for its relatively high lint percentage (176). Progenies of second and fourth backcrosses were again tested in the 1947-48 season with good results (177). The leading strain, which had resulted from seven years selection out of a second backcross appeared to be more uniform in most of the measured characters than the commercial varieties of the district. It was highly resistant to jassids and had large bolls, good quality fibre and a high ginning percentage as well as being a good yielder whether grown with or without supplementary irrigation. In an irrigation trial conducted in 1948-49 the three highest yielders were hybrids, followed by the standard Miller 41 S; and in a test of varieties for adaptation to mechanical harvesting Miller 41 S was again outyielded by one of the hybrid strains (158). Unfortunately no jassid infestations occurred in that season. Attempts are also being made to transfer jassid resistance to other cotton varieties grown in Queensland, namely Triumph, New Mexico Acala and Lone Star, using Ferguson from Trinidad and a Rhodesian strain as sources of resistance (174–176, 3).

The problem of jassid resistance in the Sudan is being tackled in several different ways. One is by transferring a gene for hairiness, \(H\), found in Tangüis to the chief Sakel strains. Both Tangüis and Sakel are varieties of \(G. \ barbadense\). This project was started with some misgivings because it had been suggested that hairiness and roughness of lint were associated, but it will be seen from the account which follows that no difficulty of this kind was encountered.

The \(F_1\) of Tangüis x NT 2/38 was grown in the 1940-41 season and crossed with NT 2/38 and X 1730 H. No conclusions as to the jassid resistance of the \(F_1\) could be reached since the attack on neighbouring cottons was not severe. The hybrids were fairly resistant to flea beetle (\(Podagrica puncticollis\) however, though less so than Tangüis since hairiness is only partially dominant (112). The first backcrosses were grown in the winter of 1940-41 and second and third backcrosses in the next season (94).

The fourth and fifth Sakel backcrosses, the latter having the composition Tangüis x NT 2/38\(^6\) and (Tangüis x NT 2/39) x X 1730 H\(^5\), where superscripts denote the number of times a
THE BACKCROSS METHOD IN COTTON BREEDING

The backcross method has been used as a parent, were grown in the following year (62). Blackarm resistant strains of NT 2 and X 1730 which had at this time become available were substituted for the original recurrent parents; and, as a first step in the transfer of hairiness to Domains Sakel, it was crossed with Tangius x NT 2/386 hybrids.

An interspecific transfer of the hairiness of Tangius to the American Upland cottons Uganda SP84R and Deltapine was also begun, the first backcross hybrids being grown in the winter of 1941–42. In the Deltapine crosses the Tangius gene, $H$, seemed to have been diluted or lost the following year for none of the backcross plants appeared to be any more hairy than Deltapine itself. Third and fourth backcrosses to SP84R were made in 1943–44 (63).

Blackarm resistant SP 84 homozygous for $B_2$ was used as recurrent parent in 1944–45. A small propagation plot of fourth backcross derivatives homozygous for $H$ was sown but they were eaten by locusts and there was no seed for resowing (64).

It was felt that satisfactory hair length and density were unlikely to be dependent on a single gene, and therefore other sources of hairiness were introduced into the breeding programme, including the G. barbadense variety Carpulla, the G. hirsutum var. Marie-galante variety St. Ignatius, the G. hirsutum varieties Kapas Purao, Ferguson and MU8b, G. tomentosum, G. anomalum (for hair length) and G. arboreum (64).

In the 1942–43 season four small lots of seed of (Acala Okra x G. tomentosum) x U4 composition had been obtained from Trinidad and the most hairy plant in each family was crossed with XA 129 (62). These hybrids reached first backcross stage in 1944–45 and second backcross seed was produced.

To return to the Sakel hybrids, the results of spinning tests carried out to see whether the $H$ gene affected lint characters in NT 2 x Tangius derivatives showed a higher hair weight but no loss of strength (65).

In the transfer of $H$, now referred to as $H_1$, from Tangius to Domains Sakel, the fifth backcross stage was reached in 1945–46; the transference of the G. arboreum race bengalense gene for hairiness reached the sixth backcross; and the transference of the hairiness gene from Carpulla to Domains Sakel reached the fifth backcross stage; while transference from G. tomentosum, St. Ignatius, MU8b, Ferguson and Kapas Purao were in their first backcross stage.

In the 1946–47 season it was shown that the main Carpulla gene occupied the same locus as the Tangius gene, $H_1$ (66), and
in the next season it was shown to be identical with it, as also were the main hairiness genes of MU8b and St. Ignatius (67).

These four varieties and also Philippines Ferguson, Kapas Purao, and the variety Kawanda belonging to *G. hirsutum* var. *punctatum* each have one major gene conferring hairiness, accompanied by minor and modifying genes which increase the length and density of the hairs. In *G. tomentosum*, on the other hand, hairiness depends on a single gene, *H*₂, alone.

In transferences from MU8b the full parental hairiness was retained in the second backcross. Ferguson hybrids also showed an excellent degree of hairiness in the second backcross.

The method of transferring hairiness to Sakel was to cross the hairy parent with Sakel and backcross the hairiest plants of the F₂ to Sakel and then from the F₂ of the backcross to select again the hairiest plants for further backcrossing and selfing. Meanwhile successive backcrosses, not alternating with selfed generations, were carried on as parallel projects for each type of cross, an *HH* type being selfed out after four or five such backcrosses and used as a temporary backcross parent in the transference of the genes modifying hair length. When the identity of any particular *H* gene with *H*₁ was established the hybrid was backcrossed to J.R. 14/5. The latter is a Domains Sakel type to which *H*₁ had been transferred by repeated backcrossing. Its lint length was not affected by the transfer of *H*₁ to it; nor was its quality visibly affected.

A different kind of jassid resistance, not dependent on hairy leaves, is also being transferred to Sakel, from *G. Armourianum* (67).

According to the most recent report (68) the full hairiness of MU8b was recovered in the F₂ of the second backcross, and third backcross progenies have been raised and selfed; work with Ferguson has also continued along similar lines. In these transferences the hairiest plants in the early backcrosses were markedly sterile, but in the third backcross material there was evidence that this sterility was breaking down.

Fifth and sixth backcrosses of MU8b hybrids to Sakel were made by crossing with BAR 14/7 and the material was then crossed with BLR 14/16 in the winter of 1948–49 to aid leaf curl resistance. A similar course was adopted with hybrids containing the *H* genes from Kapas Purao, *G. punctatum*, St. Ignatius, *G. tomentosum* and *G. mastelinum*.

V. BREEDING FOR RESISTANCE TO BLACKARM

Two species of New World cotton have for many years been included in the breeding work in the Anglo-Egyptian Sudan,
G. barbadense, referred to as Egyptian cotton, and G. hirsutum, the American Upland type. Investigations on Sakel, which belongs to the former species, indicated that no genetic factors for resistance to blackarm, an important bacterial disease in this region, were present; whereas considerable resistance was observed in American types obtained from Uganda. It was decided therefore to transfer this resistance to Sakel, and crosses between the two types were made at Shambat, near Khartoum, starting in the 1934–35 season (165, 166, 120). The Sakel strains used in the early generations were X 1530, a vigorous type selected from Sudan Sakel and particularly suited to conditions in the Gezira area, and NT2, a strain from Gash Sakel, with superior lint quality. Uganda B31 was the American type, blackarm resistant parent. The F1 hybrids were rather uniformly resistant, though less so than B31. For the purpose of classifying plants according to their blackarm reaction, 13 grades were recognized ranging from 0 for complete immunity to 12 for full susceptibility.

In the 1936–37 season 1156 plants of the first backcross (X 1530 x Uganda B31) x X 1530 were grown. In vegetative characters they resembled X 1530 much more than B31 (167). Together with plants of the parental strains and a number of F1 plants, they were sprayed with a suspension of Xanthomonas malvacearum, the causal organism, when five weeks old. Subsequent observations showed that 277 of the backcross hybrids were fully susceptible, like X 1530, and the other 879 had various degrees of resistance, the most resistant ones exhibiting infection similar to that of the F1. It therefore seemed probable that two factors were involved. These were tentatively named B1 and B2, Uganda B31 having, on this assumption, the constitution B1B2B2B2 and Sakel b1b1b2b2 (120). When plants with undesirable vegetative characters had been discarded, three resistant plants remained. These were used for backcrossing to X 1530 again and to NT2 to improve their lint.

First backcrosses of B31 x X 1530 to NT2 tested in the same year gave results similar to those for the X 1530 backcrosses, and five resistant plants, selected for resemblance to the Sakel habit, were again crossed with NT2 (167).

In second backcrosses to X 1530 and backcrosses involving NT2, tested in 1937–38, the Egyptian type characters of the recurrent parents strongly predominated (113). The ratios of segregation for blackarm resistance approached the expected 3:1. However, there were relatively fewer plants than in the first backcross showing resistance equal to that of the F1; this suggested the presence in the first backcross of modifying factors,
derived from B31, which were largely eliminated in the second backcross (120). Further backcrossing was carried out on a large scale.

The third backcrosses very closely resembled their Sakel parents in appearance and included many plants whose lint was indistinguishable from that of the parents in ordinary laboratory tests (164). Some families gave a 1 : 1 ratio for blackarm resistance, showing that plants with only one resistance factor had been used as parents. The results of tests of F_2 generations completely proved the two factor interpretation. The two factors are cumulative, B_2 having a greater effect than B_1 (120). In these experiments resistance was assessed on leaf symptoms only, but leaf resistance had been shown to be correlated with stem resistance.

A fourth backcross was effected in 1938-39 and some of the seed was sown out-of-season. In this way a further backcross was made possible the same year. The fourth backcrosses were indistinguishable in appearance from their Sakel parents (164). For the following year there is no report, but two backcrosses were evidently carried out, for in 1940-41 the eighth backcrosses to Sakel were made, using NT 2/38, NT 66/38 and X1730H as recurrent parents (112). The progenies were sown in the winter of that year and the ninth backcrosses were made. The composition of the ninth backcross progenies was as follows:

\[
\text{([[B31 x X 1530B] x NT 2/36^2] x NT 2/37) x NT 2/38^6} \\
\text{[([[B31 x X 1530B] x NT 2/36^2] x NT 2/37) x NT 2/38^2] x NT 66/38^4} \\
\text{[([[B31 x X 1530B] x X 1530A] x X 1530A^2) x X 1730G^2] x X 1730 H^4]} \\
\text{In addition, some X 1730 types were backcrossed in 1939-40 to X 1730A instead of the more recent substrain X 1730H, because X 1730A was thought likely to prove more resistant to leaf curl under Shambat conditions. Both types, however, proved equally susceptible and only the three lines shown above were carried on to the ninth backcross stage.}
\]

In 1940-41 blackarm resistant Sakel strains were propagated in bulk for the first time. Over a ton of seed of NT 2 homozygous for B_2 was produced from a 6^3/4 acre propagation plot of F_3 progenies of fifth backcrosses. Two 1^1/4 acre plots of fifth backcross NT 2 derivatives homozygous for both B_1 and B_2, and for B_1 only, yielded respectively 60 and 61 lbs. of seed. F_2

* In these formulae the convention of putting the female parent first has not been followed.
families from $B_1b_1B_2b_2$ and $B_1b_2B_2b_1$ plants in seventh backcross progenies were also grown, and $B_1B_1$ and $B_2B_2$ seed of the X 1730 type and $B_1B_1$, $B_2B_2$ and $B_1B_1B_2B_2$ seed of the NT 2 type was obtained. The fifth backcross material was of typical NT 2 appearance, and gave promising results in preliminary small scale spinning tests.

The ninth backcrosses of the NT 2 and X 1730 types were grown in the season 1941-42 but seed of the NT 66 type was stored pending further testing of NT 66 itself, as this strain has not fulfilled its earlier promise (94). Resistant hybrids were selfed and F₂ families were raised from which seed homozygous for $B_1$ and $B_2$ was obtained. In addition, one $B_1b_1$ plant and one $B_2b_2$ plant from the ninth backcrosses of the NT 2 type were each crossed with NT 2/39, and a $B_1$ and $B_2$ plant of their progeny crossed once more with NT 2/39, making the eleventh Sakel backcross. It was estimated that these progenies should contain 75.0% NT 2/39 “blood,” 24.6% NT 2/38, 0.3% earlier NT 2 types and a negligible quantity of Uganda B31 and X 1530B.

Bulk propagation plots of hybrids of the NT 2 type homozygous for $B_2$ were grown. Lint tests on replicated samples from fifth backcross derivatives showed that this hybrid material equalled the NT 2 parent in all respects except ginning outturn which was rather low. Smaller plots of seventh backcrosses were also grown, and fifth and seventh backcrosses were included in varietal tests.

In 1942-43, $B_2B_2$ plants of ninth backcross origin, in both the X 1730 and NT 2 lines, were crossed with $B_1B_1$ plants of similar origin (62). The hybrids were grown out of season and backcrossed to the $B_1B_1$ parent, so as to give a proportion of $B_1B_1B_2b_2$ plants which could be made homozygous for $B_2$ by selfing.

In the winter of that year a programme was started to transfer $B_1$ and $B_2$ from BAR 2/11 and BAR 2/10, both of ninth backcross origin, to Domains Sakel.

Bulk propagation plots of seventh, ninth and tenth backcross material homozygous for either $B_1$ or $B_2$ were grown. It was found that in the seventh backcross material, $B_2$ alone gave very marked blackarm resistance under Gezira conditions but not sufficient to enable all other control measures to be dispensed with.

In the 1942-43 season a large number of single plant selections was made from bulk sowings of the blackarm resistant material of both the X 1730A and NT 2 types (63). About 50 of the best selections of each kind were grown as single progeny rows for analysis and further selection. In this and the following
year tests were carried out at various locations in the Sudan (64).

In the 1945–46 season it was decided that the whole range of NT 2 types, having proved inferior to Domains Sakel in quality and earliness, did not merit further genetical work (65). All such work was therefore discontinued. BAR 1730L, a strain carrying \( B_2 \) derived from the seventh backcross of Uganda B31 on to X 1530 and X 1730, had then been on trial for four years. Comparison with X 1730A showed a difference in lint length of about \( \frac{1}{64} \) of an inch in favour of X 1730 and a hair weight difference in favour of BAR 1730L. In lea tests (count x strength) X 1730A showed a slight increase over BAR 1730L. For all practical purposes however the two strains could be regarded as identical in respect of effective length, hair weight and strength. Thus \( B_2 \) had been transferred to X 1730 without affecting its lint quality. Yield tests showed that there was no difference in lint yield between the two strains under conditions in which every effort was made to exclude blackarm. On the basis of these results it was decided to try BAR 1730L on a commercial scale, sowing it earlier than was possible with the susceptible X 1730A which then formed the main crop.

Data from tests carried out the following year confirmed the conclusion that BAR 1730L gave as good a lint yield as X 1730A and was a satisfactory blackarm resistant substitute for that variety (66). BAR 4/5, a ninth backcross of the X 1730 type homozygous for \( B_2 \) proved superior to X 1730A both in standard hair weight and in strength.

Selection within these strains was based primarily on yield and quality. BAR 1730L–1 a selection from BAR 1730L proved superior to the latter with respect to both these characters in 1947–48 (67). In this season 25 acres of BAR 4/5 sown on 1 August was grown commercially at Fahli Block by the Sudan Plantations Syndicate in comparison with an adjacent block of X 1730A sown at the normal time in mid-August. The earlier sowing of BAR 4/5 was made possible by its blackarm resistance. Unfortunately almost complete replanting of certain areas was necessitated by dirty land, bad preparation, poor sowing and a severe attack of flea beetle, and these conditions were probably responsible for the poor grade of BAR 4/5 which was obtained. There was little difference in yield. In hair and spinning tests BAR 4/5 had generally proved slightly superior to X 1730A in lint quality. Of the three main blackarm resistant strains of X 1730 produced in bulk, BAR 4/5 was shown by analysis of the spinning tests so far carried out to be slightly superior to BAR 1730L and BAR 4/11 which were practically identical.
with X 1730A; while, in the relative absence of blackarm, BAR 1730L had given an average yield about equal to that of X 1730A, the other two strains being inferior in this respect. In addition to the gene $B_2$, the variety BAR 4/11 contains $B_3$, another resistance factor which remains to be discussed. The superior yield of BAR 1730L was attributed to its X 1730A parentage, this variety having proved superior to X 1730H which was the last recurrent parent used in the synthesis of the other two strains, whose constitutions were BAR 4/5–[[B31 x X 1530$^4$] x X 1730G$^2$] x X 1730A$^4$ and BAR 4/11–[[B31 x X 1530$^4$] x X 1730G$^2$] x X 1730H$^3$, that of BAR 1730L being [[B31 x X 1530$^4$] x X 1730G$^2$] x X 1730H x X 1730A.

Some fourth backcrosses to Sakel of hybrids between another source of resistance, Harland’s RU4, and Sakel were shown to contain $B_2$. By further crosses with Sakel strains carrying the G. arboreum gene $R$ for reddish flowers and plant body, this gene was transferred to the blackarm resistant hybrids to make them easy to identify and keep pure [112, 94]. In 1941–42 they were of the following composition:—

(1) $[\{(RU4 \times Sakel) \times X 1530E\} \times X 1530A]$
\hspace{1cm} $x X 1730F] x NT 2/38^7$

(2) $([[[RU4 \times Sakel] \times X 1530E] \times X 1530A]$
\hspace{1cm} $x X 1730F] x NT 2/38^6] x NT 2/39$

(3) $([[[(RU4 \times Sakel) \times X 1530E] \times X 1530A] \times X 1730F]$
\hspace{1cm} $x X 1730G] \times X 1730H] \times X 1730A] \times X 1730H^3$

In 1942–43 plants from these crosses homozygous for $R$ and $B_2$ were bulked (62). Seventh backcross material of X 1730 types included in the standard variety test at the Gezira Research Farm in the following season proved to be typical X 1730 as regards such features as plant habit, yield and ginning outturn and to have a greater hair weight than X 1730A (63). Ninth backcross material showed a similar lea product to X 1730A and a lower hair weight (64). This strain was not to be bulked for commercial purposes; but it was hoped to have available a $B_2B_3$ type with red flowers and leaves by the time the ultimate, highly resistant $B_2B_3$ product was released commercially.

We turn now to work involving the third gene for blackarm resistance, $B_3$. R. L. Knight has given an account of the inheritance of this type of resistance in crosses between BAR 3 and Sakel, and backcrosses to Sakel [114]. The strain referred to as BAR 3 was discovered in 1937–38 as a single, offtype,
blackarm resistant plant in a line of the *G. punctatum* variety Schroeder 1306. The Sakel varieties used throughout as recurrent parents were X 1730H and NT 2/38.

BAR 3 carries two genes for blackarm resistance: one proved to be identical with *B₂* which had already been found in *G. hirsutum*, and the other, which was semi-dominant, was designated *B₃*. This gene is of considerable economic importance because it is stronger, in the homozygous state, than *B₂* and acts additively with *B₁* or *B₂*, so that *B₃ + B₁* and *B₃ + B₂* both confer greater resistance than *B₁ + B₂* when combined in the Sakel genome. *B₂* and *B₃* were linked together, with a cross-over value of 32-4%. It is interesting to note that in later backcrosses the recombination value increased, i.e. the linkage became weaker. This was attributed to the replacement of the *G. punctatum* chromosome segment between *B₂* and *B₃* by a *G. barbadense* segment. Since the two species are not very closely related there would probably be a greater frequency of crossing-over between two corresponding *G. barbadense* chromatids than between a *G. barbadense* chromatin and its *G. punctatum* homologue, introduced into the *G. barbadense* genome.

In the annual progress reports the first mention of breeding work involving *B₃* is for the year 1940–41 (112) when third and fourth backcross progenies from crosses involving the *G. punctatum* variety FS2 as resistant parent were grown and fifth backcrosses to Sakel were made, to give seed of the composition \([(FS₂ \times X 1530A) \times X 1730F] \times X 1730G] \times X 1730H^3\) and \([(FS₂ \times X 1530A) \times X 1730F] \times X 1730G] \times NT 2/38^3\). In the following year sixth backcrosses were made to X 1730H, and to NT 2/38 and NT 2/39, respectively (94). The results from these crosses led to the same conclusions regarding *B₃* as did the BAR 3 crosses. Two more backcrosses, the seventh and eighth were made in 1942–43 to the same recurrent parents (62). Crosses were also effected between seventh backcross material containing *B₃* and ninth backcross material containing *B₂* so as to increase the blackarm resistance of *B₂B₃* types which had proved themselves suitable for Gezira conditions. These hybrids, which were of both the X 1730 and NT 2 types, were sown out of season, and *B₂B₂B₃B₃* plants were selfed to produce seed for sowing bulk propagation plots. Seed of the X 1730 type thus made homozygous for *B₂* and *B₃* was grown in 1944–45 under the strain number BAR 4/11 (64).

In the breeding plots another backcross was carried out as an insurance against any unforeseen faults in BAR 4/11. This was apparently a backcross of BAR 4/11 to X 1730, for what
was designated ninth backcross X 1730, grown in 1945–46, was homozygous for both \( B_2 \) and \( B_3 \) (65). A small plot of \( B_1B_3 \) 1730 was also grown that year as a stage in the synthesis of a type carrying all three of the resistance genes. As stated above work on all the NT 2 types was discontinued.

BAR 4/11 proved very resistant to blackarm, and spinning tests showed that it was fully equal to X 1730A in spinning quality. We have already said, in discussing Sakel strains into which \( B_2 \) had been introduced, that BAR 4/11 yielded less than X 1730A and BAR 1730L and that this was attributed to X 1730H and not X 1730A being its most recent recurrent parent. For this reason it was decided to make two backcrosses of BAR 4/11 to X 1730A and self out a \( B_2B_2B_3B_3 \) strain.

Accordingly BAR 4/11 was crossed with X 1730A in the 1948–49 season and the \( F_1 \) was backcrossed to X 1730A. \( F_2 \) seed was produced in the winter for sowing in 1950 (68).

Another blackarm resistant variety of \( G. \) punctatum, Gambia Native, was crossed and backcrossed with Sakel but this line of crossing was soon discarded since the factors for blackarm resistance proved phenotypically identical with those obtained from FS2 (K14–1091, \( K_1E_1K \) and A12–G00).

It has already been mentioned that in 1942–43 BAR 2/11 and BAR 2/10, two strains originating from ninth backcrosses of B31 x Sakel hybrids to Sakel, were crossed with Domains Sakel as the first step in transferring \( B_2 \) and \( B_3 \) to Domains Sakel. This variety, which is the standard cotton in the northern half of the Gezira, was also crossed, in the same year, with seventh Sakel backcross material of the NT 2 type, homozygous for \( B_3 \), in order to add this gene to it as well (62). \( F_1 \)'s and first backcrosses were raised in 1943–44 and second backcross seed was obtained (63). The following year the third and fourth backcrosses, and in 1945–46 the fifth and sixth were carried out, the latest selections of Domains Sakel being used as recurrent parents (64, 65). Of the sixth backcrosses to Domains Sakel which were grown in 1946–47, the \( B_1B_1 \) and \( B_2B_2 \) types represented sixteenth backcrosses to \( G. \) barbadense and the \( B_2B_2 \) type a fourteenth backcross. \( F_2 \)'s of the sixth backcrosses were crossed with the latest leaf curl resistant Domains Sakel with a view to combining resistance to the two diseases by backcrossing to the leaf curl resistant stock (66). It was necessary to use the latter as recurrent parent since leaf curl resistance appeared to be due to a number of minor genes, some of which would almost certainly be lost in straight hybridization.
About a third of an acre of Domains Sakel homozygous for \( B_2 \) was grown in 1947–48, and seed from this was sown out of season in a five acre propagation area which yielded approximately half a ton of seed. It was of the composition \([(Uganda B31 \times X \ 1530) \times NT 29] \times DS1\), and was given the designation BAR 14/7. In addition, small propagation plots of \( B_1B_1 \) and \( B_2B_2 \) material of similar parentage were grown as BAR 14/11 and BAR 14/9 respectively. Each of the three sixth backcross types had been crossed with leaf curl resistant Domains Sakel, RDS, in the previous season, and in this season they were crossed with it twice more. RDS, however, did not prove equal in quality to the previous Domains Sakel parent, DS1. Therefore, instead of relying on the RDS crosses, advantage was taken of the high incidence of leaf curl infection to select rigorously for leaf curl resistance in the two most heavily infected areas of BAR 14/7.

Part of the seed from the plot of BAR 14/7 was used for sowing 105 acres in the Gash in the 1948–49 season, and a small quantity was sown in a replicated test at Medani, where it yielded 476.8 lbs. of lint per acre as against 387 lbs. from the parental Sakel used as control, this difference in yield being caused by a severe blackarm attack early in the season (68). Selection for leaf curl resistance within BAR 14/7 was continued, and the leaf curl resistant component which emerged was given the number BLR 14/16. In a trial at Medani, the parental Sakel, BAR 14/7 and BLR 14/16 showed 97%, 79% and 11% leaf curl infection, respectively.

The synthesis of a Domains Sakel type of similar parentage to BAR 14/7 but carrying both \( B_2 \) and \( B_3 \) was held up by a severe attack of leaf curl but the \( B_2B_2 \) plants were crossed with BLR 14/16 so as to combine leaf curl resistance with blackarm resistance.

While this work was going on other crosses were being made to transfer to Domains Sakel a fourth blackarm resistance gene, \( B_4 \), found in \( G. \ arboreum \) and a fifth, \( B_5 \), found in the \( G. \ barbadense \) variety Grenadines White Pollen. Knight has given an account of the transference of \( B_4 \) to Domains Sakel in the sixth of his series of papers on the genetics of blackarm resistance (117); the genetics of the \( B_4 \) type of resistance is described in the seventh paper of the series (118).

Crosses of the blackarm immune Multani (sanguineum), strain NT 12/30, which belongs to \( G. \ arboreum \) race hengalense Silow with Nuba Red, a semi-wild, Sudan type belonging to \( G. \ arboreum \) race soudanense and backcrosses to Nuba Red showed that the
immunity of Multani is controlled by the major gene $B_4$ together with a strong complex of modifying genes which, it is suggested, determine the difference between resistance, immunity and near immunity.

In the winter of 1940–41 Multani plants having $2n = 26$ chromosomes were treated with colchicine and were later pollinated with pollen of Sakel ($2n = 52$). $F_1$ plants, presumably having $2n = 52$ chromosomes comprising two Multani genomes and one Sakel genome were obtained from the largest seeds. In all, five backcrosses were made. Segregation in the $F_2$ of the fourth and $F_3$'s of the fourth and fifth backcrosses was observed, and it was found that a single partially dominant factor for resistance had been transferred from Multani to Sakel. Details are not given concerning the economic characters of the hybrids apart from their blackarm resistance.

The nature of the Sakel used in this breeding work is not clear. It is described by Knight in the paper referred to (117) as Domains Sakel, and no other strain is mentioned, but according to his progress report for 1946–47 (66) the eighth backcross to *G. barbadense* in the transference of $B_4$ to Domains Sakel was only the fourth backcross to Domains Sakel. Possibly the first four backcrosses in this case were to NT 2/38, for backcrosses to this strain are described in the earlier reports (94, 62, 63) but they do not seem to correspond with those described in the paper.

According to the 1947–48 report (67) a tenth backcross to *G. barbadense*, the sixth to Evelyn's selected Domains Sakel, was carried out in that year and in the following season $F_2$ plants homozygous for $B_4$ were raised.

Coses of fifth backcross plants with Sakel strains homozygous for $B_1$, $B_2$ and $B_3$ respectively showed that the segregation of $B_4$ was independent of these three genes and that $B_4$ had an additive effect in conjunction with $B_2$ and $B_3$. $B_1$ added little if anything to the resistance conferred by $B_4$ in the homozygous condition.

Three possible methods of transferring a gene or genes from *G. arboreum* to *G. barbadense* are discussed by Knight (117): (a) the allotetraploid method, (b) the autotetraploid method exemplified in the work just described and (c) straight transference via the triploid. (a) has the disadvantages that it is not always easy to synthesize the required tetraploid from a hybrid between *G. arboreum* and a diploid New World cotton and that the complication of a second foreign genome is introduced. The disadvantage of method (c) is the great difficulty
of obtaining the triploid F₁, though Harland successfully used this method when he transferred the G. arboreum gene R₂<sup>RS</sup> to G. hirsutum. In method (b) on the other hand it is easy to make the original autotetraploid by soaking G. arboreum seeds in a 0-05% colchicine solution for 48 hours and this tetraploid shows good fertility when used as female parent in crosses with G. barbadense. The F₁ obtained in this way lacks fertility but this difficulty can be overcome by raising a large F₁. A first backcross progeny of adequate size can then be obtained. In the present case a backcross progeny of 29 plants contained 3 showing a certain degree of fertility.

Another transference, referred to as the second, from tetraploid G. arboreum race bengalense to Sakal is now being made (66–68) with a three-fold objective (1) to see if B₄ will be transferred to the same locus as before, (2) to determine whether a strong intensifier of B₄, thought to exist in G. arboreum can also be transferred, and (3) to add to Sakal a G. arboreum gene for hairiness. An F₁ of 89 plants was grown in 1946–47, a first backcross progeny of 75 plants in 1947–48 and a second backcross progeny of 43 plants in 1948–49, selections from which were crossed with Sakal to form the third backcross.

It was noticed in the 1944–45 season that Grenadines White Pollen, a perennial variety of G. barbadense was resistant to blackarm. Crosses of this variety with Domains Sakal and X 1730A reached the first backcross stage in 1946–47 and a second backcross was made (66). Third backcross seed was produced the following year (67) and grown in 1948–49 (68). The resistance was found to depend on the major gene B₅ fortified by minor genes. B₅ is variable in expression but in general the homozygotes are more resistant than the heterozygotes. This gene is additive in conjunction with B₁, B₂, B₃ and B₄ (119).

It will be remembered that the gene B₂ is found in certain American Upland cottons. In order to increase the blackarm resistance of Upland types grown in the Sudan, B₂, when not already present, and the G. punctatum gene, B₃, have been added to them (112, 94, 62–68). When introducing both B₂ and B₃ into a variety Knight considers it best to transfer the two genes separately, i.e. by separate backcross programmes, and then combine the two kinds of resistant types obtained (115).

In the winter of 1940–41 third backcrosses of G. punctatum hybrids to NT 58/39 and 511D were made in order to transfer B₃ to them. These two varieties already showed a fair degree of blackarm resistance due to B₂. To make sure that any
accidental loss of a resistance factor would be recognized, a fully susceptible American variety, Durango, was also used as a backcross parent for comparison.

In 1941–42 it was found that seeds of Uganda SP84R received from the Uganda Department of Agriculture produced a proportion of plants with blackarm resistance depending on the gene $B_2$. The susceptible component of SP84R, designated SUS 7/2, was crossed with $G. punctatum$ carrying $B_3$. It was considered easier to add $B_3$ to the susceptible than to the resistant component; $B_2$ and $B_3$ could be combined later by crossing. Crosses were also made between NT 61, a Pump Scheme derivative to which $B_2$ had been transferred, and the Upland variety Deltapine as the first step in transferring $B_2$ to the latter. First backcross seed was obtained for sowing in 1942–43. To transfer $B_3$ to Deltapine it was crossed with $G. punctatum$ and the first backcross was made. Work was also carried out for the transference of $B_2$ to 51ID and of $B_2$ to XA129.

In 1942–43 the second and third SUS 7/2 backcrosses were made. In the transference of $B_2$ and $B_3$ to Deltapine the second backcrosses were grown. Similarly the second backcrosses of the 51ID and XA129 material were raised. It was decided to transfer $B_2$ and $B_3$ to BP 52 also, and for this purpose BP 52 was crossed with first backcross material of the XA129 type and the hybrids were backcrossed to BP 52.

Backcrossing was continued in 1943–44, and in 1944–45 the integration of an SP84R type homozygous for $B_2$ and $B_3$ was begun by crossing BAR 7/5 with BAR 7/1, these strains being homozygous for $B_3$ and $B_2$ respectively. Second backcrosses to Deltapine were on test, and third and fourth backcrosses were grown, thus concluding the breeding for blackarm resistance in this variety. 51ID already carried $B_2$, and enough seed was obtained from $F_2$ progenies of fourth backcrosses to grow a propagation plot of material homozygous for both $B_2$ and $B_3$, thus bringing this programme too to a close. The fourth backcross stage of XA129 was reached and material homozygous for $B_2$ was bulked as BAR 11/5. Meanwhile $B_2B_3$ had been transferred from Sakel to XA129 by four crosses and the product was crossed with BAR 11/5 to combine the two resistance genes. In the transference of $B_2$ from NT 61/38 to BP 52 the fifth and last backcross stage was reached in the winter of 1944–45, while in the transference of $B_3$ to BP 52 second backcross material was grown.

In 1945–46 BAR SP84, the blackarm resistant component of SP84R, i.e. the component carrying $B_2$, was accepted as the
future commercial cotton for Kordofan and Equatoria provinces, and all gene transference work ceased, except for the transference of \( B_0 \) to SP84R and the transference of \( B_2 \) and \( B_3 \) to Uganda BP 52. Fifth backcross BP 52 progenies and the \( F_2 \)'s of these were grown in 1945–46.

In the 1946–47 season a small propagation plot of BAR SP84 homozygous for both \( B_2 \) and \( B_3 \) was grown under the designation BAR 7/7; and BP 52 material of fifth backcross derivation, homozygous for \( B_2 \), was propagated.

The following year BAR 7/7 did not appear true to type and a later backcross was bulked as BAR 7/8. From a propagation area of this strain grown in the 1948–49 season 5000 lbs. of pure seed was produced.

The gene \( B_4 \) is not useful for transferring blackarm resistance within \( G. \) hirsutum because it is closely linked with, or possibly identical with, a gene designated \( d \), which determines an abnormality known as Dwarf-bunched (116).

It may be useful at this point to recapitulate the sources of the five blackarm resistance genes which have been transferred to cultivated cottons in the Sudan. \( B_1 \) and \( B_2 \) both occur in \( G. \) hirsutum; \( B_3 \) was found in \( G. \) punctatum (\( G. \) hirsutum var. punctatum); \( B_4 \) was derived from \( G. \) arboresum race bengalense; and \( B_5 \) was discovered in a variety of \( G. \) barbadense.

The methods used in transferring \( B_1 \), \( B_2 \) and \( B_3 \) to both Egyptian and American Upland varieties have been discussed by Knight in a research memoir published in 1946 (115). A more general paper by the same author on the backcross technique in cotton breeding has been referred to in Chapter I.

Similar techniques to those employed in the Sudan have been used in Uganda for transferring blackarm resistance to the variety BP 52 (96, 108). The blackarm resistant parent, B 181, had relatively short, harsh lint which appeared to be dominant to the long silky lint of BP 52 (147). Successive backcrosses to the latter were selfed and selected for good plant type. It was pointed out in the 1945–46 report on the work (107) that the transference was proceeding empirically with no reference to the genetics of blackarm resistance. \( B_2 \) alone appeared to be of much use in Uganda, and the presence of other named genes was suspected. In the 1946–47 season extensive series of BP 52 backcrosses were grown including first to fifth backcrosses carrying the gene \( B_2 \), from B 181 or a derivative, and two backcrosses carrying \( B_3 \), derived from the variety Gambia Native (146). B/C66, a third backcross, heterozygous for
blackarm resistance has been found to compare favourably with commercial BP 52 in both large and small scale spinning tests and has been released for multiplication (141). Thus the addition of blackarm resistance has not involved loss of the good fibre quality which is the chief asset of BP 52.

In recent years the backcross programme in Uganda has been extended to include the transference of genes for *Verticillium* wilt resistance, naked and tufted seed types, red plant body and other characters (109, 107, 140, 141).

In Georgia hybrids between Empire and Stoneville have been backcrossed to wilt resistant strains of Empire in order to introduce blackarm resistance to this variety, and crosses with the Hopi-Acala strain from California have been used in the same way to improve its fibre strength (45).

Simpson and Weindlunng have reported that hybrids between the bacterial blight (blackarm) resistant strain Stoneville 20 and susceptible varieties, and backcrosses to the susceptible parents, have proved highly resistant to the disease (159). Stoneville 20 carries the gene $B_1$.

VI. BREEDING FOR RESISTANCE TO *Fusarium* AND *Verticillium* WILTS

The Broach cotton breeding scheme was initiated by the Bombay Department of Agriculture in 1932 with the aim of developing wilt resistant strains with a high ginning percentage and high spinning capacity (153). Since none of the selections from the local material met these requirements Broach deshi (*G. herbaceum* var. *frutescens*), a high quality cotton resistant to *Fusarium* wilt, was crossed with Goghari (also *G. herbaceum* var. *frutescens*), a wilt-susceptible type inferior in quality but having a high ginning outturn, and with introduced cottons superior to Goghari in fibre qualities. Promising segregates were backcrossed to BD8. Segregates 1–2 and 1–6 from the backcross (BD8 x Goghari A20) x BD8 have given very satisfactory results and are considerably better than Broach Local (a mixture of Broach deshi and Goghari) as regards fibre qualities and spinning capacity; they are resistant to wilt and their ginning outturn exceeds that of BD8 by 7–8%. The strains were distributed as a composite variety known as Vijay.

Resistance to *Fusarium* is thought to be governed by two dominant complementary genes, $A$ and $B$, the presence of which
is essential for resistance, and a third dominant gene, $C$, which inhibits their action (110).

An improvement in the fibre length of BC 1–2 and BC 1–6 is being sought by crossing with long stapled 1027 ALF and subsequently backcrossing (153).

In a project in Louisiana to combine *Fusarium* wilt resistance with other desirable characters crosses between commercial varieties were carried out and some of the $F_1$'s were backcrossed to the resistant parents (47). This is an attempt to introduce desirable genes into a resistant variety; if the objective were to introduce wilt resistance into an otherwise acceptable strain, backcrosses would be made to the susceptible parent.

In Georgia a wilt resistant variety CSS 3720, developed by backcrossing the hybrid Cleveait $\times$ Stoneville to Stoneville has given good results (44–46).

At the Bambesa experiment station in the Belgian Congo the backcross technique has been employed for the improvement of the variety Stoneville especially as regards ginning outturn and to introduce *Fusarum* wilt resistance into it (21, 22).

According to Harrison (105) backcrossing has been successfully used in California in breeding for resistance to *Verticillium* wilt.

In Mississippi the transference of tolerance to *Verticillium* wilt to a locally adapted variety is being attempted (48).

**VII. Breeding for High Ginning Outturn**

An attempt was started in the Sudan in 1942–43 to transfer some or all of the higher ginning outturn of Deltapine to XA129 (62). In $F_1$ hybrids between these two varieties the ginning outturn was intermediate, the high ginning outturn of Deltapine being partially dominant.

In 1943–44 first backcross hybrids were grown in comparison with $F_1$'s and the parental varieties, and the following figures for ginning outturn were obtained: XA129, 26 to 35%, for individual plants, with a mode at 29%; Deltapine, 32 to 45% with a mode at 39%; $F_1$, 31 to 41% with a mode at 35%; and first backcrosses 24 to 36% with a mode at 32%. First backcross plants with 36% ginning outturn were selected for resemblance to XA129 in appearance and backcrossed again to XA129 (63).
In the second backcross progenies four plants had the desired combination of quality comparable to that of XA129 and high ginning outturn (64).

These results did not, however, have the practical value which had been intended because in the following year, 1945–46, XA129 was superseded by BAR SP84 (65).

VIII. BREEDING FOR BOLLWORM RESISTANCE AND FIBRE STRENGTH

Two Gossypium species which showed resistance to pink bollworm (Platyedra gossypiella) in the Anglo-Egyptian Sudan, G. Thurberi \((2n = 26)\) and G. Armourianum, were crossed with Sakel in 1942–43 and 1943–44 respectively in order to transfer their resistance to the latter (62, 63). The \(F_1\) hybrids in each case were sterile but a presumed hexaploid hybrid (\(2n = 78\)) between G. Armourianum and Sakel was obtained which set seed relatively freely. It was named G. armadense. In the 1944–45 season this hybrid was completely free from bollworm attack and it was thought probable that the resistance was connected with the abundant essential oils and resins found in the oil glands of the plant. Backcrosses to Sakel were carried out (64).

Attempted backcrosses to Sakel of the hybrid between G. Thurberi and Sakel were not successful, but in the 1945–46 season hexaploid plants, designated G. thurbadense, were obtained after treatment of six \(F_1\) seeds with 0.05% colchicine for 48 hours (65). These plants, which were resistant to bollworm, were crossed with Domains Sakel. The resulting backcross hybrids showed remarkable uniformity. They each, presumably, had 65 chromosomes representing a full G. barbadense somatic complement and a single set of G. Thurberi chromosomes. Resistance to pink bollworm seemed to be recessive, for it did not appear in this generation.

The backcrosses involving G. Armourianum were less uniform than those involving G. Thurberi, indicating a stronger residual homology between the G. Armourianum genome and the D genome of Sakel than between the G. Thurberi genome and the D genome of Sakel.

Second backcrosses of both types grown in 1946–47 showed some variation in fertility (66). Selections of the G. Thurberi hybrids, which also varied greatly with respect to bollworm damage, were made for further backcrossing to Domains Sakel; and the G. Armourianum hybrids, of which there were only five, were all backcrossed to Sakel.
A start was made also in the transference of bollworm resistance to American cottons. A presumed pentaploid F₁ hybrid between the hybrid referred to as *G. thurbadense* and Domains Sakel was bulk crossed with XA129, which appeared to be unusually susceptible to bollworm attack. The form designated *G. armadense* also was crossed with XA129 and the pentaploid progeny were bulk backcrossed to it.

Two types of families of *G. Thurberi* hybrids were grown in 1947–48, PE 1–22/47 representing the F₂ of the second backcross and PE 23–40/47 representing the F₁ of the third backcross of the hexaploid hybrid between *G. Thurberi* and Sakel to Domains Sakel (128). A heavy attack of bollworm was induced by sowing six acres of American Upland beside the test plot some eleven weeks before the hybrids were sown; when the hybrids were flowering freely the Upland cotton, which by this time was heavily attacked by bollworm, was cut and left lying; and in addition to this, bolls from the Upland cotton were broadcast in the test plot.

None of the forty progenies showed any appreciable bollworm resistance. It appeared that either the bollworm resistance of *G. Thurberi* could not manifest itself in tetraploid *G. barbadense* or not enough parents had been selected in the previous generations to give reasonable certainty of including resistant ones. The former possibility was thought most likely.

Of the *G. Armourianum* crosses, three progenies were grown, having the following compositions:—

PE 41/47—Amphidiploid hybrid between *G. Armourianum* and Sakel × Domains Sakel² F₁.
PE 47/47—Amphidiploid hybrid between *G. Armourianum* and Sakel × XA129² F₁.
PE 42–46/47—Amphidiploid hybrid between *G. Armourianum* and Sakel × Domains Sakel³ F₁.

Of 161 plants of the first of these progenies, 51 showed a variable amount of fertility while the other 110 failed to set a single boll. Several of the fertile plants which appeared resistant to bollworm were backcrossed again to Domains Sakel.

There were 23 plants of PE 47/47, 10 of which showed varying degrees of fertility. Two plants appeared to carry marked bollworm resistance and these were backcrossed again to American Upland.

In the families PE 42–46/47, only PE 46/47 showed any worthwhile degree of resistance, and several partially resistant plants were selected for further backcrossing.
In the 1946–47 season lint from 33 plants of the second backcross of the form referred to as *G. thurbdense* to Domains Sakel were sent to the Shirley Institute for preliminary tests of lint strength, and one of them, J. 1129/46.4, was outstanding, having a strength index of 9.99 as judged by Pressley fibre strength tests. This plant had an effective lint length of 49/32 inches and a standard fibre weight of 119. Apart from its hair characteristics it was indistinguishable from Domains Sakel in the field (67). It was backcrossed to Domains Sakel and in 1947–48, 153 third backcross plants were raised, three of which gave excellent results in lint tests and were backcrossed again, this time to BAR 14/17 instead of Domains Sakel.

The three families from these crosses were grown the following season (68). They were badly attacked by leaf curl but a small quantity of selfed seed was obtained from most of the plants, and several were selected which appeared to have the fibre strength of *G. Thurberi*.

This work has two possible uses: it offers a means of increasing the fibre strength of Sakel by some 22 or 23%, and should breeding for increased hairiness as a protection from jassids lead to increased fibre weight, this material with standard hair weights of 104–107 would be useful for reducing it.

**IX. Breeding for Deciduous Bractlets and for Suitability for Mechanical Harvesting**

Two other backcrossing projects which have recently been carried out in the Sudan must be briefly mentioned (65, 66, 128, 68).

An attempt has been made to transfer the character of deciduous bractlets from an imported Upland variety to Domains Sakel and to BAR SP84. However, this character, which was inherited as a recessive, was associated with deleterious effects on boll size, boll shedding, leaf abnormality and fertility. As this association could not be broken up, the project has now been abandoned.

With a view to producing a cotton suitable for mechanical picking, the genes for “Egyptian Short Branch” and “Cluster” have been transferred from an Egyptian and an Upland type respectively to Domains Sakel, but unfortunately they have such a weak expression, when fully transferred, as to be of no economic significance.
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CHAPTER III

THE BACKCROSS METHOD IN TOBACCO BREEDING

I. INTRODUCTION

Mosaic, wildfire (*Pseudomonas tabacum*), black shank (*Phytophthora parasitica*), black root rot (*Thielaviopsis basicola*), root knot (*Heterodera marioni*) and nematode root rot (*Pratylenchus* sp.), are all tobacco diseases to which resistance has been introduced into commercial varieties. An account follows of the backcross programmes involved and of a few others designed to transfer genes for characters other than disease resistance.

Our chief concern is with mosaic disease.

II. THE USE OF AMBALEMA IN BREEDING FOR MOSAIC RESISTANCE

Two main sources of resistance have been widely used in breeding for resistance to this virus disease: Ambalema and *Nicotiana glutinosa*. *N. rustica* has also been employed.

Ambalema is a variety of *N. Tabacum* which was discovered by J. A. B. Nolla in Colombia in 1929 (61). Hybrids involving this variety have to be backcrossed to commercial varieties before they are suitable for cultivation because they inherit low smoking quality and unsuitable leaf characters as well as the desired mosaic resistance from the resistant parent.

The resistance of Ambalema is determined by two pairs of recessive factors, designated by Nolla $r_{m1}$ and $r_{m2}$. Clayton, Smith and Foster (30) who refer to these genes as $a_1$ and $a_2$ reported the existence also of modifying genes which influence the degree of resistance. Such modifying factors present some difficulty in breeding by the backcross method.

J. A. B. Nolla's breeding work with Ambalema as a source of mosaic resistance was started in the autumn of 1929 in Puerto Rico and continued at the Universities of Cornell and Wisconsin, and then in Puerto Rico again (1, 59, 60). Ambalema was first crossed reciprocally with the Turkish variety Samsun from Greece. Other susceptible varieties used in the crosses were White Virginia No. 9, a native Puerto Rican tobacco and
No. 144-9-1, a *Phytophthora* resistant line selected from the cross Cuban x Turkish.

The $F_1$ hybrids from the crosses with Samsun were susceptible to mosaic. In the $F_2$ a ratio of 15 susceptible segregates to one resistant was obtained, and in four out of five progenies from the backcross of the $F_1$ to the susceptible parent the ratio was 3 : 1, further showing that resistance is determined by two recessive factors, which was confirmed in the $F_3$. Thus certain $F_3$ lines gave a 3 : 1 segregation as in the backcross and these were made use of in the breeding programme. Owing to the recessiveness of the characters and the consequent small proportion of resistant segregates it was necessary, of course, to grow large progenies. Morphological characters, length of growing period, burning and smoking quality, resistance to black shank and other characters were selected for in the mosaic resistant lines. Nolla remarks (60) that backcrossing did not prove as useful in this project as in other crop improvement investigations. It does not appear to have been used to any great extent in subsequent work at the Tobacco Institute of Puerto Rico after Nolla's resignation as director (1).

In Java, Ambalema was crossed reciprocally with Kanari and selection for mosaic resistance carried out in the $F_2$ (32). Promising plants which were reasonably satisfactory as regards quality and leaf shape were backcrossed with Kanari. Mosaic resistant Kanari-like forms from the $F_3$ of Ambalema x KW10 were crossed with Timor Dj. to improve the quality and introduce *Phytophthora* resistance (56). Selection for mosaic resistance was to be begun in the $F_2$ and repeated backcrosses made to Vorstenland plants so as to combine disease resistance with the necessary quality. In 1938 the cross with Timor Dj. was inspected and found to be little better in quality than the KW10 crosses. The plot which showed the greatest resistance was worst in quality, so seed from high-quality infected plants was collected because, mosaic resistance being recessive, the chances of combining resistance and quality in the progeny of such plants were considered good. Unfortunately no further reports of the Experiment Station for Vorstenland Tobacco, subsequent to the 1938-39 one (57), are available.

Breeding for the Ambalema type of mosaic resistance is referred to by Nelson (58) as an example of the way in which new strains are developed in the plant breeding programme of the Tobacco Division of the Dominion Department of Agriculture in Canada.
The method is to inoculate with mosaic virus the F₂ plants from crosses of Ambalema with commercial varieties in order to determine the resistant segregates. Some of these are then both selfed and backcrossed to the commercial parent. If the F₃ plants obtained by selfing are not resistant, all seed from the backcross with the parent selection has to be discarded. The F₄ of the backcross is subjected to the same treatment as the original F₂ population, and the process is repeated for several generations in order to obtain a resistant selection with the characters of the commercial parent.

This backcross method was begun in 1937 when the whole tobacco breeding programme at the Central Experimental Farm, Ottawa, was reorganized (54). It was found that 6 to 7% of the resistant plants in an F₂ progeny were usually of the Ambalema type, but after three or more backcrosses had been carried out many of the undesirable characters had been eliminated. The majority of the mosaic resistant hybrids are now quite similar to their respective mosaic susceptible parents (54).

From 1937 to 1948, 103 progeny strains from crosses of burley varieties with Ambalema were tested for mosaic resistance, about 50 plants of each being individually inoculated by hand, and resistant plants were selected each year for further work. The burley varieties first chosen as recurrent parents were Kelley, Harrow Velvet and Judy's Pride. In 1948 these lines were in the fourth and fifth backcrosses of the F₁ to F₃ generations.

It was decided, also, to incorporate mosaic resistance into White Mammoth, Yellow Mammoth, Bonanza and Warne, four widely grown flue cured varieties which had many desirable characters such as good quality and yield but were badly damaged in some years by mosaic. Up to 1948, 136 progeny strains were inoculated with the available strains of the mosaic virus and selection for resistance was carried out on the basis of the results; in that year the breeding material consisted of two selections of Bonanza, seven of White Mammoth, one of Warne and three of Yellow Mammoth, all in the third and fourth backcrosses of the F₁ to F₃ generations. All these strongly resembled their susceptible recurrent parents but were, for the most part, highly resistant to mosaic.

The introduction of mosaic resistance into cigar varieties was initiated in 1942 when the three most popular varieties of this type, Connecticut Havana 38, Comstock Spanish Pomeroy and Resistant Havana 211, were crossed with a resistant F₃ strain of Judy's Pride x Ambalema, which was the most resistant
strain available in that year since no Ambalema stock had been
grown later than 1939. From 1941 to 1948, 62 cigar tobacco
progeny selections were tested, five of Comstock Spanish Pomeroy,
two of Resistant Havana 211 and four of Connecticut Havana 38
being inoculated in 1948. These selections, which were in the
third and fourth backcrosses of the F₁ and F₄ generations,
appeared to be quite similar, apart from their mosaic resistance,
to their susceptible parents.

Resistant Havana 211 obtained from Ottawa is now being
used in Chile for the transference of the Ambalema factors for
mosaic resistance to susceptible varieties (22).

W. D. Valleau, working on mosaic resistance in dark and burley
tobaccos at the Kentucky Agricultural Experiment Station has
used the backcross method for introducing both the resistance
of Ambalema and that of N. glutinosa into commercial varieties
of tobacco and for combining the two types of resistance (70).
He found that although it was possible to backcross F₂ plants
of crosses between Ambalema and burley tobacco with a
susceptible variety four consecutive times and still retain mosaic
resistance, there was some question as to whether the resistance
was as great as in the original Ambalema selections. Resistant
burley varieties obtained by backcrossing showed some unde­sirable characters: they had a somewhat objectionable plant type
and a lower yield than the Ky 16 parent and the majority of
them wilted in hot weather with the result that scald occurred
in one or more leaves. In 1946 Valleau stated (71) "In over
ten years' breeding no satisfactory varieties of burley or dark
fire-cured tobacco containing the Ambalema factors for resistance
have been developed. Plant type is not satisfactory and the
leaves are inclined to wilt and scald under conditions where
other varieties are not injured."

But a note of optimism appears in the Experiment Station
Report for the following year. A variety distinct from the
rest was noted as being more promising (9). It was of the stand­
up type and highly resistant to black root rot and mosaic, and
for three years had shown no signs of wilting and scalding. It
seemed possible that the factor for scalding had been eliminated
by crossing over. So at last there was some hope of developing
satisfactory burley varieties for Kentucky with the Ambalema
factors for mosaic resistance.

At the Trelawney Tobacco Research Station, Southern
Rhodesia (2), Ambalema was crossed with Jamaica Wrapper,
and the hybrid was backcrossed to the latter and selfed, after which the mosaic resistant selections were again crossed to Jamaica Wrapper and selfed. Three plants from this second selfing were sown in 1945. In one family of about 350 seedlings fourteen immune seedlings were obtained, while the other two families were completely susceptible. The immune selections were very similar in growth type and leaf shape. They showed none of the twisting characteristics of Ambalema, but were easily distinguished from the flue cured varieties of tobacco under cultivation. Ten of the immune plants were crossed on to White Stem Orinoco. Eleven resistant lines grown the following year all had as complete a resistance to mosaic as the original Ambalema. Crosses between immune plants and White Stem Orinoco, Jamaica Wrapper and Bonanza were also grown and selfed.

Hybrids between Pennsylvania and Ambalema have been used in breeding for disease resistant cigar tobacco at the Pennsylvania Agricultural Experiment Station. In 1945 several seventh backcross hybrids were notable for their good quality, acceptable leaf shape and desirable colour (12). Pennsylvania R5A, a line combining resistance to mosaic and black root rot had a high leaf count and other desirable characters, and in 1947 it was reported to be acceptable in nearly every respect (13). Other such hybrids were also of desirable type (12, 14). Their pedigrees are not given.

In New Zealand (15–20), crosses have been made between flue cured tobacco and Ambalema, and the segregates for mosaic resistance have been backcrossed to the flue cured parent. Highly resistant lines have been obtained but these still fall short of the desired flue cured type.

III. THE USE OF N. glutinosa AND N. rustica IN BREEDING FOR MOSAIC RESISTANCE

The response of N. rustica to the mosaic virus takes the form of systemic necrosis, determined by a dominant gene, $N$, the action of which may be modified, according to Holmes, by a recessive gene, $d$.

In N. glutinosa a dominant factor, $N$ (or $Vr$ according to Kostov), is responsible for localizing the virus in necrotic spots if the infection is light or may bring about systemic necrosis if it is heavy (70, 71). This factor can be transferred to N.
Tabacum and since the resistance is expressed in all hybrids carrying the gene, these are easily picked out in successive backcross generations, selfing as in the case of recessive factors being unnecessary. Valleau has recently reported (73) that N. glutinosa carries, in addition to N, a dominant factor for mosaic susceptibility. He interprets the findings of McKinney and Clayton on the effect of temperature (55) as showing that a temperature of 97° F. causes the N factor to become temporarily non-functional and allows the factor for susceptibility to be expressed.

F. O. Holmes transferred the necrotic reaction of N. rustica to N. paniculata (40, 41). The response of the interspecific hybrid to the virus infection resembled that of N. rustica. By repeated backcrossing to N. paniculata of hybrids giving this response, followed by selfing after the third or fourth backcross, self fertile plants resembling N. paniculata but homozygous for the necrotic reaction were obtained.

Holmes states that these hybrids would be identified as N. paniculata if found growing wild and the new strain may, for practical purposes, be considered a necrotic type variety of N. paniculata; but it may differ from this species in ways not then recognized, for a chromosome segment and not just a single gene was probably carried over from N. rustica.

In the backcresses, N. paniculata was used as male parent. In most cases the ratios obtained in the progenies from selfing and backcrossing agreed with the hypothesis that the necrotic reaction is governed by a single main dominant gene, N. The necrotic response was not the same in all cases: backcross progenies gave what was termed the unmodified necrotic type, whilst some of the progenies from selfing the fourth backcross gave what was termed the delayed necrotic type, somewhat resembling the response of N. rustica. The delayed type appeared to be governed by the recessive gene d segregating independently of N.

Subsequently Holmes reported the transference of the necrotic factor from the backcross material referred to above to plants of N. paniculata x N. Tabacum backcrossed twice in succession to N. Tabacum (42). In the backcross generations there were considerable deviations from the expected 1 : 1 ratio of necrotic types to mottling types.

It may be mentioned, incidentally, that Lammerts, in a cytogenetical study, had obtained a series of true breeding lines by making repeated backcrosses of the hybrid between N. rustica
and *N. paniculata* to *N. paniculata* (52). These lines, however, were quite distinct from the recurrent parent. Backcrossing to *N. rustica* var. *pumila* similarly gave rise to derivative types distinct from each other and from *N. rustica* var. *pumila* (53).

Holmes also transferred the *N. glutinosa* type of resistance to *N. Tabacum* (43, 44) by the use of the amphidiploid hybrid between *N. glutinosa* and *N. Tabacum* obtained from R. E. Clausen. This amphidiploid, referred to as *N. digluta*, had the advantage of being fertile whereas ordinary hybrids grown by Holmes had proved consistently sterile.

When pollinated with pollen of *N. Tabacum* var. Connecticut Broadleaf, the amphidiploid plants readily set seed. All the 132 plants from this cross gave the *N. glutinosa* response to mosaic infection. In further backcrosses to *N. Tabacum*, three varieties of this species were used: Connecticut Broadleaf, White Burley and Samsun. The segregation ratios for response to the mosaic virus were different in the different crosses. No 1 : 1 backcross or 3 : 1 selfed ratios occurred in the first few generations.

After the first backcross generation of the "*N. digluta*" x *N. Tabacum* hybrid to *N. Tabacum* there was little visible indication of any *N. glutinosa* characteristic in the hybrids, which soon acquired the distinctive characteristics of the recurrent parents. A line homozygous for *N* was obtained by repeatedly selfing the first backcross to Samsun. Homozygous lines could not be obtained from backcross plants of Connecticut Broadleaf or Burley 16 parentage. The homozygous line was self and cross fertile and Holmes believed that it would prove useful for the introduction of the *N* type of resistance into locally desirable varieties of *N. Tabacum*. It will be seen from what follows that it did in fact prove very useful for this purpose.

He thought also that *Nn* plants resulting from a greater number of backcrosses to *N. Tabacum* would be useful in such breeding projects since, in them, there would have been more opportunity for crossing over between the *N. glutinosa* chromosome carrying the *N* factor and the corresponding *N. Tabacum* chromosome and therefore more chance of the unwanted parts of the *N. glutinosa* chromosome being eliminated. It will be seen however that W. D. Valleau obtained disappointing results with fifth backcross strains from Holmes' material and that Gerstel's cytological studies showed that crossing over such as Holmes had in mind was not as frequent as he had hoped.
Kostov, like Holmes, failed to obtain seed from backcrosses to *N. Tabacum* of hybrids between this species and *N. glutinosa*, and used the amphidiploid hybrid for transferring mosaic resistance to *N. Tabacum* (46, 51). By selfing selections from the second backcross of *N. Tabacum* x “*N. digluta,*” three families were obtained which gave the local necrotic reaction to mosaic and had the normal *N. Tabacum* chromosome number, \(2n = 48\).

*N. rustica* var. RL was also used by Kostov (47, 48) in combination with “*N. digluta.*” From the cross (*N. rustica* var. RL x *N. Tabacum* var. Basma) x “*N. digluta*” he obtained a plant possessing two genomes of *N. Tabacum* and one each of *N. rustica* and *N. glutinosa*. This plant, which gave the desired necrotic reaction was backcrossed to *N. Tabacum*. Nine plants resembling *N. Tabacum* but exhibiting the necrotic reaction were obtained in the first backcross, and the most fertile of them was again backcrossed to *N. Tabacum*. Selected second backcross plants were selfed for two generations and gave rise to three fertile families homozygous for local necrosis. These families, also, had the normal *N. Tabacum* chromosome number. The family with the greatest morphological uniformity has been designated *N. Tabacum* var. *Virii*.

Crosses were made between *N. Tabacum* var. *Virii* and several different varieties of tobacco (51). The data indicated that *N. Tabacum* var. *Virii* carried both the \(N\) genes of *N. glutinosa* and the genes for the reaction of *N. rustica* var. RL which at ordinary temperatures is the local necrotic reaction and at higher temperatures “flowing” necrosis.

Breeding work in Russia to utilize the mosaic resistance of *N. glutinosa* has been reported by Ternovskii (65–68). It was begun in 1936. Like Holmes and Kostov, Ternovskii found that hybrids between *N. glutinosa* and *N. Tabacum* were sterile and therefore useless for breeding purposes, but by growing large numbers of hybrids fertile amphidiploids were obtained. In the progeny of the first backcross (*N. glutinosa* x Dubec) x Dubec and in subsequent backcrosses segregation for resistance occurred in different ratios. The deviation from Mendelian ratios was attributed to elimination of certain chromosomes, gametes or zygotes. Some families with regular meiosis gave regular 3 : 1 ratios. Some bred true for resistance up to the eighth generation and in all other respects resembled the commercial parent Dubec 44/39, although sometimes varying in time of maturity, height and other characters.
According to Ternovskii, resistant hybrids in no way inferior in quality to Dubec 44 appeared from the fourth or fifth generation onwards and comparison of immune and susceptible plants from different backcrosses showed no correlation between immunity and quality. Moreover, 6 out of 18 lines tested excelled Dubec in flavour.

The fertile hybrids and their backcrosses tended to be inferior to Dubec in yield and vigour, but in the later backcross generations immune types appeared with yields surpassing that of Dubec by 14 to 19%. One immune form was included in the state variety trials in 1940 only four years after the work on mosaic resistance was started.

A number of hybrids combining immunity to both mildew (Peronospora tabacina) and mosaic with yield, quality and morphological characters equal to those of Dubec were also produced.

Immune forms of all the main commercial types are reported to have been obtained by crossing the mosaic immune Dubec hybrids with other standard varieties. They include Samsun 311 which exceeds the standard Samsun 57 in yield and equals it in quality, American 232 which surpasses the standard American 572 in yield, gives a more aromatic product and shows more rapid growth, Tyk-Kulak 220 which equals Trebizond 92 in yield and is superior in aroma, and Trebizond 117 which exceeds the standard Trebizond 1272 in yield and quality.

Valleau (70) found that transference of the N factor of N. glutinosa to the N. Tabacum genome was often accompanied by transference of other, less desirable characters. Of three strains homozygous for N isolated from a fifth backcross bred by Holmes in which the burley variety Ky 16 had been used as the recurrent parent, two were lighter in colour than Ky 16, had smaller upper leaves, bloomed much lower and had very tough suckers, while the third was of the same colour as Ky 16 and grew nearly as large but yielded about 25% less tobacco. Several other NN strains of burley bred at the Kentucky Experiment Station were isolated but many had to be discarded because of slow growth, low yield and other undesirable characters. Strains 48-7, 48-9 and 48-11, for instance, which were tested in 1940 (3), tended to blossom early and to produce small upper leaves and tough suckers which were hard to break off. In comparative tests in 1941 Ky 48-7 yielded only 77% as much tobacco per acre as Ky 16. It thus appeared that the N factor carried with it other factors which affected plant type when in
the homozygous condition. There were, however, some NN strains which appeared promising, and four years later Valleau was able to report (71) that, after as many as nine backcrosses of hybrids between Ky 16 and N. glutinosa to Ky 16, varieties with NN resistance, somewhat earlier and lower yielding than Ky 16 but otherwise satisfactory, had been obtained. NN strains tested in 1943 (6) proved to have inherited the black root rot resistance of the recurrent parent, Ky 16, as well as exhibiting the mosaic resistance of the N. glutinosa parent.

It has now been reported (73) that some of the NN varieties obtained, viz. Ky 52, Ky 56, Ky 151 and Ky 160 have been grown commercially with satisfactory results regarding plant type, quality, yield and freedom from mosaic under ordinary conditions.

Very promising results were achieved with dark tobacco in the experiments to introduce the N type of resistance. By crossing Holmes' NN Samsun with the susceptible dark fire cured varieties Little Crittenden, Little Orinoco and Brown Leaf, and the air cured variety One Sucker, and then backcrossing four or five times, mosaic resistant varieties apparently otherwise identical with the original varieties were obtained (71, 7).

Comparative yield data in pounds per acre for these mosaic resistant strains and the susceptible varieties from which they were derived (except for One Sucker) are given in the 1947 Report of the Kentucky Station (9). In three year averages, although not in each separate year, the mosaic resistant varieties outyielded the parents. Their quality was quite similar to that of the parents.

The mosaic resistant Little Orinoco produced in Kentucky is now being used in Chile for introducing mosaic resistance into air cured and cigar tobaccos grown there (22).

In New Zealand experiments to introduce the N factor into flue cured varieties have been begun in which NN hybrids of burley and dark tobacco received from Valleau are being used as resistant parents.

A cross between burley and the amphidiploid hybrid between N. glutinosa and N. Tabacum obtained by Holmes was used at the Trelawney Research Station, Southern Rhodesia as a source of the N type of mosaic resistance (2). Successive backcrosses were made to the variety Bonanza. After only two backcrosses, the hybrids were closely similar to that variety in
appearance, and the proportion of plants showing the local necrotic reaction to those with systemic infection approximated to the theoretical $1:1$ ratio. After four backcrosses the plants were indistinguishable in appearance from the recurrent parent, but they were markedly slow growing and lacking in vigour. In 1945, seven backcrosses to Bonanza had been made. Five hundred seedlings grown that year from seed of selfed backcross hybrids and inoculated with the tobacco mosaic virus gave the expected $3:1$ ratio of necrotic to systemic plants. Twelve of the most vigorous of the necrotic plants were bagged, and seed from these gave two double dominants and ten single dominants. One of the former was included in a varietal test. Unfortunately this had to be abandoned owing to waterlogging of the soil, but from field observations the mosaic resistant strain seemed to be slower growing and to produce smaller plants. Its leaf was of good quality and indistinguishable from Bonanza in colour, feel, and aroma. Backcrosses were made to Bonanza, Jamaica Wrapper and White Stem Orinoco.

The transference of mosaic resistance from $N. glutinosa$ to $N. Tabacum$ is of particular interest because something is known from cytological observations of the mechanism of transfer. According to D. U. Gerstel (35-3) mosaic resistance was introduced into the variety Holmes' Samsun by substitution of the $N. glutinosa$ pair of chromosomes designated $H_g$, carrying the resistance gene, for the $H_t$ chromosome pair of Samsun. Unfortunately for the breeder, factors of $N. glutinosa$ which reduce yield are carried on the same chromosome, and Gerstel found that in heterozygous plants the $H_g$ and $H_t$ chromosomes normally fail to pair so that the resistance factor and the yield reducing factors are inherited together, there being no crossing-over. This explains Valleeau's difficulty in obtaining satisfactory resistant plants. It was shown, however, that occasionally the chromosomes do come together and exchange of segments may occur. This apparently is what happened when the linkage group was broken up and commercially satisfactory mosaic resistant tobaccos were obtained.

Somewhat different conclusions are reached by D. Kostov who finds Gerstel's observations unconvincing and thinks his material should be reinvestigated.

Kostov studied meiosis in the pollen mother cells of the F$_1$ of $N. Tabacum$ var. Virii (alba) x the variety Nevrokop Basma of $N. Tabacum$ and of $N. Tabacum$ var. Virii (alba) x the $N. Tabacum$ variety Serska Basma (49, 50). In the first hybrid 24 bivalents
were found in 108 pollen mother cells and 23 with 2 univalents in 8 pollen mother cells (7.4%). In the second hybrid 82 pollen mother cells had 24 bivalents, and 4 (4.7%) had 23 bivalents plus 2 univalents. The results show that the *N. Tabacum* var. *Virii* chromosome carrying the mosaic resistance factor nearly always conjugates with its *N. Tabacum* partner. Kostov interprets these data as evidence that transference of a chromosome segment carrying the gene *N* (or *Vr* as he calls it) has occurred and attributes the small proportion of cases in which conjugation fails to the existence of the non-homologous segment.

These results can be reconciled with Gerstel’s by supposing that although pairing between the *Ht* and *Hg* chromosomes is unusual, they did come together in the breeding of *N. Tabacum* var. *Virii* and an exchange of segments took place. Apparently Kostov was unaware of Gerstel’s publication of 1948 (38) in which he states that exchange of segments between the two chromosomes in question may in fact occur and evidently has done so in Valleau’s breeding work.

IV. COMBINATION OF THE AMBALEMA AND *N. glutinosa* FACTORS FOR MOSAIC RESISTANCE

The combination of the Ambalema type of mosaic resistance with the *N. glutinosa* type at the Kentucky Station was found to be more effective than the use of the *N* factors alone in that the necrotic spots developed much more slowly in a hybrid carrying both kinds and the plants could be regarded as almost completely immune (4). *Ky 52* was developed by backcrossing the mosaic resistant amphidiploid hybrid between *N. glutinosa* and *N. Tabacum* with burley tobacco carrying the Ambalema factors for resistance (5). It showed complete freedom from mosaic even though inoculated, made rapid, vigorous growth in soil infested with the black root rot organism and produced tobacco of excellent quality. Valleau (70) reports the production of ten such strains of burley by backcrossing *NN* hybrids with the Ambalema type of resistance. These strains were set in the field in 1941 and inoculated with the mosaic virus 25 days after setting. They were heterozygous for *N* and had not been selected for the *a* type of resistance. Of 294 plants, 245 showed no evident signs of infection. In the greenhouse, *Nn* *a_1a_2* *a_3* plants rarely showed systemic necrosis under conditions where nearly all *Nn* plants would be destroyed.

A. Goenaga (39) reports that a fertile hybrid of the cross *N. Tabacum* × *N. glutinosa* was obtained in 1944 at the Tobacco
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Institute of Puerto Rico and backcrosses made to commercial varieties and to some of the mosaic resistant strains from crosses with Ambalema in an effort to develop a variety with no character of N. glutinosa except the necrotic reaction to the mosaic virus. The F₂ plants were not however completely immune in inoculation tests.

V. THE USE OF N. longiflora IN BREEDING FOR WILDFIRE RESISTANCE

The wild species N. longiflora is immune to wildfire, a major disease of tobacco caused by the bacterium, Pseudomonas tabacum. Beginning in 1934, E. E. Clayton tested N. Tabacum collections from various parts of the world but did not discover a single genotype which was highly resistant to this disease. He therefore attempted to cross the two species in order to transfer the immunity of N. longiflora to cultivated tobacco (27, 28). From a cross between tetraploids of the two species, a few plants weak in growth and completely sterile were obtained. One of these produced shoots from callus tissue which were vigorous and set seed freely when pollinated with N. Tabacum pollen. From the F₁ generation of the backcross progeny thus obtained, line TL 106 was selected. This line was resistant to wildfire at all stages of growth. It also resisted water soaking after heavy rains and was highly resistant to blackfire (Pseudomonas angulata). TL 106 was crossed with five standard varieties of tobacco and the progeny were tested for wildfire resistance in 1946. Of 1350 plants only five showed infection after repeated inoculations, and in field plantings the plants remained practically free from infection throughout the season. Thus resistance is completely dominant. Many plants in the F₂ populations of the backcrosses proved resistant to wildfire and some of them closely resembled the susceptible parent varieties in appearance. The ratio of susceptible to resistant plants was 5:25 : 1, the actual numbers of plants in each category being 1219 and 232 respectively. Further backcrosses were made to the susceptible cultivated varieties. The ratios obtained indicate that, even in advanced backcross generations, considerable chromosome irregularity still persists as a consequence of the interspecific hybridization. The segregates maintained their resistance even in the presence of prolonged, storm-induced water soaking of the leaves, and field studies of resistant progeny from the third and fourth backcrosses showed that resistance was not linked with any undesirable growth characters.
In 1940, after prolonged attempts, Clayton secured a cross
between diploid plants of *N. longiflora* and *N. Tabacum* (26). The *F₁* of the first backcross was self and cross fertile. An
immune strain, T.I.106, was selected from the *F₆* generation,
and was crossed with commercial types of tobacco. Both
T.I.106 and the *F₁* hybrids from these backcrosses showed the
wildfire resistance of *N. longiflora*; T.I.106, like T.L.106 proved
to be resistant to blackfire as well as to wildfire.

Valleau, too, has used *N. longiflora* as a source of resistance
to wildfire (72, 8–10). In 1946 he crossed Ky 23 burley tobacco
with *N. longiflora*, the latter being the pollen parent. Forty
fertile seeds were obtained and were treated with colchicine to
convert them into amphidiploids. Of 31 plants obtained in this
way four proved to be fertile when selfed or backcrossed. Back-
crossing to *N. Tabacum* was carried out in every hybrid generation
so as to eliminate as quickly as possible the unwanted *N. longi-
flora* chromosomes. Plants carrying the resistance gene could
be recognized because, as mentioned above, this character is
dominant. In order to introduce resistance to other diseases in
addition to wildfire, Valleau chose for recurrent parents
varieties carrying resistance to mosaic (NN) and black root rot
or to mosaic, black root rot and *Fusarium* wilt. Some excellent
burley type plants were obtained in the second backcross genera-
tion; in the third, all the progeny were tobacco-like and an
appreciable number of plants were selected which were typical
of burley tobacco in plant type but appeared to be as resistant
to wildfire as *N. longiflora*. By this method of breeding it is
hoped to develop new varieties practically immune to the four
diseases mentioned.

VI. THE USE OF *N. Gossei* AND *N. glauca* IN BREEDING
FOR RESISTANCE TO VIRUS STREAK

Other work at the Kentucky Experiment Station has included
the use of an Australian species *N. Gossei* as female parent in
crosses with burley tobacco in order to introduce resistance to
the virus streak disease into the latter (8). Most of the seedlings
from such crosses die when they are small from a breakdown of
the roots, but one plant was grown to maturity and a few back-
cross seeds were obtained after treatment with colchicine. *N.
glauca* also has been crossed with burley and the hybrid made
fertile by colchicine treatment and backcrossed to burley. In
1947 the second backcross generation was being tested for streak
resistance (9). It was reported the following year (10) that this attempted transfer of resistance had not succeeded.

VII. Breeding for Black Shank Resistance

An example of the transference of a character showing a more complicated mode of inheritance than mosaic or wildfire resistance is the breeding of flue cured tobacco resistant to black shank (*Phytophthora parasitica*).

The development by intraspecific hybridization of four strains resistant to this disease in North Carolina will now be described. The strains have been designated Oxford 1, Oxford 2, Oxford 3 and Oxford 4 (25).

In extensive tests of tobacco varieties, four strains of cigar wrapper tobacco developed by the North Florida Experiment Station were found to be highly resistant to black shank in North Carolina. Three of them had objectionable characteristics such as small number of leaves, short internodes, short blunt leaves with large auricles, extensive sucker growth and shattering of the seeds at maturity. So the fourth one, No. 301, was alone used for introducing resistance into flue cured tobacco. This strain had been developed from a cross between resistant Big Cuba and resistant Little Cuba. Its disadvantages from the commercial standpoint included susceptibility to frogeye (*Cercospora Nicotianae*) and brown spot (*Alternaria longipes*) and absence of a bright colour after flue curing and of the taste, aroma, texture and body desired for flue cured leaf.

In the summer of 1932, strain 301 and other cigar wrapper strains were crossed with several flue cured varieties, and the \( F_1 \) hybrids were grown and selfed in the greenhouse during the following winter. Later, all the crosses were discarded except 301 x Warne and its reciprocal, Virginia Bright Leaf x 301 and White Stem Orinoco x 301.

All later breeding and selection work was carried out on heavily infected soil in the field. The hybrids were self pollinated in most cases and selected for three or more generations or until a line fairly uniform for type and resistance could be obtained, quality being always taken into account in making the selections. Those plants combining the most desirable flue cured characteristics with adequate resistance to black shank were selected for future testing. Lines obtained after five to seven generations of selfing without backcrossing, though uniform for resistance and type, were too much like the resistant parent; so, in 1935, resistant \( F_3 \) and \( F_4 \) lines were backcrossed to the flue cured
parent. Plants showing a greater number of flue cured characters than the resistant parent were easily found in the second and third generations after the first backcross but their resistance was generally lower. A few strains with fairly high resistance were, however, selected.

Second backcrosses to the flue cured parent were made in 1938, and the process of selfing and selecting repeated. Desirable plants in the F₂ of the second backcross were again crossed with the flue cured parent. F₃’s from the second backcross and F₂’s from the third were planted out the following season. When the former hybrids produced lines which were fairly uniform for type and resistance they were continued along with the third backcross selections.

Four F₃ selections from the second backcrosses were released as Oxford 1, Oxford 2, Oxford 3 and Oxford 4. The first of these could hardly be distinguished from the flue cured parent, Virginia Bright Leaf, and the second is similar but with rather different leaf characters; Oxford 3 resembles White Stem Orinoco and Oxford 4 is similar in growth habit to Warne.

It was realized at the time of release of these varieties that further improvements with respect to quality and uniformity of product were desirable but their release was considered to be justified by the urgent need for effective control of black shank.

Later tests (23) showed that Oxford 2 and 3 had retained the full resistance of Florida 301 but were inferior in other respects to Oxford 1 which is less resistant.

Smith and Clayton have reported (64) that resistance to black shank is determined by multiple factors. Presumably Oxford 1 carries only some of these while Oxford 2 and 3 carry them all but also possess undesirable genes from Florida 301. The transference of resistance is somewhat complicated owing to the relatively large number of genes involved and it is necessary to breed larger populations than in transferring a simply inherited character such as the mosaic resistance of N. glutinosa. One encouraging feature of the black shank resistance genes, however, is that they appear to be linked with those for bacterial wilt and there seemed to be a possibility, as pointed out by Smith and Clayton (64), of breeding varieties resistant to both diseases.

This has since been done, two new varieties, Dixie Bright 101 and Dixie Bright 102 combining resistance to black shank and wilt having recently been produced (33). Details of their ancestry are not given but both are reported to inherit their wilt resistance from T.1.448 and their black shank resistance
from Florida 301 and to have both Virginia Bright Leaf and 400 as flue cured parents.

Backcrosses have been made also in other disease resistance programmes in North Carolina but only the very early stages are reported in the literature so far available.

In Mauritius, backcrosses of hybrids between the cigar wrapper tobacco Rg and established flue cured varieties have recently been made in an attempt to introduce black shank resistance into the latter (21).

In Java too, backcrossing has been used in breeding for Phytophthora resistance in Timor-Vorstenland hybrids as well as for various other characters such as mosaic resistance, which we have already mentioned, and fine leaf veining in combination with Kanari characters (31, 32, 56, 57). The advantages of the backcross method in connexion with tobacco breeding in Java have been discussed by Tollenaar and Middelburg (69).

VIII. BREEDING FOR RESISTANCE TO BLACK ROOT ROT

In Ottawa, resistance to black root rot caused by Thielaviopsis basicola has, since 1937, been introduced by means of the backcross technique into commercial tobacco varieties of three types (54).

Resistant Havana 211, a variety resistant to this disease, was crossed with four outstanding varieties of cigar tobacco. Resistant selections were backcrossed to their respective susceptible parents in 1938 and succeeding years. In 1945, 18 strains were selected for replicated yield and quality trials, and in 1948, 26 strains were being grown which showed a high degree of resistance to the disease. These were in the fourth or fifth backcross of the F₅ to F₉ generations and included six Connecticut Havana 38, nine Pennsylvania Broadleaf, five Comstock Spanish Pomeroy and six Connecticut Broadleaf strains.

Three popular burley varieties were also chosen for improvement by the incorporation of resistance to black root rot. Harrow Velvet was the resistant parent used. In 1948 nine selections representing third and fourth backcrosses of the F₁ and F₂ generations of crosses with the three susceptible varieties were under observation. In certain strains considerable difficulty has been experienced in obtaining resistant segregates resembling the susceptible parent.
One dark tobacco variety, Greenwood, has been included in the black root rot resistance programme, Harrow Velvet again being used as the source of resistance. Up to 1948 three strains in the sixth backcross of the $F_4$ had been selected as being considerably more resistant than Greenwood.

In New Zealand (15–20) the chief commercial varieties of flue cured tobacco were crossed with Little Dutch, a black root rot resistant cigar variety. The hybrid material was grown on infected ground and the resistant plants backcrossed to the flue cured parents in 1946. Further backcrosses were made in 1947. It is learned from R. Thomson, the director of the Tobacco Research Station, that some very promising lines have now been obtained as a result of further backcrossing. They equal the flue cured parent as regards yield, are of good leaf type and are highly resistant to black root rot. Some difficulty has been encountered however in eliminating the cigar aroma of Little Dutch from the hybrids.

In Massachusetts a strain of tobacco, Havana K2, resistant to black root rot, was obtained by crossing the Havana Seed tobacco known locally as the Sandman strain with Havana 211 and backcrossing to Havana Seed (45). Havana 211, the resistant parent, had been developed from a cross between Havana 38 and the black root rot resistant strain, Page's Comstock.

**IX. BREEDING FOR RESISTANCE TO ROOT KNOT AND NEMATODE ROOT ROT**

Clayton and Graham (29) used a selection designated T.I.706 for breeding for resistance to root knot (*Heterodera marioni*) and nematode root rot (*Pratylenchus* sp.). The full resistance of this parent was recovered after crossing with susceptible tobacco and after the first and second backcrosses. All $F_3$ lines from the backcrosses showed segregation but some $F_4$ lines were homozygous for resistance. Homozygous lines from the $F_4$ and $F_5$ generations of the second backcross appeared slightly more resistant to both root knot and nematode root rot than the original selection, T.I.706.

**X. BREEDING FOR EARLINESS**

There are a few cases to be mentioned of transference of characters other than disease resistance.
HE BACKCROSS METRO IN TOBACCO BREEDING

Eghis (34), a Russian investigator breeding for earliness, obtained segregates in the F₂ of a cross between Sumatran wrapper tobacco and a very early hybrid of *N. Tabacum* x *N. sylvestris* which were of the Sumatran type and possessed the desired earliness. These he backcrossed to the original Sumatra in order to improve their quality while maintaining their earliness. A similar procedure was followed with early F₂ segregates from a cross between Maryland Broadleaf, which is too late for cultivation in the USSR, and a tri-species hybrid chosen for its earliness. Other crosses between Bright and early Syrian and Persian tobaccos showed that the backcross generation contains a lower proportion of early segregates than the F₂ does but includes a greater number of forms with the desired quality.

In Canada a breeding programme to develop early maturing varieties of flue cured, burley, cigar and dark leaf tobacco was begun in 1934, with the variety Petit Havane as the early parent for all four types (54). This variety has smaller leaves, lower yielding ability and leaf quality typical of pipe tobacco but is ten or more days earlier than most commercial varieties.

The three widely grown cigar varieties Pennsylvania Broadleaf, Connecticut Broadleaf and Resistant Havana 211 were hybridized with Petit Havane to improve their earliness and were then subjected to systematic selection and backcrossing to the cigar type varieties in the usual way. Eleven strains resulting from this procedure were tested together with their recurrent parents in randomized replicated yield and quality trials in 1947.

The flue cured strains chosen for crossing with Petit Havane were White Mammoth, Yellow Mammoth, Warne, Bonanza and Virginia Bright. In 1948 most of the strains were sixth and seventh backcrosses of F₃ and F₄ hybrids and were ready for final selection in the areas producing flue cured tobacco.

Greenwood was the only dark variety used. In 1948 two eighth backcrosses of the F₄ were ready for regional variety tests in 1948.

Details of the work with burley varieties are not given.

XI. BREEDING FOR LOW NICOTINE CONTENT

Strains of tobacco resembling burley but very low in nicotine content have been developed by Valleeu (74) by crossing low nicotine strains of Cuba tobacco with the black root rot resistant varieties Ky 5, Ky 7, Ky 14 and Ky 16 and then backcrossing the hybrids to these burley varieties. The resulting low nicotine
strains have been recognized by the United States Department of Agriculture as a subtype of burley and designated Type 31-V. They have the recessive light colour of burley tobacco.

Low nicotine content was recessive but there was no sharp distinction between high and low nicotine content among the $F_2$ segregates, possibly because both nicotine and non-nicotine were reported as nicotine. Some low nicotine $F_2$ plants gave only low nicotine progeny in the $F_3$ while others produced $F_3$ plants with higher contents than in the $F_2$. The low nicotine strains have been successfully grown under field conditions. They fall into two groups: those with 28% or less of the total alkaloid content in the form of nicotine, and those with 73% or more the total alkaloid as nicotine. In general, however, when the nicotine content of segregates is low it constitutes a small percentage of the total alkaloid content, although strains could be isolated with about 1% total alkaloid nearly all of which was non-nicotine. Thus it would appear that there are two sets of genes governing nicotine and non-nicotine content: one set determining total alkaloid production and one set controlling the conversion of nicotine to non-nicotine in the leaf.

O. E. Street has used backcrossing in the breeding of low nicotine strains at the Tobacco Research Laboratory, Lancaster, Pa. (II) but details of the work are not available.

The beginning of a programme to transfer freedom from nicotine from $N. glauca$ to $N. Tabacum$ has been reported by T. Oka in Japan (62).

XII. Breeding for Improved Smoking Quality

M. Benincasa (24) mentions a cigar tobacco hybrid with excellent smoking quality designated Kentucky Italia, which was derived from the variety Italia bred by L. Angeloni from a cross of Kentucky with Sumatra backcrossed to Angeloni’s Kentucky.

In Mauritius, backcross hybrids involving the varieties Bonanza and Amarello have been made with a view to improving quality (21).

XIII. Breeding for Yellow Leaf Colour

In Canada chlorophyll deficiency has been transferred from the yellow leaved variety Consolation to the burley varieties
Halley's Special, Harrow Velvet and Judy's Pride, the flue cured varieties White Mammoth, Yellow Mammoth, Warne and Bonanza, and the cigar varieties Connecticut Havana 38, Resistant Havana 211 and Comstock Spanish Pomeroy (54). As the character is determined by a recessive gene, chlorophyll deficient \( F_2 \) segregates were used in the backcrosses. In 1948 third and fourth backcrosses of the \( F_1 \) to \( F_3 \) generations of the burley hybrids had been obtained. These required selfing before being placed in varietal tests with the parental varieties. Most of the flue cured varieties were in the fourth backcross \( F_4 \) and showed considerable resemblance to their recurrent parents. Work with the cigar varieties, which began in 1941, was less advanced.

XIV. BREEDING FOR PELIOLATE LEAVES

The standard flue cured varieties White Mammoth, Bonanza, Virginia Bright and Warne, grown in Canada, have a winged portion at the base of the leaf which interferes with the stringing of the leaves at harvest. To eliminate this, these varieties were crossed in 1939 with a strain developed from a hybrid involving \( N. sylvestris \), \( N. Tabacum \) and \( N. tomentosiformis \) (54). The petiolate character of this strain is determined by a pair of dominant genes which can be quite simply transferred. From 1939 to 1948, 128 cultures were grown for the purpose of selecting hybrids suitable for backcrossing. Three sixth backcross \( F_4 \) hybrids were retained in 1948 which were very similar, apart from the petiolate character, to their recurrent parents and were ready for replicated yield trials in the flue cured tobacco growing areas.

XV. TRANSFERENCE OF A GENE CONTROLLING PHOTOPERIODIC RESPONSE

The transference to \( N. rustica \) of a recessive gene, "mammoth," which, in \( N. Tabacum \), restricts flowering to short day conditions, has been reported by H. H. Smith (63). After five generations of backcrossing it was concluded from the phenotype of the hybrids, their chromosome number of \( 2n = 48 \) and the production of 3:1 ratios by selfed heterozygotes that the gene was in relatively pure \( N. rustica \) germ plasm. The "mammoth" segregates of \( N. rustica \) differed from those of \( N. Tabacum \) in that they failed to flower after exposure to short photoperiods. Other examples such as this of the differential response of genes to different germ plasms are to be found in the chapter on cotton.
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CHAPTER IV

THE BACKCROSS METHOD IN TOMATO BREEDING

I. INTRODUCTION

The technique of repeated backcrossing has been extensively used in tomato breeding, especially in the United States of America, for introducing disease resistance and other characters of wild tomatoes into cultivated varieties. The tomato is a native of Peru and adjacent areas. Botanists have searched these and elsewhere for plants which could contribute useful genes to new varieties of the edible tomato, Lycopersicon esculentum, and various species and varieties of Lycopersicon thus obtained have been crossed with cultivated tomatoes. The resulting hybrids usually inherit undesirable as well as desirable characters from the wild parents and must therefore be repeatedly backcrossed to the cultivated parent or one or more other cultivated varieties so as to eliminate the unwanted characters, while those which are to be introduced are retained by appropriate selection. The hybrids have, for instance, fruits which are too small for commercial purposes but segregation for fruit size occurs in the backcross generations and the larger fruited segregates can be selected out.

II. THE USE OF L. pimpinellifolium IN BREEDING FOR RESISTANCE TO Fusarium Wilt

L. pimpinellifolium is a wild Peruvian species bearing small red fruits about the size of peas. It is often referred to as the Red Currant tomato. Several characters of the species have been made use of in breeding programmes. Its resistance to Fusarium wilt caused by F. oxysporum is considered first, not for chronological reasons but because it is the most important.

The breeding of Pan America (100, 102) is a good example of the application of the backcross method to tomato breeding. This variety was developed from a cross between a L. pimpinellifolium strain known as P.I.79532 and Marglobe, the latter being chosen as the L. esculentum parent because of its good horticultural characters, its resistance to nailhead spot (Alternaria
Tomato), its intermediate resistance to Fusarium wilt, its vigorous growth and its heavy yield of high quality fruit. It was used as the female parent and L. pimpinellifolium as the male.

The F₁ hybrid had globular fruits about an inch in diameter. Three backcrosses were made to inbred lines of Marglobe, each backcross generation and the five subsequent generations of line selections being tested for wilt resistance. Altogether 10,021 plants were included in these tests. In all the tests of Pan America’s parent lines selected in 1938 and later, 95–100% of the samples tested were entirely free from any evidence of Fusarium wilt infection.

Pan America was released by the United States Department of Agriculture in 1941 as the most wilt resistant variety so far tested. Its fruit characters are good and it ripens a little earlier than Marglobe. Since its release it has proved very useful in soils heavily infested with Fusarium and has been widely used as a source of wilt resistance in tomato breeding.

Two examples of this use deserve mention because the backcross method was used in each case, Pan America being the recurrent parent in one instance and the non-recurrent parent in the other.

The first example is the development of the new collar rot (Alternaria Solani) resistant variety Southland (46, 47). A productive, collar rot resistant selection from the cross Devon Surprise x Indiana Marglobe, made in 1940, was crossed with Pan America, and selected hybrids from the cross were successively backcrossed to Pan America and crossed with Rutgers. Southland combines resistance to collar rot with near immunity to Fusarium wilt and moderate resistance to early blight (also caused by A. Solani) and one form of late blight (Phytophthora infestans). It resembles Pan America more than Rutgers.

The other project is an attempt to combine earliness with resistance to Fusarium wilt (87). For this purpose, a very early variety, First Early, was crossed with Pan America which, though resistant to wilt, matures late. The F₁ generation was backcrossed to First Early and plants were selected from the progeny solely on the basis of wilt resistance and shortness of the period from sowing to first bloom. Undesirable fruit size and shape were ignored so as not to eliminate genes for earliness which might be linked with these characters. Small families were grown from selfed seed of 34 plants of this first backcross generation. It is proposed to backcross one or two plants from each family and to select from the backcross progenies for wilt resistance and short periods of development.
At the Missouri Agricultural Experiment Station, Accession 106, a different strain of *L. pinnatellifolium* from that involved in the breeding of Pan America, has been used. Its high resistance to *Fusarium* wilt was found to be controlled by a single dominant major gene (designated *I*) and it was easy therefore to transfer the character to *L. esculentum* (58, 59, 92, 111). The F₁ hybrids between Accession 106 and susceptible varieties were immune, and of the 1784 first backcross generation hybrids tested, 854 were susceptible and 930 immune. In the second backcross generation there were 458 susceptible to 461 immune plants, which approximates to a 1:1 ratio. The use of resistant instead of susceptible commercial varieties as recurrent parents did not appreciably affect the proportion of susceptible segregates, the resistance factors of these commercial varieties, if inherited by the progeny, not being sufficiently potent.

The potency of the *L. pinnatellifolium* gene for immunity did not seem to be decreased in association with large numbers of genes from commercial varieties. It was concluded from observation of the segregation ratios that this gene was linked with a factor for increased effectiveness of the pollen.

Promising hybrids homozygous for immunity were selected from successive generations obtained by backcrossing the hybrids with different commercial varieties. It was necessary of course, in making these backcrosses, to bear in mind the characters other than immunity to wilt which were required in the hybrids. An important one is fruit size. Since Earliana and Bonny Best which were used for the first generation hybrids, have relatively small fruits, various other varieties including Bison, Break O'Day, Early Baltimore, Greater Baltimore, Louisiana Pink, Oxheart, Ponderosa, White Beauty and Yellow Ponderosa were used as parents in later generations. Many of these, particularly the ones with large fruits, had various undesirable characters and so were not used repeatedly in backcrosses; thus most of the hybrids in later generations had several commercial varieties in their pedigrees.

In making selections from non-infected plants in the field an attempt was made to maintain the desirable characters of Accession 106 and of the various commercial parents. Successive backcross generations produced progressively larger fruits. From 374 immune plants of the first backcross of Bonny Best x Accession 160 to Bonny Best, five were selected (on the basis of other characters besides fruit weight) with fruits averaging 28.5 to 33.5 grm. Among 116 immune selections of the second backcross to the same variety, five selected hybrids had fruits
averaging 42.0 to 70.0 grm. Higher weights than these were obtained in other second backcross progenies.

Among later generations tested in 1938, progenies obtained by backcrossing were more uniform in all characters than those from self pollinated hybrids. Several plants in all progenies and particularly in the backcross ones had fruits similar in many respects to fruits of commercial varieties, some of them weighing as much as 100 grm. Several plants from the cross Earliana x Accession 106 backcrossed to Break O’Day, selfed, backcrossed to Ponderosa and selfed again, had fruits weighing 260 grm. Considering that the fruits of Accession 106 weighed only about 1 grm., this is a striking example of the elimination of an undesirable character of the immune parent by means of backcrossing. It was expected that repeated selfing of selected hybrids would yield a tomato variety homozygous for desirable morphological characters as well as for immunity to Fusarium.

In 1945–46 about 300 hybrid lines were grown in the breeding plots and about 600 individual yield records were made (110). All the lines were inoculated with the wilt organism. On plots at Columbia some lines outyielded commercial varieties by 75%; at both Columbia and Movett the better hybrids equalled or exceeded the best commercial varieties in fruit size and percentage of marketable fruits. Moreover several hybrid lines grown in commercial tomato producing areas proved completely resistant to Fusarium wilt under field conditions, yielded well and were favourably received by growers.

One of the selections was sent to Durban and thence to Nelspruit. It has been successively grown at the Nelspruit Research Station where it is being selected for trueness to type, with a view to distributing it to growers under the name of Durbot (95).

The gene I, possessed by the hybrids we have been discussing confers immunity to the usual strain of Fusarium but not to a new strain designated race 2 which has recently appeared in Ohio. One or more accessory factors in addition to the main one seem to be necessary for resistance to the new strain.

It has recently been shown, by inoculating hybrids with virulent isolates of the pathogen from tomatoes containing the L. pimpinellifolium type of Fusarium resistance, that another resistance factor in addition to I exists in L. pimpinellifolium (110).

Work in Australia (77) has suggested the presence of modifying factors which influence the proportions of wilt immune segregates.

Some of the interspecific hybrid seed from the Missouri Research Station was sent to South Africa where the plants
proved completely immune from *Fusarium* wilt although the numerous well known varieties which had been imported from other countries all succumbed to the disease under South African conditions (72). The hybrids did not however compare favourably with the best varieties in other respects and they were therefore backcrossed to commercial types. Hofmeyer reported in 1942 (72) that new varieties were hoped for in two to three years but there appears to be no record in the literature of any having been produced.

Material from Missouri was used also by L. J. Alexander (52, 53, 55) working at the Ohio Experiment Station on the development of a wilt resistant tomato of the Globe type for greenhouse cultivation. The Missouri lines used as sources of resistance were M-8-2 and M-21-2. The pedigree of the former is given as Earliana x *L. pimpinellifolium* x Break O’Day x Break O’Day x Ponderosa, selfed in the field, backcrossed again this time to Greater Baltimore and twice selfed in the field. That of M-21-2 was Earliana x *L. pimpinellifolium* x Break O’Day x Bonny Best x Ponderosa, selfed in the field, hand selfed, and finally twice selfed in the field. The two lines were crossed with Globe and then again to that variety or selections derived from it. Three selections which were tested gave higher spring and autumn yields than Strain A Globe in 1946 and equalled or exceeded it in earliness. Seed of the three lines was distributed to growers in Ohio for further testing. As regards their *Fusarium* resistance, selections 1 and 3 appeared to be immune to the widely distributed race 1 of *Fusarium oxysporum* f. *Lycopersici*. Selection 3 was finally chosen as the most desirable and was released as Ohio W–R Globe (54, 55). Its pedigree is Livingston Globe x M–8–2 x Association Globe x Selection A Globe, self-fertilized twice in the field and once in the greenhouse and bulk selected three times. After each of the crosses, tests for *Fusarium* wilt resistance were carried out and susceptible plants were discarded.

Ohio W–R Globe is highly resistant to race 1, the widely distributed form of the pathogen, but highly susceptible to race 2. Its average yield equals that of the standard variety, Strain A Globe which it also resembles in plant and fruit characters, but is slightly earlier.

Accession 106, the selection of *L. pimpinellifolium* used in Missouri was also the one employed in the wilt resistance project at Purdue University Agricultural Experiment Station in
Indiana (20-29), where it was crossed to Baltimore and Rutgers, and successive backcrosses carried out. Selfed seed from plants approaching the commercial types after the third to fifth backcross was planted out for selection. In 1944, there had been produced many promising new strains combining the desirable commercial characters of Baltimore and Rutgers with high wilt resistance. They showed no *Fusarium* injury in inoculation tests in which varieties such as Rutgers and Pritchard were usually wiped out. Eleven promising new lines had been selected from the hybrids in 1945 but needed further testing. In the preliminary tests six proved as productive as Indiana Baltimore and had good fruit type and plant characteristics in addition to being highly wilt resistant. In 1948 it was reported that a group of lines apparently identical with Indiana Baltimore and Rutgers but highly resistant to *Fusarium* wilt had been obtained.

Marglobe and Rutgers were used as backcross parents in a wilt resistance programme in Texas (61). Lines obtained by backcrossing hybrids between *L. pimpinellifolium* and commercial tomatoes to the above varieties were selected through several generations for adaptability and resistance to *Fusarium* wilt. After that they were crossed with Pritchard, Oxheart and T.723. In this way plants with large fruits and good quality were obtained.

At the Georgia Experiment Station (3-6) hybrids between *L. esculentum* and *L. pimpinellifolium* which were resistant to *Fusarium* wilt and also to nematode root knot (*Heterodera marioni*) and *Septoria* were backcrossed to large fruited commercial varieties. Suitable commercial qualities were obtained in selections from the F₂ of backcross hybrids. Second backcross hybrids retained the *Fusarium* and root knot nematode resistance but were less resistant to *Septoria Lycopersici*. Several F₅ selections from the third backcross tested in 1947 were free from wilt symptoms but none were found to be entirely free from root knot or *Septoria*. One very prolific strain has been increased for more intensive testing.

III. THE USE OF *L. pimpinellifolium* IN BREEDING FOR RESISTANCE TO LEAF MOURD

*L. pimpinellifolium* has also been used as a source of resistance to leaf mould, a widespread disease of greenhouse tomatoes caused by the fungus *Cladosporium fulvum*, of which there are several physiological forms showing differences in pathogenicity.
Sengbusch and Loschakowa–Hasenbusch reported in 1932 (108) that *L. pimpinellifolium* showed immunity to *C. fulvum* (i.e. to the only form then known) whereas not one out of 41 cultivated varieties tested possessed immunity, Sterling Castle being, however, highly resistant. *L. pimpinellifolium* was crossed with cultivated varieties, and small fruited hybrids were obtained. Their segregation showed that immunity to leaf mould was determined by a single dominant factor. The resistance of Sterling Castle, on the other hand, proved to be recessive.

Guba (7, 8), working at the Massachusetts Agricultural Experiment Station, believed that limited or partial resistance to the disease was all that could be expected from intraspecific *L. esculentum* crosses, but found that the F₁ generations from crosses of *L. pimpinellifolium* with three varieties of *L. esculentum*, Belmont, Break O'Day and Success, were completely immune, and that, in the F₂, there appeared to be a ratio of three immune segregates to one susceptible, showing that the immunity was inherited as a dominant factor. In 1935 the F₃ generations were selected for resistance to *Cladosporium* and some of them were crossed with Field Station, Lloyd and Baltimore to improve their fruit size (9). From the F₁'s of these crosses, 49 selections were made and used as parents for the F₂ generation. Good commercial qualities were introduced into some of the lines by crossing them three times to the variety Waltham Forcing, and it was from the F₂ of the third cross that the variety Bay State was selected (10–12, 68, 69). This variety resembled Waltham Forcing except for its resistance to *Cladosporium*, greater earliness and freer branching of the fruiting cluster. It outyielded Waltham Forcing only under conditions of leaf mould infection. In 1940 and 1941, however, Bay State was attacked by a new physiological race of *Cladosporium* to which it proved susceptible (13). So did Globelle and Vetomold, which were also developed from crosses with the Red Currant tomato for resistance to the disease. *L. pimpinellifolium* itself was infected, and *L. hirsutum* too, which like *L. pimpinellifolium* is resistant to the original form.

But some highly resistant or immune types were found (14, 15) and when crossed with Bay State gave progeny which segregated in the F₂ for various degrees of susceptibility and for immunity. The most useful source of immunity was Plant Introduction No. 112, 215, a *L. pimpinellifolium* type from Ecuador. By introducing the immunity of this type into varieties which had proved susceptible to the new physiological form of *Cladosporium*,
the resistant varieties Improved Bay State, Improved Vetomold-121, Leafmold Resistant Marglobe and Leaf Mold Resistant Waltham Forcing were obtained (16, 17). The first of these proved particularly satisfactory. Similar resistance was introduced into several English forcing varieties such as Carter’s Sunrise, Kondine Red, Hundredfold, Best-of-All and Market King and the hybrids have been placed under observation in an effort to obtain a range of commercially acceptable resistant types (18, 19).

The *L. pimpinellifolium* gene for *Cladosporium* resistance is designated *Cf*$_{pl}$. Langford (83, 84) has reported that hybrids carrying this gene develop a severe non-parasitic necrosis if they are homozygous for the *L. esculentum* gene *Ne* but not if they have the dominant allele *Ne* derived from *L. pimpinellifolium*. The necrosis is regarded as an expression of incompatibility between *Cf*$_{pl}$ and a chromosome complex largely derived from *L. esculentum*. It illustrates one of the difficulties which may arise when genes are transferred from one species to another.

L. J. Alexander (48-51) used as a source of *Cladosporium* resistance two exceptional plants with very small fruits and coarse growth which appeared to be hybrids from a chance cross between *L. pimpinellifolium* and the *L. esculentum* variety, Globe. The F$_2$ and F$_3$ segregation indicated that leaf mould resistance was determined by a single dominant factor, and this was confirmed by backcrossing the heterozygote to the recessive parent. A long programme of backcrossing and selection was necessary in order to eliminate some of the wild characters of the hybrids and incorporate desirable commercial ones. Globe and Marhio were used as recurrent parents, and new strains were obtained with a yielding ability apparently equal to Globe in the absence of leaf mould infection and much superior to it when leaf mould was serious. One of the selections was released as the leaf mould resistant variety Globelle mentioned above. In the 14 generations in which it was developed, four backcrosses to *L. esculentum* were effected. The new variety produced pink fruits similar to those of Globe but of higher quality.

IV. THE USE OF *L. pimpinellifolium* IN BREEDING FOR RESISTANCE TO FRUIT SPLITTING

Fischer and Sengbusch (64) used *L. pimpinellifolium* as a source of resistance to fruit splitting, which appeared to depend
on the shape of the fruits. Different varieties of *L. esculentum* were crossed with *L. pimpinellifolium* and non-splitting segregates selected from the F2. The hybrids, which were, of course, small fruited types, were backcrossed to *L. esculentum* so as to combine the non-splitting character with satisfactory fruit size.

V. THE USE OF *L. pimpinellifolium* IN BREEDING FOR RESISTANCE TO SPOTTED WILT

A new tomato variety, Pearl Harbour, has recently been developed at the Hawaii Agricultural Experiment Station from hybrid material involving *L. pimpinellifolium* (79). It is resistant to spotted wilt, a virus disease which constitutes a limiting factor in tomato production in Hawaii, and was selected from the F9 generation of a cross between Bounty and an F6 selection of 133–6 x Red Currant (*L. pimpinellifolium*) backcrossed to 133–6. Its resistance is apparently determined by a single dominant gene.

When tested in New Jersey its resistance broke down owing to the presence of a strain or strains of the pathogen not present in Hawaii. New sources of adequate resistance were found however (75, 76): the variety Rey de los Tempranos [King of the Earlies] and selections of Manzana [Apple] from Argentina proved to be resistant under both artificial and natural infection.

The resistance appears to be monogenic, but in this case recessive; so it probably would not be very difficult to transfer to other varieties. As Rey de los Tempranos and Manzana, when tested in Hawaii, did not exhibit the same resistance as Pearl Harbour, it has been suggested that the two types of resistance should be combined.

In order to obtain resistant types with larger fruits than Pearl Harbour, this variety was crossed with others including Pritchard, Coopers Special, Grothens Globe and Pearson (80) but the isolation of early resistant lines with larger fruits than Pearl Harbour is not easy, possibly because of linkage.

This difficulty over fruit size has been experienced also in attempts made in Australia to utilize the resistance of *L. pimpinellifolium* to spotted wilt (96).

Hutton and Peak (78) have reported work at Canberra with the aim of breaking the apparent linkage between resistance and undesirable growth characteristics. In 1946 crosses were made between Bounty, as female parent, and Porter's strain of *L. pimpinellifolium* and eighty seedlings were obtained, all of
which were susceptible. Two reciprocal backcrosses were made to the variety Sioux. The segregation ratios showed that resistance was recessive and appeared to be determined by multiple factors. In crosses with Sioux as female parent the general level of resistance tended to be lower than in the reciprocal crosses. By the fourth generation the spotted wilt resistance was becoming stabilized through intensive selection.

The resistant hybrids obtained at Canberra are not yet commercially acceptable but are nevertheless a distinct improvement on *L. pimpinellifolium*. Further improvement is being sought by means of continued backcrossing and selection.

### VI. The Use of *L. pimpinellifolium* in Breeding for Various Other Characters

Daskalov (62, 63) has reported that backcrosses of hybrids between the tomato varieties Zarja and Plovdiv and various strains of *L. pimpinellifolium* gave better yields, larger fruits and a higher dry matter content than that of the parents; and first backcrosses to Zarja and Plovdiv exceeded these varieties in earliness as well as giving good yields of fruits averaging in most cases 50 grm. each in weight.

In India, *L. esculentum* x *L. pimpinellifolium* hybrids have been backcrossed to *L. esculentum* and selected for earliness together with other desirable characters including ascorbic acid content. The latter, unfortunately, was highest in small fruited selections (97, 41–44).

This negative correlation between ascorbic acid content and fruit size was encountered also in crosses between the two species made at the Purdue University Agricultural Experiment Station (89). Plants with fruit size approaching that of the commercial parents and nearly twice as much ascorbic acid have now been obtained however by backcrossing the hybrids to Rutgers and Indiana Baltimore and intercrossing segregates rich in ascorbic acid.

### VII. The Use of *L. chilense* in Breeding for Resistance to Various Diseases

The Chilean species, *L. chilense*, is highly resistant to curly top, a virus disease of considerable importance in the United States. In 1939, F. O. Holmes reported (73) that a seed from a twelve year old herbarium specimen of this species had remained
viable and given rise to a seedling which bore greenish, hairy fruits that became creamy white and about 1 cm. in diameter when mature. The species was crossed with *L. esculentum* and produced vigorous hybrids with intermediate foliage characters. Some of the *L. chilense* material was tested for curly top resistance at two places in Idaho and proved highly resistant (112). A breeding project was therefore initiated with the object of transferring the resistance to commercial tomato varieties. Backcrosses of the interspecific hybrid to *L. esculentum* were made and the resistant progenies were used for further breeding (30). In 1941 progenies from the cross Bison x (Marglobe x *L. chilense*) survived a severe attack of curly top which killed all the common varieties included in the test (37). However, the resistant plants still possessed other characters which made them unsuitable for commercial production. But three which were of a fairly good type were selected and seed from them was tested the following year with promising results (32). In 1944, about 1200 plants representing 15 selections of fourth generation progeny from the cross between Marglobe and *L. chilense* and 53 backcrosses to commercial varieties were tested for yield and quality. The quality of several of the backcross selections was of the necessary commercial standard, although further selection for resistance to curly top was necessary. More tests were conducted in subsequent years and further selection was carried out (33–35). There appeared to be linkage in some lines between large fruit size and roughness, and between small fruit size and smoothness. Some of the resistant plants produced rough fruits weighing over a pound.

In 1947 a severe attack of curly top eliminated the commercial tomatoes in the breeding plots before they even flowered but some of the selections showed no symptoms of the disease (36).

P. A. Young (117) crossed *L. esculentum* as female parent with Holmes’ *F*₁ hybrid between *L. chilense* and *L. esculentum*, and obtained among the resulting progeny, segregates which were nearly immune to *Fusarium* wilt.

Holmes reported in 1943 (74) that *L. chilense* tended to escape infection by tobacco mosaic and suggested that the incorporation of this character into *L. esculentum* might be possible. The *F*₁ plants from the cross *L. esculentum* x *L. chilense* were intermediate in susceptibility. One individual capable of escaping the disease was obtained from the seed of a plant of the first backcross generation to *L. esculentum*. This tendency to escape infection is to be distinguished from symptomless infection. If the plants
do become infected they respond in much the same way as cultivated tomato varieties.

Plants resistant to mosaic, i.e. showing only very slight leaf symptoms when inoculated with a virulent strain were reported by Lesley (87) to have been obtained in a family derived from *L. esculentum* x *L. peruvianum* var. *dentatum* by six generations of backcrossing or selfing. *L. peruvianum* var. *dentatum* is regarded by Müller (94) as synonymous with *L. chilense*.

In Hawaii (39) backcrosses to *L. esculentum* of a complex hybrid involving *L. hirsutum* and *L. pimpinellifolium* as well as *L. esculentum* and *L. chilense* have been carried out in an attempt to develop acceptable types with at least mildness of mosaic symptoms.

In another backcross project reported by Lesley (87) *L. esculentum* was crossed with *L. peruvianum* var. *dentatum* (*L. chilense*) and four backcrosses were made to *L. esculentum*. The resulting plants, when selfed, gave rise to progeny in which the large fruit size, determinate growth and red flesh colour of *L. esculentum* were combined with resistance to *Verticillium* wilt, apparently derived from *L. peruvianum* var. *dentatum*.

**VIII. THE USE OF *L. hirsutum* IN BREEDING FOR RESISTANCE TO Septoria AND Alternaria LEAF BLIGHTS**

*L. hirsutum*, a species producing small pubescent fruits of a greenish ivory colour with green stripes, is a source of resistance to defoliation diseases and mosaic.

Locke (90) has studied the resistance to *Septoria* and *Alternaria* leaf blights of *L. esculentum* x *L. hirsutum* hybrids and backcrosses. He found that the F₁'s were as resistant as *L. hirsutum* to *S. Lycopersici* but intermediate with respect to *A. Solani*, whereas the first backcross generation to *L. esculentum* gave approximately a 1 : 1 segregation for *Septoria* resistance, suggesting that a single dominant gene may be involved.

Lincoln and Cummins (88) working at the Purdue Experiment Station with *L. hirsutum* PI 126445 have also obtained segregation ratios consistent with the dependence of *Septoria* resistance on a single dominant gene. This gene, moreover, appeared to be identical with the factor for resistance in the *L. esculentum* variety 'Targinnike Rea'.
Experiments to transfer the *Septoria* and *Alternaria* resistance of *L. hirsutum* PI 126445 to commercial varieties of tomatoes have been in progress for some years (21–26, 28, 29, 90). Crosses were made with Rutgers and the progeny were backcrossed to this variety. In other crosses and backcrosses involving *L. hirsutum* the variety Baltimore was used, segregates with the highest resistance to *Septoria* being selected for backcrossing. In the second generation tests were made for *Alternaria* resistance, and the plants which survived two inoculations were included in the breeding plots for further hybridization. After a few years all the hybrid lines were homozygous for red fruit colour. The single fruit weight averaged 5 oz. in the 1945–46 season; and of 24 selections with desirable fruit and plant characters made in the 1947–48 season, all but five had a fruit weight of 6 oz. or more. The work has progressed through six backcross generations to the stage of making varietal selections. None of the selections in the advanced generations is as resistant to *Septoria* as the resistant parent.

**IX. The Use of *L. hirsutum* in Breeding for Mosaic Resistance**

J. W. Lesley (87) reports that a family derived from *L. esculentum* × *L. hirsutum* by two generations of backcrossing and one of selfing had only very slight mosaic symptoms like *L. hirsutum* and that some of the plants produced a fair crop, although rather late in the season.

At the Hawaii Agricultural Experiment Station, on the other hand, first and second backcrosses of *L. esculentum* (Pan America) × *L. hirsutum* to *L. esculentum* (Pearl Harbour) had shown uniformly severe infection when tested for their reaction to mosaic (81) but seedlings showing promise with respect to mosaic resistance have been bred from a cross involving *L. esculentum*, *L. hirsutum*, *L. chilense* and *L. pimpinellifolium* and have been crossed to *L. esculentum* to improve their fruit and plant characters (39). Repeated backcrosses have been made also in connexion with the rather complicated *Stemphyllium Solani* resistance project at this station (37, 38, 66, 67, 70).

**X. The Use of *L. hirsutum* in Breeding for High β-Carotene Content**

In the course of a survey carried out at the Purdue Experiment Station of 240 tomato varieties, wild types and hybrids, it was
found that a single plant selection, 4079-5012, from the F₃ of the cross Indiana Baltimore x F₁ (Rutgers x L. hirsutum 126445) was exceptionally rich in β-carotene content (82). In spite of its otherwise poor quality, low yield and small fruits, this selection was therefore extensively used as a parent in breeding for high β-carotene content. The results of selection within line 4079-5012 led to the conclusion that the factors primarily responsible for richness in β-carotene were fixed relatively early in the selection process, although minor factors probably remained heterozygous.

When 4079-5012 was backcrossed to Indiana Baltimore, F₁ plants with intermediate or low β-carotene content were obtained, but high β-carotene content reappeared in the F₂ with a frequency suggesting that the number of major factors necessary in addition to those present in Indiana Baltimore is small. Later it was reported that only a single gene was involved (29). Selection for fruit size was carried out in the F₁, and plants were obtained which combined a β-carotene content of 83 micrograms per gram with fruit size equal to that of many commercial varieties.

XI. The Use of L. peruvianum

L. peruvianum, another wild species valuable for its disease resistance, has proved somewhat difficult to cross with L. esculentum. However, P. G. Smith (109) obtained hybrids between L. esculentum and L. peruvianum PI 128657 by means of embryo culture. Pollen from an F₁ plant of his cross with Michigan State Forcing as the cultivated parent was used by V. M. Watts (114) for fertilizing various lines of L. esculentum with the object of obtaining strains resistant to nematode (Heterodera marioni). Three seedlings were obtained, two of which were highly resistant as shown by the fact that the clonal plants to which they gave rise survived five inoculations in the course of 15 months without developing any root knots. The progeny of one of these plants, the only self fertile one, was tested for nematode resistance, and the data obtained suggested that resistance in the early stages of growth was determined by two dominant genes.

Only the self fertile plants of the progeny were retained. Four of them which proved resistant when young were found to be susceptible later on. The ten which survived bore fruits varying from one to two inches in diameter, of a deep orange to bright red colour and resembling commercial varieties in taste.

Some of the seed from the self fertile resistant plant and from one of its derivatives was sent by Watts to Hawaii where selections
were made from the progeny (65). Only one plant gave progeny which all appeared highly resistant to root knot. After further backcrossing with *L. esculentum* four highly resistant lines with improved horticultural characters were obtained. Further crossing will probably be necessary in order to obtain commercially acceptable types.

Another project in Hawaii involving the backcrossing of derivatives of *L. peruvianum* and *L. esculentum* is an attempt to combine high vitamin C content with disease resistance by the method of convergent improvement (39). The original hybrid was a cross made by Yeager of New Hampshire between *L. peruvianum* and Michigan State Forcing, which significantly exceeded any commercial variety tested as regards vitamin C content. Two derivative lines were crossed with the high quality, triple disease resistant line 2958 and the progeny were backcrossed to both parents. Plants of the backcross generations high in the characters of the non-recurrent parent were to be selected and selfed and then crossed with other selections to converge the opposing trends.

Porte and Walker (101) obtained several hybrids by pollinating *L. esculentum* varieties with pollen of *L. peruvianum*. All the fruits were seedless except those of the hybrids with the variety Prince Borghese as female parent. The seeds from these hybrids were viable and gave rise to vigorous F₁ plants which produced some seed when open-pollinated in the field. The F₂ progeny, which showed marked phenotypic differences, consisted mostly of sterile plants. But several outcrosses were made to Pan America, Rutgers and various hybrid combinations of *L. esculentum*. From the segregating progenies thus obtained promising selections were made.

No. 44B292, an outcross to Pan America, was backcrossed to Prince Borghese, and the wide range of phenotypes obtained from this cross are being studied at the Massachusetts Agricultural Experiment Station for their reactions to *Cladosporium* and to root knot nematode (16).

At the New Hampshire Agricultural Experiment Station (116) just a single seed was obtained from the cross Michigan State Forcing x *L. peruvianum* PI 126946. The F₁ plant was vigorous and apparently completely fertile however, and bore long clusters of small, round, orange-red fruits with 2 to 3 locules. From the F₂, plants with high ascorbic acid content and relatively
large fruit size were selected, and these were backcrossed to
*L. esculentum*, the varieties used being New Hampshire Victor
and Red Skin, not the original cultivated parent. The third
generation of the cross involving Red Skin contained plants
with an ascorbic acid content of 43–67 mg. per 100 grm., the
corresponding value for standard varieties being 19 mg. per
100 grm. One hybrid, from a cross between a selection with
high ascorbic acid content and New Hampshire Victor, combined
fruits of commercial size and shape with an ascorbic acid content
of 39 mg. per 100 grm. It has been suggested that such selections
might be valuable as parents in the production of hybrid tomatoes.

XII. THE USE OF OJO DE VENADO AND RED PEACH
IN BREEDING FOR RESISTANCE TO CURLY TOP

Experiments at the Utah Agricultural Experiment Station (113)
led to the discovery of resistance to curly top in a Mexican wild
tomato, Ojo de Venado (Deer’s Eye) and in a dwarf selection
of the novelty tomato, Red Peach. Of about 800 commercial
varieties and strains tested prior to 1938, none had proved
sufficiently resistant to this virus disease; so resistant selections
of Ojo de Venado and Red Peach were crossed, with commercial
varieties in an attempt to combine the curly top resistance with
desirable commercial characters. The *F₂* and *F₃* generations
were lacking in both resistance and fruit quality, but crosses
and backcrosses were repeated and in 1941 large fruited selections
from crosses with different varieties, chiefly Stone, Baltimore and
Century were obtained (1). The resistance of some of the
selections was almost as good as that of the resistant parent.

The green fruited types *L. glandulosum* C. H. Mull., *L. peruvianum* var. *humifusum* and *L. peruvianum* var. *dentatum* later
proved to have even better curly top resistance than Ojo de
Venedo and Red Peach, but repeated attempts to cross them
with *L. esculentum* varieties were unsuccessful (113). Crosses
were made with *L. esculentum* x *L. hirsutum* hybrids but the
progenies from them were sterile or almost so (1).

XIII. THE USE OF L. ESCULENTUM VAR. CERASIFORME IN BREEDING
FOR RESISTANCE TO VERTICILLIUM WILT

Resistance to *Verticillium alboatrum* closely approaching im-
munity was found, in Utah, in *L. esculentum* var. *cerasiforme*
and *L. pimpinellifolium*, while one of the green fruited species,
*L. glandulosum*, appeared to be partly immune (114). *L. esculen-
tum* var. *cerasiforme* hybridizes easily with commercial varieties.
Plants with fruit of approximately commercial size were selected from among its hybrids with Stone and Century and some of the selections were backcrossed and outcrossed in an effort to improve size and quality (1). The resulting plants were, however, highly susceptible to wilt. *L. pimpinellifolium* was also used in crosses but the fruit size of the hybrids was inferior to that of the *L. esculentum* var. *cerasi forme* hybrids. *L. glandulosum* is more difficult to cross with cultivated tomatoes. Poor fruit set and late ripening were so persistently associated with resistance in the various hybrids obtained that these characters appeared to be genetically linked (57).

XIV. THE USE OF TI 706 IN BREEDING FOR RESISTANCE TO ROOT KNOT AND NEMATODE ROOT ROT

Clayton and Graham (60) used selections from a collection known as TI 706 as sources of resistance to root knot (*Heterodera marioni*) and nematode root rot (*Pratylenchus* sp.). The full resistance was recovered after a cross with susceptible tobacco and two backcrosses. F₃ lines of the backcrosses segregated but some F₄ lines were homozygous for resistance. Homozygous F₄ and F₅ lines from the second backcross have been selected which appeared even more resistant to the diseases than TI 706.

XV. BREEDING FOR AN EXTENSION OF THE FRUITING PERIOD

Under the hot, dry conditions of the summer in Texas, ordinary, large fruited varieties of tomatoes are unable to set fruit, and their fruiting period is therefore short. Certain small fruited types, on the other hand, continue to set fruit throughout the summer. Yarnell and Hawthorne (115) introduced this ability to fruit under unfavourable conditions into large fruited varieties. From the seed of a hybrid between Bonny Best and Red Cherry a type designated Large Cherry was obtained and was backcrossed in 1933 to the original large fruited parent, Bonny Best. In 1936 four generations had been grown from the backcross seed, and fruits seven to nine times as heavy as those of Red Cherry were being produced. These found a ready sale in the local markets when the only other large fruited tomatoes available were those brought into Texas from elsewhere. Some of the selections were eventually distributed together under the name Summerset.

Other crosses between large and small fruited types were made by growing the two types in close proximity and allowing cross pollination to occur. The large fruited varieties on which hybrid
fruits were produced included: Dwarf Champion, Globe, Marglobe, Gulf State Market and a cross between Stone and Gulf Market. The small fruited male parents were of the cherry, plum and pear types. The fruit size of the hybrids was increased by crossing them with the large fruited types, Bonny Best, Kanora and Marglobe. Crosses with Marglobe were very successful in this respect. On the other hand a globe type from France known as Globularia proved unable to contribute factors for large fruit size. Fruit size is influenced by environmental conditions as well as genes and adaptability should therefore be selected for. Factors for drought resistance appeared to be of value in permitting the increased expression of genes for fruit size under unfavourable conditions.

XVI. The Intraspecific Transference of Genes for Uniform Fruit Coloration

Two backcross programmes involving intraspecific hybridization have been started at the John Innes Horticultural Institution in England; one to introduce the recessive gene for uniform coloration of the fruit into Potentate and the other to introduce it into Radio (45). The source of the gene in both cases is the variety Stoner’s M.P.

XVII. The Intraspecific Transference of a Mutant Gene for Male Sterility

Functional male sterility determined by a recessive mutant gene has recently been discovered in the variety John Baer (86). In view of the possible value of such sterility in the production of hybrid seed, the gene is being transferred to other tomato varieties (85).

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THE BACKCROSS METHOD IN TOMATO BREEDING


CHAPTER V
THE BACKCROSS METHOD IN POTATO BREEDING

I. INTRODUCTION

The range of parental material available to potato breeders has been considerably increased in recent years by the introduction of new varieties of the cultivated potato, *Solanum tuberosum* and other species of *Solanum* from the original home of the potato in America. This new material, collected by botanists on expeditions sent from Russia, Germany, the United States, Sweden and the British Commonwealth, constitutes a new source of genetic variation containing genes which determine valuable characteristics not previously available. The backcross technique has proved to be the best method of incorporating these genes into commercially cultivated potato varieties.

The most important of the introduced species of *Solanum* is *S. demissum*, the use of which will be dealt with first. Salaman (40) gives a list of sources of the characters which are required for introduction into commercial varieties, and Hawkes (20) lists the American species showing resistance to various diseases. The results of tests for various qualities carried out in Russia on the wild *Solanum* species are reported by Kameraz (21).

There are two chief points to be borne in mind in connexion with the application of the backcross method to this particular crop: one is that owing to the well known difficulties arising from sterility it is not always possible to follow a preconceived plan of hybridization; and the other is that selfing so as to obtain homozygosity with respect to dominant characters is not necessary in potatoes as it is in crops which are ordinarily propagated by seed.

II. THE USE OF *S. demissum* IN BREEDING FOR RESISTANCE TO BLIGHT, FROST AND THE COLORADO BEETLE

1. Blight and frost resistance.

One of the valuable characters referred to above is resistance to late blight, caused by the fungus *Phytophthora infestans*. Such resistance is found in several species of *Solanum*, but the Mexican species *S. demissum* has proved the most useful as a breeding
parent because the others are either sterile or less resistant. Certain strains of *S. demissum* carry dominant genes for immunity to blight and are also resistant to frost and to the Colorado beetle (20).

The species has $2n = 72$ chromosomes whereas *S. tuberosum* has $2n = 48$, and meiotic irregularities lead to sterility in the hybrids. L. O. Schnell (43) has recently studied meiosis in hybrids between the two species and in the first to fourth backcrosses to *S. tuberosum*. He observed various irregularities in all the generations studied, and even the fourth backcross hybrids retained chromosome numbers approximating to those of the $F_1$ as well as the concomitant undesirable characters of *S. demissum*. There was some evidence of autosyndesis of the chromosomes of the two species. Schnell concludes from these results that breeding for blight resistance by using *S. demissum* × *S. tuberosum* must remain primarily a trial and error method.

In backcrossing the interspecific hybrids to *S. tuberosum* a single variety of this species is not usually used as recurrent parent throughout the breeding programme. According to Bukasov (15) and Reddick (34) it is advisable to make backcrosses to a variety other than that which was employed in the original cross, because dwarfed and less vigorous progeny usually result from the use of a single variety throughout.

Salaman, who reports having demonstrated genetic resistance to blight in *S. demissum* as early as 1908 (38), has played a prominent part in breeding for blight resistance in England. Opposite is a typical pedigree given by him (40) of one of the lines he developed (the accompanying remarks are quoted from his paper). It shows how the wart resistance (*Synchytrium endobioticum*) and good table quality of Sutton’s Abundance and the virus X resistance of Katahdin as well as the blight resistance of *S. demissum* were introduced. The domestic seedlings were chosen for their ability to transmit high yielding capacity to their offspring.

This illustrates the general procedure followed in the early attempts to transfer the blight resistance of *S. demissum* to commercial varieties. Salaman’s methods have now been improved on to some extent, and modern breeders usually employ less selfing or none at all. Reddick (33) for instance advised avoiding selfing altogether. No characters of the wild species other than its blight resistance are wanted and the rest must be eliminated by a series of backcrosses.
The breeder’s work with respect to disease resistance is never finished because, as new resistant varieties are produced, new biological races of the pathogen tend to arise which can infect plants that were previously resistant. The existence of such

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<thead>
<tr>
<th>Generation</th>
<th>Matings</th>
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<tr>
<td>I</td>
<td><em>S.</em> demissum x Seedling of domestic type</td>
<td>A combination of Resistance to Blight and no Yield with susceptibility to blight; very high yield, white, but indifferently shaped tubers.</td>
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<tr>
<td>II</td>
<td>Selfed</td>
<td>Selection of the most vigorous types with best yields. Crops small and tubers of poor shape and size.</td>
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<td>III</td>
<td>Selfed</td>
<td>Continuance of selection, some better crops secured.</td>
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<tr>
<td>IV</td>
<td><em>x</em> Domestic seedling</td>
<td>Strengthening of the domestic characters of haulm and tuber. Selection of most desirable types with much improved yields.</td>
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<tr>
<td>V</td>
<td>Selfed</td>
<td>Further selection on same lines with elimination of all blight-susceptibles.</td>
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<tr>
<td>VI</td>
<td>Selfed</td>
<td>Continuance of selection and elimination of blight-susceptibles.</td>
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<td>VII</td>
<td><em>x</em> Sutton’s Abundance</td>
<td>Introduction of resistance to Wart Disease and improved table qualities. Selection for resistance to wart and blight.</td>
</tr>
<tr>
<td>VIII</td>
<td><em>x</em> Katahdin</td>
<td>Introduction of resistance to virus ‘X’ infection, and continued selection.</td>
</tr>
<tr>
<td>IX</td>
<td></td>
<td>Several seedlings combining blight resistance, wart resistance, and possibly resistance to virus ‘X’ with good economic qualities.</td>
</tr>
</tbody>
</table>

biological races in *Ph. infestans* was discovered in Germany in 1932, and in the same year a new race appeared in England. The relation, if any, between the German and English races is not clear. Unfortunately there is no universally adopted system of classification of *Phytophthora* strains. Salaman’s seedlings had shown complete blight resistance of both haulm and tuber for several years but when the new biotype of *Phytophthora* appeared they began to show signs of infection.

A source of resistance to the new biotype was found, however, in a potato which, according to Salaman (40), was undoubtedly
a derivative of S. demissum hybrid stock. This stock, which proved completely resistant to both the old and the new biotypes of the fungus, was crossed with a series of suitable domestic varieties and with the previously resistant seedlings. Selection was carried out for resistance to the two biotypes and further backcrosses were made. In this way several types with "double resistance" were obtained, though they lacked some of the economic qualities which are necessary in cultivated varieties (39).

In Germany, breeding for blight resistance was begun before the first world war. In 1932 when the Streckenthin strain of blight first made its appearance, the only lines not attacked were certain S. demissum x S. tuberosum hybrids which, like the parental S. demissum, proved immune to both the new and old strains of the fungus (41). Other material, derived from Müller's W races, which was resistant only to the old strain, will be referred to below in the appropriate section.

At the Biologische Reichsanstalt für Land- und Forstwirtschaft at Berlin-Dahlem, backcross selections of S. demissum x S. tuberosum resistant to Phytophthora and giving up to 75% of the yield of cultivated varieties had been obtained in 1939 (37).

According to the British Intelligence Objectives Sub-committee report on potato breeding in Germany (14), eight groups of related Phytophthora strains are now recognized in Germany and many hybrid seedlings resistant to all of them have been bred but these cannot compare with commercial varieties in their other characteristics. Among the promising seedlings undergoing field trials in Germany in 1946 there were several showing resistance to five strains of the fungus. Half the new varieties approved in Germany in recent years were bred from hybrids made by Müller who obtained a great deal of blight resistant material from crosses with S. demissum. At the Bayerische Landessaatzuchtanstalt in the US Zone the main aim in potato breeding is to develop varieties resistant to virus diseases and blight. In backcrossing the S. demissum x S. tuberosum hybrids to commercial varieties, types showing some resistance to virus diseases are therefore chosen as recurrent parents. In this way blight resistance and virus resistance have been combined.

S. demissum has been used in Russia for its combined resistance to blight and frost. In 1935, hybrids of S. tuberosum and S. andigenum with S. demissum, all resistant to −5°C, had been obtained (7). Although they were self sterile, backcrosses with domestic potatoes were successful and gave rise to segregating
progenies some of which were fairly high yielding. Only about 1% of them were attacked by blight in the field. Bukasov reported in 1938 (15) that 150 different varieties of *S. tuberosum* had been crossed with *S. demissum*, and, in order to determine the most favourable series of varieties to use in the backcrossing process, a study of 600 *S. demissum* backcrosses had been started. Some of the blight resistant hybrids of *S. Antipoviczii* and *S. demissum* with *S. tuberosum* gave yields of up to 3 kg. and more per plant and were thoroughly desirable as regards their other characteristics.

At the Scottish Plant Breeding Station in Edinburgh, high yielding, blight resistant varieties were obtained (2) by the usual method of making hybrids between *S. demissum* and *S. tuberosum* and backcrossing them several times to the latter. Susceptible seedlings were eliminated by mass selection following artificial infection with blight spores in the greenhouse. About 40% of the progeny in the later backcross generations were immune to blight (9). In 1943 it was reported (3) that selections resistant to both common blight and a virulent local strain had been obtained. Some difficulty was experienced in making the crosses owing to pollen sterility but a 48-chromosome hybrid of *S. demissum* (2n = 72) x *S. Rybinii* (2n = 24) was found to cross readily with cultivated varieties. The selfed progeny and backcross progeny of the triple hybrid showed exceptionally high fertility and many of them were resistant to both strains of blight, but in 1943, the most advanced hybrids had shown resistance to only the common strain of blight.

Genetical data reported by W. Black have shed some light on the problem of breeding for resistance. He found that immunity from the *Phytophthora* strains A and B is determined by two major genes designated *Ra* and *Rb* (10, 11). *Ra* gives immunity to strain A only, and *Rb* to both A and B. Two further dominant genes were later shown to be involved in the determination of blight resistance (12). *Rc* confers immunity from strain A and another new strain, C, and *Rbc* to strains A, B and C. In addition, minor genes appear to be present which determine the degree of susceptibility in susceptible varieties and act as modifiers in resistant ones.

With repeated backcrossing some of these genes are lost together with the undesirable ones which the crosses are designed to eliminate. Consequently the new blight resistant commercial varieties which are bred do not possess the full degree of blight resistance found in *S. demissum*. Black has suggested (13) that...
by intercrossing different resistant breeding lines which have been secured by the backcross method it might be possible to reassemble the various resistance genes to the required concentration.

In the United States also, *S. demissum* has been used as a source of blight resistance for many years. Empire, a blight resistant variety developed in 1940 at the Cornell Agricultural Experiment Station, Ithaca, New York and released in 1945 has been described by Reddick and Peterson (35). It was derived from a cross between *S. demissum* and a hybrid *S. tuberosum* seedling followed by a series of backcrosses to different varieties of the latter species as follows:—

\[
\begin{align*}
S. \text{demissum} & \ \varphi \times 103-14 \ \sigma \\
756-2 & \ \varphi \times \text{Katahdin} \ \sigma \\
\text{EW-4} & \ \varphi \times 860 \ \sigma \\
\text{No. 9} & \ \varphi \times \text{AZK-3} \ \sigma \\
\text{Empire} & \ \text{(CRH-7)}
\end{align*}
\]

No. 9 is a high yielding selection from Rural New Yorker No. 2 and was one of the parents of 103-14, the other one being a variety named 52, the identity of which was unknown. Seedling 860 is tolerant of drought and has strongly rugose leaflets, a character inherited by Empire. After each cross, plants susceptible to blight were eliminated by inoculation and the immune plants transferred to the field, where selection was carried out primarily for size, shape and appearance of the tubers.

Empire is drought tolerant as well as resistant to blight and has several of the characteristics of Rural New Yorker. In yield tests in different localities in New York State in 1944 it yielded as well as or better than the standard varieties, and in 1945 when blight infection was a factor it exceeded the standard by as much as two to one.

In 1946 however when Empire was tested again, on the south fork of Long Island, both its tubers and foliage became infected with blight and it was decided that the use of the variety should be discouraged (36) in case it should prove the means of raising the level of virulence of *Ph. infestans*.

Four other new varieties resulting from the same breeding programme, viz. Placid, Virgil, Ashworth and Chenango were described in 1947 by Reddick and Peterson (36), the breeding methods employed being the same as for Empire.
Placid was derived from a cross between a hybrid resulting from hybridizing *S. demissum* with Smooth Rural and then backcrossing twice to *S. tuberosum* and another hybrid resulting from thrice crossing with *S. tuberosum* and selfing an *S. demissum* x *S. Fendleri* hybrid. The authors say the "fantastic chart of parentage" of Placid illustrates "the gropings of the earlier efforts and to some extent the often repeated remark that in the end one takes what he can get."

Virgil's pedigree is rather simpler, this variety being derived from a third backcross as follows:

\[
\begin{align*}
S. \text{demissum} \, \varphi & \times \text{Pirola} \, \varphi \\
812 \, \varphi & \times \text{Pirola} \, \varphi \\
\text{IW-1} \, \varphi & \times 860 \, \varphi \\
1145 \, \varphi & \times \text{ZH-2} \, \varphi \\
\text{Virgil}
\end{align*}
\]

The first cross was made in May 1931 and produced seven seeds, the first backcross in 1932, the second in 1934 and the third in 1939.

In tolerance of heat and drought, Virgil is superior to Placid, which it appears to surpass also in blight resistance. Ashworth, like Placid, has a somewhat complicated parentage but as no significance is attached to the exact method in which it was developed, it suffices to say here that it came from a cross between two plants each derived from crosses and repeated backcrosses of hybrids between *S. demissum* and a heterozygous variety erroneously termed *S. Maglia* to varieties and unnamed seedlings of *S. tuberosum*. Ashworth has tubers similar in size, shape and appearance to those of Katahdin, to which two backcrosses were made, and is equal or superior to that variety in cooking quality as well as being apparently immune to blight.

A cross between *S. demissum* and *S. Fendleri* followed by six crosses to *S. tuberosum* led to the production of the other new variety, Chenango, which is early maturing and has proved immune to late blight in greenhouse tests and field plots.

In Holland according to Koopman and Mastenbroek (23) *S. demissum* blossoms freely, sets many berries though hardly any tubers and is easily crossed with cultivated potato varieties. Selection for blight resistance in the first backcross progenies is carried out after soaking and spraying the seedlings with suspensions of *Phytophthora* spores in water at the stage when
two or three leaves have developed, and as many as possible of the resistant selections are again backcrossed with a cultivated variety. Further selection is carried out in the resulting second backcross generation which is grown the following year.

In 1945 while this procedure was going on, three apparently new biotypes of the fungus appeared which attacked previously resistant varieties. Fortunately, however, some of the seedlings proved resistant to the three new strains as well as the two old ones.

It was thought that after another two backcrosses had been made as many good varieties might be expected as would result from an ordinary cross between two cultivated varieties. Selection for wart immunity, yield, taste and other qualities in addition to blight resistance would then be possible.

Backcrossing of S. demissum x S. tuberosum hybrids at New Delhi to cultivated varieties, particularly the variety Gloriosa received from Russia, has given rise to resistant forms with good tuber shape and high yield (5).

2. Colorado beetle resistance.

As mentioned above, another desirable characteristic of S. demissum besides its immunity to blight is its resistance to attack by the Colorado beetle (Leptinotarsa decemlineata). Consequently attempts have been made, though not very successfully, to transfer this quality to commercial varieties of potatoes. It would appear to be determined by a relatively large number of genes which cannot all be retained in a backcross programme.

Trouvelot (50) found that F₁ hybrids of S. demissum x S. tuberosum inherited the resistance of S. demissum to Colorado beetle in varying degrees, some of them being almost as resistant as the S. demissum parent but not very productive of tubers. In his backcrosses to S. tuberosum the resistance was usually very much diminished, but he considered that adequate resistance might possibly be combined with good yield if a sufficiently large number of plants were bred.

At the Biologische Reichsanstalt für Land- und Forstwirtschaft in Berlin results have been so discouraging that the work has been discontinued (14).

K. Sellke (45) tested some 1520 clones arising from crosses of S. tuberosum with S. demissum, S. acaule, S. chacoense and S. andigenum, together with a number of wild species, by growing the young larvae of the Colorado beetle on the leaves in moist
Petri dishes. *S. demissum* and *S. polyadenium* proved resistant, and four other species partially resistant, the degree of resistance varying in different races of *S. demissum*; and some of the *S. demissum* x *S. tuberosum* hybrids were resistant, some partially resistant and some susceptible. In the second and third backcross generations only 3% to 4% were resistant, while in later backcross generations (44) the resistance of *S. demissum* was much diminished or even lost. Hybrids which survived a heavy field attack or artificial infection seemed to owe their success to morphological features or to favourable regeneration and growth characteristics.

Müller and Sellke (31, 32) reported that the resistance to Colorado beetle of the *S. demissum* parent was not recovered either in F₂ *S. demissum* x *S. tuberosum* hybrids or in the first backcross to *S. tuberosum*. The mortality of the larvae on F₁ plants varied from 5% to 95% and on F₂ plants from 5% to 75% (32). Since the resistance of the backcross generation was no less than that of the F₂, it was concluded that inheritance of resistance is through the female parent only. After a few generations of backcrossing the chromosome number of the hybrids was reduced to 2n = 48 and the plants became progressively more like *S. tuberosum*. Unfortunately the genes for resistance were eliminated together with the *S. demissum* chromosomes. The authors suggest that selection for regeneration capacity within *S. tuberosum* might give better results.

According to Crépin (17) two German clones from the cross *S. demissum* x *S. tuberosum*, three clones from a single backcross and one obtained by backcrossing twice to *S. tuberosum* showed considerable resistance to attack by the Colorado beetle.

Having considered how *S. demissum* has been used in breeding for resistance to blight, frost and Colorado beetle, we turn now to the use of other sources of these and various other characters.

### III. The Use of Müller’s W Races in Breeding for Blight Resistance

In Germany Müller's W races and the Ef strains from which they were derived (42) have been used as sources of late blight resistance. The W races are also immune to mosaic (25). The Ef strains were complicated 48-chromosome hybrids of some primitive forms from the central region of South America (26).

Until the Streckenthin strain of *Phytophthora* appeared in 1932, the W races and their hybrids were immune but, as we have said,
they then succumbed to attack while the *S. demissum* x *S. tuberosum* hybrids retained their immunity (41, 24, 30).

The varieties Erika, Frühundel and Robusta (4, 28) were obtained from crosses with these W varieties and were resistant only to biotype A of *Ph. infestans*. The resistance gene *R₁* was not difficult to transfer to cultivated varieties since it is independent of other characters of economic importance (29). Ten varieties carrying this gene have now been registered in Germany.

This type of resistance is apparently of some value in the USA. The W varieties were introduced there for breeding purposes and subjected to field tests at Presque Isle, Maine, from 1934 to 1936 when many of them proved to be resistant to blight. One of the seedlings, No. 3895–13, was used in the breeding of the new, blight resistant variety Kennebec (8).

Selections from a cross between this seedling and Earlainde were among the best of the progenies from the various crosses made between the seedlings of the W races and commercial varieties. Two of them, 96–44 and 96–56, were highly resistant if not immune to the common races of blight in Maine besides being early and self fertile. They also approached early commercial varieties in yield and cooking quality but were inferior in yield to such standard varieties as Green Mountain, Chippewa and Katahdin. So they were backcrossed to high yielding varieties and seedlings. From the cross B127 (a hybrid between Katahdin and Chippewa) x 96–56, seedling B70–5 was obtained. This was the best of the seedlings from the cross, which was made in 1940 in the greenhouses of the Plant Industry Station, Beltsville, Maryland, although several others were close competitors, and it was given the name Kennebec. Thus, Kennebec was obtained by selection from a backcross of a hybrid between a W seedling and a commercial variety to a high yielding hybrid between two commercial varieties as follows:—

\[
3895–13 \times \text{Earlainde} \quad \text{Chippewa \times Katahdin} \\
95–56 \quad \times \quad \text{B127} \\
\text{Kennebec}
\]

The variety is described as combining high yield and good cooking quality with a high degree of resistance to late blight in both tops and tubers besides having shown no symptoms of mild mosaic or net necrosis in field exposure tests. It is expected to replace Katahdin and Sebago in some places; though its value in commercial culture remains to be seen.
IV. THE USE OF S. semidemissum IN BREEDING FOR COMBINED RESISTANCE TO BLIGHT AND FROST

S. semidemissum (2n = 60) has been used in Russia for breeding for resistance to blight and frost. In 1935 hybrids between S. tuberosum and this species were reported to be resistant both to Phytophthora and to −7° C. of frost (1). S. semidemissum is difficult to cross with cultivated varieties but Filippov (19) obtained a number of hybrid seeds in 1938 by crossing it with Smyslovskii [Fürstenkrone] after subjecting it to short days and low temperature for 25–30 days. Further hybrids were obtained in 1940 from the cross S. semidemissum x Rosafolia. The F₁ generations were very promising and were superior to S. demissum hybrids in starch content, tuber yield, earliness and frost resistance, but had small tubers. The best seedlings when backcrossed to Fürstenkrone gave rise to plants of the cultivated type resembling hybrids between domestic varieties. Many were resistant to blight and frost, yielded fairly well and matured early. They all had short stolons and some had quite well-shaped tubers. Those classed as blight resistant were grown under field conditions of very heavy infection and proved more resistant than the blight resistant variety 8670. About 30% of the seedlings were resistant to blight, and 15% withstood temperatures of −2.5° C. to −3° C.; the best resisted −5° C. Up to 65 tubers per plant were produced but these were of small size. About 40% of the backcross seedlings produced fertile pollen. Most of them had 2n = 54 chromosomes.

V. THE USE OF S. acaule IN BREEDING FOR RESISTANCE TO FROST AND POSSIBLY BLIGHT

Tkachenko (48) crossed S. acaule, a 48-chromosome wild species, with Fürstenkrone and backcrossed the hybrid to S. tuberosum. The F₁ hybrid was resistant to −4.5° C. but was low in yield. The backcross hybrids also gave low yields but showed vigorous growth, and two of them were blight resistant.

Filippov (18) reported that a relatively high-yielding seedling from a cross involving S. acaule and Fürstenkrone was backcrossed to the latter and gave rise to 136 seedlings which showed certain S. acaule characters including frost resistance and long stolons but were otherwise of the domestic type. The pollen fertility varied from 0% to 90% and some of the plants set seed spontaneously. Some were not damaged by −3° C. to −3.5° C. However none of them were blight resistant.
VI. The Use of \textit{S. chacoense} in Breeding for Resistance to Colorado Beetle

\textit{S. chacoense} is perhaps more promising than \textit{S. demissum} as a source of resistance to Colorado beetle. Hybrids were made at the Cornell University Experiment Station (6, 7) between tetraploids of \textit{S. chacoense} and commercial varieties and backcrossed to the pollen-producing varieties Katahdin and Earlaine. Some of the hybrids showed blight resistance and good commercial qualities; some of the backcross seedlings yielded fairly good tubers and showed insect resistance. Further backcrossing is still necessary.

Breeding along similar lines has not been successful in Germany, since the resistance of \textit{S. chacoense} has become dissipated with each successive backcross generation (14).

Toxopeus (49) crossed \textit{S. chacoense} with \textit{S. Antipoviczii}, doubled the chromosome numbers of the hybrids with colchicine and backcrossed the amphidiploids to \textit{S. chacoense}. An average of six seeds per berry was obtained from the backcross progenies. He designated the amphidiploid \textit{S. artificiale}. In crosses with \textit{S. tuberosum} as pollen parent, abundant seeds were produced and many of the F\textsubscript{1} plants were fertile and could be backcrossed to \textit{S. tuberosum}.

VII. Crosses Involving \textit{S. andigenum}

\textit{S. andigenum} (2n = 48) has been claimed to be another source of blight resistance as well as other desirable characters, though tests at the Commonwealth Potato Station, Cambridge, have failed to confirm its resistance. Veselovsky (51) reported a combination of the following characters in backcrosses of \textit{S. andigenum} x \textit{S. tuberosum} hybrids to early commercial varieties: early formation of tubers, short period of tuber development, early normal completion of the vegetative period and high productivity. Outstanding crosses were Early Rose x F\textsubscript{1} (\textit{S. andigenum} var. Taccia x Fürstenkrone), Epicure x F\textsubscript{1} (\textit{S. andigenum} var. tocanum x Centifolia) and Early Rose x F\textsubscript{1} (\textit{S. andigenum} var. tocanum x Centifolia).

VIII. Crosses Involving \textit{S. leptostigma} and \textit{S. Molinae}

\textit{S. leptostigma} and \textit{S. Molinae} are two species with high drought resistance. Their hybrids with \textit{S. tuberosum} are described by
Kameraz (22) as possessing, in some cases, resistance to drought and giving moderate yields of tubers with a fairly high starch content but being unsatisfactory in other respects in the $F_1$, $F_2$ and $F_3$ generations, so that, as in the case of other interspecific Solanum hybrids, backcrossing to $S. tuberosum$ is essential. Three backcrosses to $S. tuberosum$ would appear to give the best results.

**IX. Crosses Involving $S. Antipoviczii$**

$S. Antipoviczii$ crosses with $S. tuberosum$ only with difficulty. Sidorov (46) obtained three crosses with Mirabilis, Epicure and Imperator respectively. The hybrids were all blight resistant and resembled $S. Antipoviczii$ more than $S. tuberosum$; their yield was very low. $F_2$ and backcross progenies were obtained from the Mirabilis hybrid which alone was sufficiently fertile, and these, again, were all resistant to Phytophthora and showed a marked resemblance to $S. Antipoviczii$. The backcrosses with $S. tuberosum$ gave higher yields than the $F_2$ plants but were less fertile.

Kameraz (21) states that, whilst the $F_1$ to $F_4$ generations of hybrids between $S. Antipoviczii$ and $S. tuberosum$ are of low quality, backcrosses with $S. tuberosum$ have given seedlings with high yields approaching that of the standard, with normal clusters of tubers free from any bitter flavour and with resistance to blight.

**X. Crosses Involving $S. Punae$**

Another species difficult to cross with $S. tuberosum$ is $S. Punae$. According to Bukasov (16), only a few hybrids were obtained out of thousands of crosses made in the Soviet Union. On backcrossing to $S. tuberosum$ 72-chromosome hybrids with the characters of $S. Punae$ and therefore of no economic value were obtained. From the second backcross, however, 60-chromosome hybrids exhibiting frost resistance were obtained. Kameraz (21) states that although $S. Punae$ itself is not blight resistant some of its hybrids with domestic varieties, including Fürstenkrone, have proved resistant to both blight and blackleg (Erwinia phytophthora). Some of the backcrosses such as [(S. Punae x Fürstenkrone) x Centifolia] x Fürstenkrone or Centifolia combine frost resistance with the necessary commercial qualities.
XI. Crosses Involving S. Schreiteri

*S. Schreiteri* possesses valuable frost resistance. According to Zvereva (52) the difficulty of hybridizing it with *S. tuberosum* was overcome by the method of vegetative *rapprochement* and it was successfully crossed with the varieties Epicure and Smyslovskii as female parents. One of the twelve hybrid plants was backcrossed to a domestic variety, and gave seedlings showing much variation which were vigorous and mostly produced seed when selfed or backcrossed. In a yield test most of the hybrids surpassed Early Rose and Wohltmann, two exceeded Lorh by 7%, one equalled this variety, and four others came very near. Some had starch contents up to 23.5%. About 30% of the hybrids were discarded because of susceptibility to crinkly mosaic apparently inherited from *S. Schreiteri*. Of seventy hybrids tested in the field in 1945, three withstood a frost of −5°C, accompanied by strong wind, which completely destroyed all commercial varieties.

XII. Crosses Involving a Chilean Strain

In breeding for resistance to degeneration, Müller developed the variety 9089 (27) by crossing an Indian potato from Chiloé with Dolkowski's variety Świteź, backcrossing the hybrid with one of Broili's land races and then selfing. The new variety yielded better in its tenth year of cultivation than the best of the older varieties in their fourth. It showed a high degree of tolerance to leaf roll (virus) and both resistance and tolerance to mosaic but its yield was low; so it was backcrossed to a number of the best commercial varieties. The seedlings were grown for six successive years in Dahlem and some lines proved distinctly superior to the most virus resistant cultivated varieties known.

XIII. Various Interspecific Crosses Made in Java

Some breeding work with wild *Solanum* species in Java remains to be mentioned. According to T. H. Thung (47) backcrosses have been made on interspecific hybrids bred in the Netherlands and reciprocal crosses made in Java. Progenies of crosses of *S. tuberosum* with the following species have been tested for resistance to various diseases: *S. andigenum*, *S. Antipoviczii*, *S. Caldasii*, *S. chacoense* and *S. demissum*. Further backcrosses are to be made to raise the hybrids to the required standard.
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