THE GENETICS OF BLACKARM RESISTANCE

II. CLASSIFICATION, ON THEIR RESISTANCE, OF COTTON TYPES AND STRAINS

III. INHERITANCE IN CROSSES WITHIN THE *GOSSYPIUM HIRSUTUM* GROUP

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(With Three Text-figures)

CONTENTS

Introduction

In an earlier paper the authors (1939) discussed the genetics of blackarm resistance in an American × Sakel[1] cross and the transference of the factors for resistance from the American to the Sakel genotype. The work described in the present paper was started before that on the transference of resistance to Sakel types, but had to be subordinated to the latter owing to the extreme urgency of this problem.

Now that the production of blackarm-resistant Sakels is nearing completion, the problem of adding resistance to American Upland strains will again come to the fore.

In the Southern Sudan, American Upland cotton is grown under rain conditions and, often, on the same site for several years. Clearly this present lack of rotation favours the spread of the disease, and under such conditions blackarm is likely to develop into a major problem as it has in Uganda (Hansford, 1934). Indeed, it seems certain that it would have done so already were it not for the smallness and isolation of most of the plots of cotton in the rain areas. Moreover, seed disinfection and plant hygiene as methods of blackarm control, although partially successful in the Gezira,[2] will not be practicable in the Southern Sudan for many years to come.

It is clear, therefore, that the only satisfactory approach to the problem of combating this disease in the more inaccessible parts of the Sudan is by the breeding of resistant types. A necessary approach to this problem was an examination of the blackarm resistance potentialities within the genus *Gossypium*. Part II of this series gives a classification, based on resistance, of a wide range of cotton types, whilst an account of the inheritance of resistance in some of the crosses which have been undertaken is given in Part III.

Previous work

Knight & Clouston (1939) briefly described a technique for infecting cotton plants with blackarm on a standardized basis by spraying with a water suspension of the causal organism (*Bact. malvacearum* Sm.) obtained from infected plant material. A system of grading blackarm resistance, with grade "0" representing immunity and "12" full susceptibility, was also defined in detail.

[1] Sakel, an abbreviation for Sakellaridis, is a variety of *G. barbadense*. American Upland cottons belong to the species *G. hirsutum*.

[2] The Gezira is an area lying between the Blue Nile and the White Nile and irrigated from the Sennar dam.

In the same paper it was shown that the resistance of the American Upland (*G. hirsutum*) strain, Uganda B. 31, is due to the presence of two dominant, cumulative factors, $\mathbf{B}_1$ and $\mathbf{B}_2$ (together with a modifier complex). These factors, when transferred to a Sakel (*G. barbadense*) genotype, gave grade "10. 1" and "7" resistance respectively and clearly defined ratios were obtained in F_2 and in backcross progenies on the expected basis for a two-factor difference.

II. CLASSIFICATION, ON THEIR RESISTANCE, OF COTTON TYPES AND STRAINS

The resistance of Uganda B. 31 is marked, but, though the transference of B. 31 resistance factors to Sakel affords considerable protection against blackarm, it was desirable to discover whether other factors for resistance existed, with a view to their ultimate incorporation in Sakel and American varieties.

With this end in view, seed of a large number of cotton types was sown in one plot, the varieties being plentifully interspersed with controls of known blackarm grade. Six weeks after sowing, all the plants were sprayed with blackarm suspension and, after a suitable incubation period, graded for resistance. The results of this examination are given below. Such a list, including as it does over one hundred and sixty varieties and strains of cotton, should be of direct use to a plant breeder suddenly faced with the necessity of breeding cotton varieties resistant to this disease. It must be remembered, however, that this classification is based solely on leaf attack and that no account is taken of the ability or otherwise of the plant to "grow away" from the disease. Tissue resistance is the criterion and not the quality of vigour which may enable a plant to recover from an attack—this latter is a separate problem. Stem resistance was not recorded, but the authors (1939) have shown that stem and leaf resistance are positively correlated in crosses involving factors $\mathbf{B}_1$ and $\mathbf{B}_2$, and observation indicates that this correlation is general.

Hansford (1934), writing of blackarm in Uganda, attributes the major damage to stem infection but states that this occurs in 99% of cases as the result of the extension of leaf attack and that, without the latter, infection of the stem will not occur. Uganda appears to differ, in this respect, from the Sudan where leaf infection alone is capable of considerably reducing the yield. It matters little, however, for plant breeding purposes, whether the crop loss is a direct or indirect sequel to leaf infection, since control of the latter still remains the key to the problem.

(1) *Peruvian group* (G. barbadense *Linn.*)

(*a*) *Sakels.* Some forty strains and substrains of Sakel have been tested and all showed full susceptibility (grade "12" symptoms).

(*b*) "*Egyptian*" *types.* Sixteen types have been examined, namely, "310", NT. 25/24, Nahdah, Garofallou, Pima, Nazli, and Giza nos. 3, 7, 12, 15, 19, 24, 25, 26, 27, 28. All these proved fully susceptible except that Giza nos. 7 and 12 might have contained a very slight degree of resistance—a difference too slight to be measured on the "0"–"12" scale.

(*c*) *Pure Sea Island and strains of Sea Island origin.* Thirteen strains were examined: D. 3. 2, D. 1. 8, D. 14. 1, NT. 4/33, "897", "898", AN, NT. 12/34, NT. 13/34, and Shambur nos. III and IV; all showed grade "12" symptoms. V. 135 and "Montserrat" were graded as slightly under "12"—a degree of resistance so slight that place effect could readily account for it. In addition, a single plant was found in "898" showing grade "7" resistance.[1]

(*d*) *Ishan.* Ishan A is fully susceptible.

(*e*) *Hybrids.* The following types were found to be fully susceptible:

K. 3 ×S. 5. 39 (Kidney ×Sea Island)
K. 3 ×S. 5. 58 (Kidney ×Sea Island)
K. 3 ×S. 5. 124* (Kidney ×Sea Island)
K. 3 ×S. 1. 74* (Kidney ×Sea Island)
K. 3 ×S. 1. 99 (Kidney ×Sea Island)
K. 3 ×S. 1. 107 (Kidney ×Sea Island)
K. 3 ×S. 1. 118* (Kidney ×Sea Island)
K. 3 ×S. 1. 160 (Kidney ×Sea Island)
K. 3 ×S. 1. 238* (Kidney ×Sea Island)
Red Sea Island (Kidney ×Sea Island)
NT. 5/33 (Afifi ×Burd's Sea Island)
508 B (Sea Island ×Sakel)
NT. 8/34 (Peruvian ×Sea Island)
NT. 40/36 (Ishan ×Sakel)
NT. 37/36 (Ishan ×Sakel)

[1] A paper on the genetics of the resistance of this plant is in the course of preparation by the senior author.

* In the following classification an asterisk signifies that less than ten plants were examined.

(2) *American Upland group* (G. hirsutum *Linn.*)

Sixty-six strains and substrains were examined. They were classified first according to whether they were pure breeding for the degree of resistance shown, and secondly, on average blackarm grade.

(*a*) *Types showing little or no variation in blackarm symptoms.*

(i) *Blackarm grade* "9"–"10". Delta Webber 6, Webber nos. 38 and 49. 2, Uganda S.G. nos. 26, 27 and 29*, Willett's Red Leaf, Rustam 82*, 514, 514 A, 514 B, 514 D, 514 E, N.T. 6/34*, Dekhan 169, Batyr 508, Ak Dzhura, Schroeder 1306*, Columbia 44*, Wild's no. 1, Bolland Upland nos. 29, 99*, and 105*, XA 129*, XA 1129, Triumph nos. 145. C. 51. 30*, 143. J. 4. 119, and 143. K. 2. 130*, NT. 60/39, NT. 68/39, NT. 75/39 and NT. 77/39.

(ii) *Blackarm grade* "7"–"8". Meade*.

(iii) *Blackarm grade* "5"–"6". 513, 513 A, 513 B, 513 E, N.T. 58/39, NT. 61/39, NT. 84/39, Parnell's U. 4. Nyasa 5, NT. 15/35, 511 A, 511 C, 511 E, Triumph 145. C. 52. 32*, NT. 7/34.

(iv) *Blackarm grade* "3"–"4". Uganda B. 31/21, Uganda B. 31/10/12/11.

(*b*) *Types impure for blackarm resistance.*

Type	Modal grade	Range
Rustam 124*	"9"	"7"– "9"
Columbia 40	"11"	"9"–"12"
Columbia 43	"9"	"9"–"11"
Delrect I	"10"	"7"–"10"
Parnell's U. 4*	"5"	"5"– "7"
Parnell's U. 4. 4. 2	"5"	"5"–"11"
Parnell's U. 4. Nyasa 4	?	"5"– "9"
Parnell's U. 4. Nyasa 8	?	"5"–"10"
Parnell's U. 4. Nyasa 9	"6"	"5"– "9"
Parnell's U. 4. Nyasa 10	"6"	"5"– "9"
511	"6"	"6"–"10"
Pump Scheme Strain	"10"	"7"–"12"
NT. 74/39	"5"	"4"–"10"
NT. 63/38	?	"4"–"12"
NT. 69/39	"5"	"5"–"10"
NT. 78/39	"9"–"10"	"5"–"10"
NT. 83/39	"5"– "6"	"5"– "8"

(3) *Bourbon group* (G. purpurascens *Poir.*)

"Serido" and "Moco" were fully susceptible but the sample of the latter contained one grade "10" plant.

(4) *Punctatum group* (G. punctatum *Sch. & Thon.*)

"Gambia native" and XBA 22039 possessed grade "1"–"2" resistance whilst samples of "Hindi Weed" (? *G. punctatum*) from the commercial Sakel crop were pure for grade "5"–"6" resistance where they had not outcrossed with Sakel.

(5) *Interspecific hybrids and other types*

Type	Modal grade	Range
Verdao* (American Upland × Brazil perennial)	"12"	—
R.U. 4 (36) 23–1 (Asiatic × New World)	"3"	—
Titsiros	"12"	"10"–"12"
Kawa Baladi	"9"	"9"–"10"

(6) *Old World* (13 *chromosome*) *cottons*

Five types were tested: Abu Hareira, *G. cernuum* and *G. sanguineum* proved immune; "Chinese Indigenous" gave a range of grades from "0" to "9", whilst Nuba Red was pure breeding for grade "9".

Discussion

In the American Upland group resistance ranged, in pure types, from grade "3" to "10", whilst some of the types impure for resistance contained fully susceptible plants. It would appear that grade "9"–"10" is the normal "full susceptibility" in American varieties, and this probably represents the grade "12" of *G. barbadense* modified by such factors as hairiness, rapid maturity and hardening of leaves. Recent work by the senior author indicates the probability that $\mathbf{B}_2$ is the major factor responsible for the resistance of most of the American strains of grade "7" and under.

From the results obtained, the Bourbon group appears to contain little, if any, resistance, but a much more varied sample would be required to determine the resistance potentialities of this group with any certainty. Harland (1939), writing of *purpurascens* types obtained from Serido, noted that "One type was so badly attacked that it was almost impossible to carry the plants past the seedling stage, and the susceptibility was fully inherited in the next generation. Another type proved to be practically immune". This statement is particularly interesting because of the strong suggestion of seed infection as a factor determining the severity of attack on the first variety. In view of the fact that these Brazil types are often heterozygous for fuzzy seededness, it is possible that the suggestions made below with regard to the St Vincent results might also explain Harland's findings.

In the Punctatum group, Gambia native and XBA 22039 (a derivative of an "off-type" plant found in "Schroeder") show outstanding resistance and this is the strongest resistance so far found in New World types.

No indication of blackarm resistance was discovered in the Peruvian group with the exception of the single (? mutant) plant referred to in paragraph 1 (c). Other workers, however, have claimed the existence of marked resistance in *G. barbadense*. Lambert (1938) noted the remarkable power of recovery from blackarm possessed by the X 1530 and X 1730 types as compared with ordinary Sakel. This, however, is due to the greater vigour of the former which enables the plant to "grow away" from the disease, an effect which can be observed in ordinary Sakel growing under good conditions.

Bailey (1928, 1929) recorded varying "susceptibility" on six Egyptian types under test and noted the same order of varietal susceptibility at each of three stations[1] within the same year. In the following season, the results from the three stations again agreed closely, but the order of susceptibility of the six varieties differed markedly from that of the previous season. In view of the inconsistency of the results of the two years' work the intervarietal differences noted could not be attributed to genetic resistance and Bailey therefore suggested that the varying attack might be due to differential seed infection. As the seed supply of these varieties came from districts known to differ markedly in blackarm severity, this assumption seems reasonable. Under standard conditions these varieties have since been shown to be equally and fully susceptible.

This illustrates the divergent results which might be obtained in a search for true resistance in the absence of standardized inoculation and provides a possible explanation of the failure to find, at Shambat, the resistance claimed by Burd, Harland and Evelyn for certain Sea Island strains and hybrids.

Burd (1925), working in St Vincent, described the Sea Island strain "AN" as "somewhat resistant to angular leaf spot", whilst Harland & Evelyn (1933) considered that all their pedigree cultures possessed a "considerable degree of resistance". In the following year Evelyn & Harland (1934) reported: "A striking feature of the Red Sea Island strains...is their apparent immunity to Angular Leaf Spot" and again "with the exception of the Moco strains, Ishan and the hybrid Ishan × V. 135, the strains can be regarded as being highly resistant, particularly the Red Sea Island strains which appear to be completely immune." Finally, Evelyn (1936) wrote: "The Red Sea Island strains are in general highly resistant to Angular Leaf Spot."

Of the strains handled by these workers "AN" and Red Sea Island proved fully susceptible at Shambat, whilst V. 135 showed a degree of

[1] Shambat, near Khartoum, and Wad Medani and Barakat in the Gezira.

resistance so slight that place effect could readily account for it. On the other hand, Evelyn (1937) recorded his Asiatic × New World strains as being highly resistant, and these strains tested at Shambat did show considerable resistance (para. 5).

It is a matter of some importance to know whether blackarm resistance factors may operate in one place and not in another. The lack of agreement between the St Vincent and Shambat results therefore deserves consideration. From the published reports of the St Vincent workers it would appear that the incidence of blackarm, as measured by the percentage infection of the crop, was the criterion on which varietal resistance was based. Thus Evelyn & Harland (1934) stated that, for angular leaf spot, counts were made at weekly intervals, plants attacked being marked to avoid re-examination. As these observations were made on plants not subjected to any standard infection but which contracted the disease naturally, it seems highly probable that factors other than, or in addition to, true tissue resistance were operating. As already stated plant vigour is an important factor in blackarm incidence and, as Bailey (1929) showed, comparison of intervarietal attack can be readily vitiated by the degree of primary infection of the respective seed lots used. Some such effect might explain the divergence between the St Vincent and Shambat results. In this connexion it is interesting to note that the strains found to be susceptible in St Vincent are, in general, those with most fuzz on the seed, e.g. Moco, Ishan and to a lesser extent Montserrat, which Harland (1939) described as "rather susceptible". Obviously seed fuzz provides a foothold for the bacterial slime, and the amount of primary infection[1] should be positively correlated with the degree of fuzziness.

Experience in the Sudan has clearly shown the supreme importance of seed infection, and though seed disinfection is not absolutely effective it has removed the risk of complete crop failure which previously obtained in this country as a result of early blackarm attack. It seems, therefore, that the resistance obtained in St Vincent might be due almost entirely to absence of seed fuzz with the concomitant reduction of primary infection. Where, however, true resistance occurs (e.g. in the Asiatic × New World types) the presence or absence of fuzz would be relatively unimportant. Moreover, judged on Sudan results, the very vigorous growth obtained in St Vincent would accentuate differences due to differential seed infection, whilst the heavy rainfall, during the

[1] Primary infection is the attack on the cotyledons resulting from *B. malvacearum* carried on the seed coat or fuzz.

"dead" season for cotton, would largely inactivate blackarm debris, thereby further accentuating the importance of primary infection. In this connexion it is noteworthy that Squire (1938), working on the survival of pink bollworm, stressed the rapidity of disintegration of cotton debris in the West Indies.

III. INHERITANCE IN CROSSES WITHIN THE *GOSSYPIUM HIRSUTUM* GROUP

(1) *Uganda B.* 31 × 514 *crosses*

The object of this cross was to transfer, by backcrossing to the 514 parent, the blackarm resistance of Uganda B. 31.

514 was bred in the Sudan from a selection made in Pump Scheme Strain and is an erect, "open", rather tall type with good quality lint. This strain possesses only very slight (grade "10") blackarm resistance, and it was thought that any increase in this resistance would be of marked value in the rain areas.

Uganda B. 31, when grown at Shambat, is a short, dark green type of very unattractive appearance and low yielding capacity. The leaves are extremely susceptible to attack by sucking insects. The main stem internodes are condensed and the sympodia very short. In the Southern Sudan, however, B. 31 has a very different appearance: the internodes are longer, the leaves are healthier and the type is not unattractive but the yield is poor. The value of B. 31 lies in its very marked (grade "3") blackarm resistance.

F_1 *of Uganda B.* 31 × 514.

In 1934–5 season a number of F_1 families were grown, these being the result of crossing Uganda B. 31 with substrains of 514. At this stage no standard system of infecting the plants nor of grading for resistance had been evolved.

The F_1 plants, together with the parent types, were sprayed with blackarm suspension 7 weeks after sowing and were later examined for the disease after an adequate incubation period had elapsed. The severity of attack was found to be intermediate between the marked resistance of B. 31 and the susceptibility of 514, though there was a range from true intermediacy down to resistance as marked as that of B. 31, due, undoubtedly, to the inaccuracy of infection and grading referred to.

In subsequent seasons the sowing and grading of this F_1 and of the parent types was repeated. With the knowledge of spraying gained by experience and working on a more perfectly defined system of grading, a much more even result was obtained. B. 31 was found to have an average blackarm grade of "3" with a range from "2" to an occasional "4" and 514 was graded steadily between "9" and "10" whilst the F_1 was graded at "6" with little variation.

First backcross to 514.

In 1935–6 season the first backcross to 514 was grown, sprayed with blackarm inoculum 6 weeks after sowing and later graded. The summarized results of this grading are tabulated below, and graphed in Fig. 1.

Table 1. *Summation of blackarm classification of first backcross to* 514

	Blackarm grade												
	"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
	—	25	82	170	33	10	35	88	129	37	—	—	609
Percentages	—	4·1	13·5	27·9	5·4	1·6	5·7	14·4	21·2	6·1	—	—	99·9

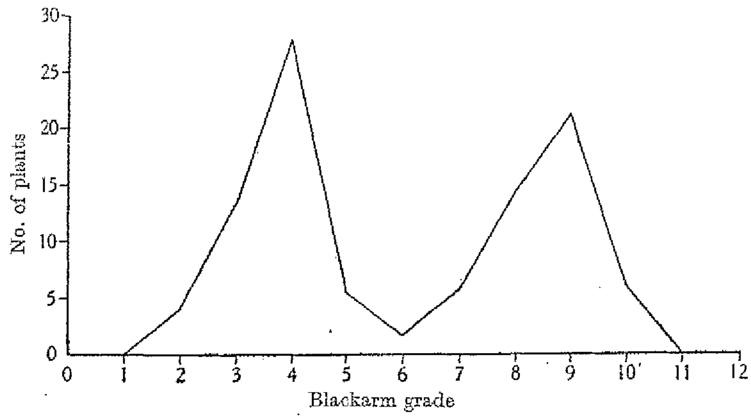

Fig. 1. (Uganda B. 31 × 514) × 514.

These figures give very little information as to the factorial nature of resistance, but, if the frequencies are split into two groups omitting grade "6" (the point of minimum frequency), the ratio of 289 less-resistant to 310 more-resistant plants is obtained and this hints at a 1 : 1 ratio.

F_2 of Uganda B. 31× 514.

In 1935–6 season a number of F_2 families were grown. These were sprayed with inoculum and graded.

Normal spacing for cotton at Shambat is 50×90 cm., and, where blackarm grading is to be done, sowing is carried out at one seed per hole or else the plants are thinned at a very early stage to one plant per hole. The 1935–6 F_2 families shown in Table 2, however, were sown at 25 × 90 cm. spacing, with up to four plants per hole according to the amount of seed available. This was done because, though it was necessary to have a large population to work with, considerations of available land and labour precluded the adoption of normal spacing.

When blackarm grading was carried out it became obvious that this overcrowding must have affected the efficacy of spraying and it seemed likely that the shade effects produced by overcrowding might also have vitiated the results (Knight, 1935). A second large F_2 was, therefore, grown at normal spacing in 1936–7 to check the previous season's data. The two seasons' results are compared in Table 2 and those for the latter

Table 2. *Summation of blackarm classification of F_2 of Uganda B.* 31 × 514. *Comparison of* 1935–6 *with* 1936–7 *results*

	Blackarm grade												
	"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Totals
Distribution													
1935–6	173	91	140	171	159	72	46	24	57	61	57	17	1068
1936–7	183	156	256	632	475	119	22	42	284	172	83	70	2494
Percentages													
1935–6	16·3	8·6	12·4	16·1	15·0	6·8	4·3	2·3	5·4	5·8	5·4	1·6	100·0
1936–7	7·3	6·3	10·3	25·3	19·0	4·8	0·9	1·7	11·4	6·9	3·3	2·8	100·0

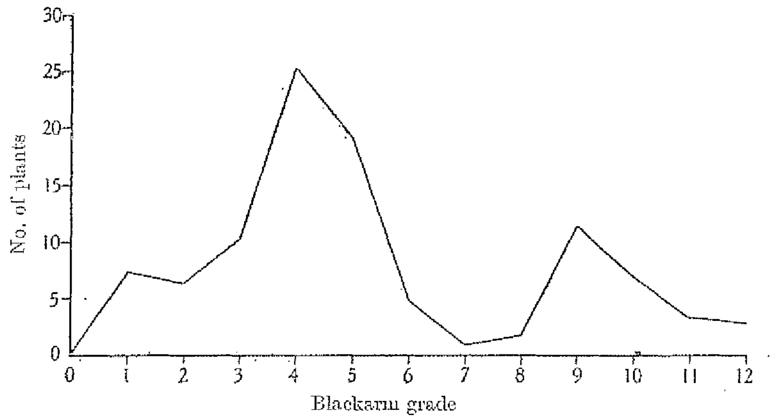

Fig. 2. Uganda B. 31 × 514 F_2.

season are graphed in Fig. 2, the earlier results being omitted on account of the considerations stated above.

A comparison of the two seasons' results shows that the normal spacing has brought about a drift from grades "1"–"3" into grades "4" and "5" and from "6"–"8" into grade "9". It is unlikely that this change was due to climate as the grading standard in each season was based on numerous controls of the parent types. These results further stress the absolute necessity for complete standardization in this work.

A number of markedly dwarfed[1] plants, about 8 in. high, appeared in F_2 and also in the F_2 of the first backcross to 514. This dwarfing has been found to be due to complimentary factors, and it is closely linked

Table 3. *Summation of blackarm classification of F_2 of first backcross to 514*

	Blackarm grade												
	"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
	139	139	195	781	949	410	141	193	386	96	60	31	3520
Percentages	3·9	3·9	5·5	22·2	27·0	11·6	4·1	5·5	11·0	2·7	1·7	0·9	100·0

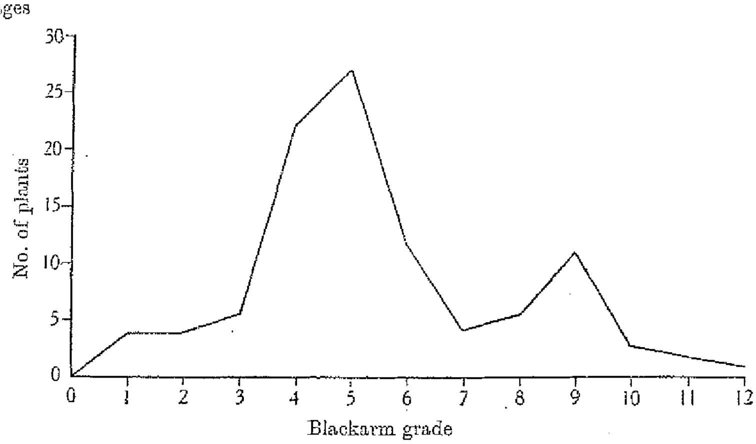

Fig. 3. (Uganda B. 31 × 514) × 514 F_2.

with factor $\mathbf{B}_1$. These dwarfs do not occur in all American Upland crosses involving Uganda B. 31, nor do they appear in crosses between this strain and Sakel.

F_2 of first backcross to 514.

All plants in the first backcross showing grade "4" or less infection were reselected in the field for nearness to 514 appearance and, later, in the laboratory, for lint quality and ginning out-turn. Plants of grade "3" and "4" only remained after this rigorous selection. Self-bred seed of these was sown in 1936–7 season and, 6 weeks after sowing, the plants were sprayed with blackarm suspension and, later, graded. The grading of all these families is summarized in Table 3 and graphed in Fig. 3.

[1] A paper on the genetics of this character is in course of preparation by the senior author.

Discussion.

In crosses between Sakel and 514 (unpublished work) the F_1 was fully susceptible whilst, in F_2, resistance ranged, with no clear-cut groups, from the grade "10" of the 514 parent to the full susceptibility of Sakel. This suggests that several minor factors are responsible for 514 resistance and that these are in the main recessive.

It is known that Uganda B. 31 contains two blackarm resistance factors, $\mathbf{B}_1$ and $\mathbf{B}_2$, and in crosses between this variety and Sakel, clear-cut ratios of three resistant to one fully susceptible occur in the first and second Sakel backcrosses. With the almost complete removal of the B. 31 modifier complex in the third and later backcrosses, ratios of 2 : 1 : 1 of the following composition were obtained (Knight & Clouston, 1939):

		Grade in 5th Sakel backcross
Phenotype A 1	$\{\mathbf{B}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{b}_2\}$ $\{\mathbf{b}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{b}_2\}$	"7" + "6" + "5"
Phenotype B 1	$\mathbf{B}_1\ \mathbf{b}_1\ \mathbf{b}_2\ \mathbf{b}_2$	"10. 1"
Phenotype C 1	$\mathbf{b}_1\ \mathbf{b}_1\ \mathbf{b}_2\ \mathbf{b}_2$	"12"

Crosses between Sakel heterozygous for factor $\mathbf{B}_1$ and 514 yield, in F_1, a 1 : 1 ratio of grades "10. 1" to "12" (unpublished work), grade "10. 1" being the type of resistance produced by $\mathbf{B}_1$ in the Sakel genotype. On the other hand, 514 to which factor $\mathbf{B}_2$ has been transferred is graded as "5" though $\mathbf{B}_2$ gives grade "7" resistance in a Sakel leaf (NT. 61/39 in para. 2 (*a* iii) of Part II is of this type and though classified in the grade "5"–"6" group, this type produced no grade "6" lesions). The inference is that 514 contains no modifiers for factor $\mathbf{B}_1$ but does possess modifiers for $\mathbf{B}_2$.

514 was selected from Pump Scheme Strain which arose mainly from Nyasaland Upland (Bailey, 1927). The origin of Uganda B. 31 is obscure but it seems probable that it, also, arose from Nyasaland Upland. It is reasonable to assume, therefore, that some of the Uganda B. 31 resistance modifier complex is present in the 514 genotype. Thus, in the backcross (B. 31 × 514) × 514, the 3 : 1 ratio which obtains in early Sakel backcrosses would not be expected, since the absence of $\mathbf{B}_1$ modifiers in 514 and the presence of $\mathbf{B}_2$ modifiers would result in a widening of the gap between $\mathbf{B}_1\mathbf{b}_2$ and $\mathbf{B}_1\mathbf{B}_2$ or $\mathbf{b}_1\mathbf{B}_2$ plants. It is suggested that the 1 : 1 ratio shown in Fig. 1 is made up of phenotype A (above) on the one side and B + C on the other and that B and C merge owing to the incorporation of a number of the 514 weak resistance factors. In this connexion it should be noted that "10. 1" resistance is slight so that phenotype B is

not far removed from C and any merging of the two would therefore readily account for the curve at the more susceptible end of the scale in Fig. 1.

Early Sakel backcrosses, involving Uganda B. 31, yield, in F_2, 15 : 1 ratios of resistant to fully susceptible plants whilst later ones give the expected ratio of 12 : 3 : 1. Though no 12 : 3 : 1 ratio is clearly defined in the F_2 of B. 31 × 514, Fig. 2 shows a basic distribution similar to this ratio and Fig. 3 confirms this. Fig. 3 tails off, at the susceptible end, more rapidly than Fig. 2, because of the inclusion of more weak 514 resistance in the first backcross F_2 than in the straight F_2. The subsidiary peak at grade "1" is partly due to the presence of dwarf types which showed an increased "resistance" owing to their shortened main stem and branch internodes, which rendered spraying of their leaves difficult.

(2a) *Uganda B.* 31 × 513 *crosses*

The object of this cross was to find out whether the resistance of 513 could be combined with that of Uganda B. 31 with the possibility of obtaining complete immunity to blackarm.

513 was selected in the Sudan from an importation of Punjab American Upland cotton. It is an early maturing, heavy yielding strain of medium quality. It is very hairy but requires rather frequent irrigation and is not very well suited to the Southern Sudan though it has proved of great value in the North. 513 is graded for blackarm attack as "5"–"6" at Shambat.

F_1 of Uganda B. 31 × 513.

In 1934–5 season a number of F_1 families were grown but, as was noted earlier, no standard system of infecting the plants nor of grading for resistance had been evolved at that stage so that the F_1 grade was not noted except that the blackarm symptoms were intermediate between Uganda B. 31 and 513.

First backcross to 513.

A number of first backcross families were sown in 1935–6, sprayed 6 weeks after sowing, and, later, graded (Table 4). As these families all gave similar results only the totals have been tabulated.

Table 4. *Summation of blackarm classification of first backcross to* 513 *parent*

Blackarm grade												
"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
—	27	245	394	35	2	—	—	—	—	—	—	703

It is clear, from the absence of any fully susceptible types or, indeed, of any plants showing greater susceptibility than 513 (grade "5"–"6" resistance), that 513 and Uganda B. 31 have at least one resistance factor in common.

F_2 of Uganda B. 31 × 513.

The F_2 of Uganda B. 31 × 513 was grown in 1935–6 and gave the following distribution of blackarm grades.

Table 5. *Summation of blackarm classification of F_2 of Uganda B.* 31 × 513

Blackarm grade												
"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
77	170	378	361	119	33	14	—	—	—	—	—	1152

A comparison of the distribution shown in the foregoing table with that given in Table 2 for the F_2 of Uganda B. 31 × 514 is instructive. It has been shown that 514 contains no major genes for resistance so the difference in distribution must be due to the resistance of 513, and again the absence of fully susceptible plants shows this resistance to be genetically identical with part of the resistance of Uganda B. 31.

F_2 of first backcross to 513.

A number of selections were made in the first backcross for breeding purposes. The seed of these was sown in 1936–7 season and a routine blackarm examination made later gave the following figures.

Table 6. *Blackarm classification of F_2 of (Uganda B.* 31 × 513) × 513

Family no.	Grade of parent	Blackarm grade "1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
HA 12/36	"3"	—	—	5	64	21	—	—	—	—	—	—	—	90
HA 14/36	"3"	—	—	22	19	1	—	—	—	—	—	—	—	42
HA 15/36	"3"	—	1	27	54	11	—	—	—	—	—	—	—	93
HA 16/36	"3"	—	2	5	15	11	—	—	—	—	—	—	—	33
HA 19/36	"3"	—	7	13	11	10	—	—	—	—	—	—	—	41
HA 27/36	"3"	—	—	—	11	49	8	—	—	—	—	—	—	68
HA 10/36	"4"	—	—	1	33	45	1	—	—	—	—	—	—	80
HA 11/36	"4"	—	2	26	53	43	5	—	—	—	—	—	—	129
HA 17/36	"4"	—	—	—	5	31	—	—	—	—	—	—	—	36
HA 20/36	"4"	—	2	6	9	13	4	—	—	—	—	—	—	34
HA 22/36	"4"	—	—	—	24	36	13	1	—	—	—	—	—	74
HA 23/36	"4"	—	—	2	12	96	48	1	—	—	—	—	—	159
HA 24/36	"4"	—	—	—	21	31	1	—	—	—	—	—	—	53
HA 25/36	"4"	—	—	9	19	51	2	—	—	—	—	—	—	81
HA 13/36	"5"	—	—	—	5	28	5	—	—	—	—	—	—	38
Totals	"3"	—	10	72	174	103	8	—	—	—	—	—	—	367
Totals	"4"–"5"	—	4	44	181	374	79	2	—	—	—	—	—	684
Grand totals		—	14	116	355	477	87	2	—	—	—	—	—	1051

The distribution in families derived from parents of grade "3" resistance and those in families derived from grade "4"–"5" parents are totalled separately in Table 6. The value of selecting grade "3" plants is obvious, for their progenies have a mode at grade "4" whereas the modal point for the progenies of grade "4"–"5" plants is at grade "5". Had family HA 27/36 been omitted from these totals the difference would have been greater and it seems probable that the parent of this family was incorrectly graded.

(2b) *Crosses between* 513 *and Sakel*

The object of crossing 513 with Sakel was the transference of the 513 resistance into Sakel by repeated backcrossing. It was hoped that it might prove possible to add the resistance of 513 to that of the factors B_1 and B_2, the inclusion of which in the Sakel genotype is now accomplished.

F_1 of 513 $\times$ *Sakel.*

The resistance of the F_1 was similar to that of the 513 parent.

First Sakel backcross.

The grading of the first Sakel backcross was as follows.

Table 7. *Blackarm classification of first Sakel backcross*

	Blackarm grade											
"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
—	—	—	—	10	87	64	—	—	—	7	128	296
					161						135	
	Expected (1 : 1)				148						148	

$\chi^2 = 1{\cdot}14$ and P is approximately 0·3.

If the grade "11" plants are included with the fully susceptible group a ratio of 161 resistant to 135 fully susceptible plants is obtained, and this is a fair approximation to a 1 : 1 ratio.

F_2 of 513 $\times$ *Sakel.*

An F_2 of 513 $\times$ Sakel was grown in the same season as the backcross, sprayed with inoculum 6 weeks after sowing and, later, graded with the following results.

Table 8. *Blackarm classification of F_2 of* 513 $\times$ *Sakel*

	Blackarm grade											
"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
—	—	—	9	134	210	137	5	8	6	36	61	606

Double F_1 (Sakel × Uganda B. 31) × (Sakel × 513).

In the hope of obtaining clearer results by eliminating a portion both of the B. 31 genotype and of the 513, a double F_1 was made by crossing the F_1 of Sakel × B. 31 with that of Sakel × 513. The results from the grading of this hybrid are tabulated below.

Table 9. *Blackarm classification of double F_1 (Sakel × Uganda B. 31) × (Sakel × 513)*

Blackarm grade												
"1"	"2"	"3"	"4"	"5"	"6"	"7"	"8"	"9"	"10"	"11"	"12"	Total
—	2	2	14	37	65	60	—	3	29	3	31	246
				180				32		34		
	Expected (6 : 1 : 1)			184·4				30·8		30·8		

Discussion.

The absence, in the backcross (B. 31 × 513) × 513 (Table 4), of any plants even approaching full susceptibility indicates that Uganda B. 31 and 513 have at least one resistance factor in common. The F_2 of B. 31 × 513 (Table 5) bears out this conclusion and the grading of the F_2 families of the first backcross to 513 (Table 6) also agrees with the assumption that 513 and Uganda B. 31 share at least one resistance factor.

In crosses between Sakel and 513 the production of a 1 : 1 ratio in the first Sakel backcross (Table 7) indicates that 513 contains only one major factor for resistance. In the F_2 of Sakel × 513 (Table 8), however, the clear-cut 3 : 1 ratio which would be expected with a monofactorial difference is not obtained.

It is suggested that 513 contains the strong factor $\mathbf{B}_2$ together with a number of weak factors and that it is these weak factors which are responsible for the distribution which obtains in the F_2 of Sakel × 513 shown in Table 8.

If 513 contains $\mathbf{B}_2$ and no other major factors for resistance, then, in the double F_1 shown in Table 9, the following types should appear.

1 $\mathbf{B}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{B}_2$ }
2 $\mathbf{B}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{b}_2$ } Grades "7" and under
1 $\mathbf{b}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{B}_2$ }
2 $\mathbf{b}_1\ \mathbf{b}_1\ \mathbf{B}_2\ \mathbf{b}_2$ }
1 $\mathbf{B}_1\ \mathbf{b}_1\ \mathbf{b}_2\ \mathbf{b}_2$ Grade "10. 1" in Sakel but "10" and under in B. 31 × Sakel crosses, according to the proportion of B. 31 genotype
1 $\mathbf{b}_1\ \mathbf{b}_1\ \mathbf{b}_2\ \mathbf{b}_2$ Grade "12" in Sakel

The agreement between expectation on this 6 : 1 : 1 basis and the results tabulated in Table 9 is so close that there can be no doubt that the genetic make-up of 513, from the resistance standpoint, is as stated, and it is, therefore, impossible to combine the resistance of 513 with that of Uganda B. 31 in new strains. There is no point in adding the factor $\mathbf{B}_1$ to the 513 genotype as, regardless of blackarm resistance, 513 is not well suited to rain cultivation in the Southern Sudan.

Summary

Part II of this series gives a classification, based on blackarm resistance, of over 160 varieties and strains of cotton. Complete immunity was not found in any New World types but exists in some of the Old World species. Several of the results disagreed with statements by St Vincent workers, some of the strains classed as "somewhat resistant", "highly resistant" and "immune" by them being found at Shambat to be fully susceptible. It is suggested that St Vincent results were based on differences in primary infection (seed infection), rather than on true tissue resistance and that these differences were accentuated by the presence or absence of seed fuzz and by plant vigour.

Part III shows the type of blackarm resistance inheritance obtaining in the crosses Uganda B. 31 × 514 and B. 31 × 513 (all three are American Upland types) the latter results being further clarified by crosses between 513 and Sakel.

Uganda B. 31 contains resistance factors $\mathbf{B}_1$ and $\mathbf{B}_2$ plus modifiers and shows grade "3" resistance; 514 contains no major resistance factors but numerous minor ones and is graded as "10" (grade "0" represents immunity and "12" full susceptibility). The first backcross to 514 gives a bimodal curve with peaks at grades "4" and "9" and displaying an approximate 1 : 1 ratio instead of the 3 : 1 ratio expected. In F_2 and in the F_2 of this first backcross, bimodal curves are again obtained, but these bear some resemblance to the 12 : 3 : 1 ratio expected. The reasons for these anomalies are discussed.

It is shown that 513, a selection from a Punjab American Upland importation with grade "5"–"6" resistance, contains factor $\mathbf{B}_2$ together with several very weak resistance factors.

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