THE GENETICS OF BLACKARM RESISTANCE

V. DWARF-BUNCHED AND ITS RELATIONSHIP TO B_1

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(With Plate 5)

CONTENTS

Introduction

In the course of breeding work designed to produce blackarm-resistant American Upland types, crosses were made between Nye's Uganda B31 and 514. A number of bunched-up dwarfed plants appeared in the F_2 of this cross and, as dwarfing appeared to be associated with blackarm resistance, a knowledge of its genetics became desirable from the plant-breeding standpoint. In the present paper it is shown that one of the factors responsible for Dwarf-bunched is either identical with the blackarm-resistance gene B_1, or else is so closely linked with it that the two may be treated as one for practical plant-breeding purposes It is for this reason that the present paper has been included in the series on the genetics of blackarm resistance.

Previous work

The resistance to blackarm of Uganda B31 was shown by Knight & Clouston (1939) to be due to two dominant cumulative factors, B_1 and B_2, together with a modifier complex. By repeated backcrossing to Sakel these factors were separated from their modifier complex, and it was demonstrated that B_1 confers weak resistance (grade '10·1'), whereas B_2 is a strong factor giving grade '7' resistance ('0' represents immunity and '12' full susceptibility).

Knight & Clouston (1941) described the nature of blackarm-resistance inheritance in the cross Uganda B31 × 514, and they inferred that 514 contains no modifiers for $\mathbf{B}_1$ though it possesses $\mathbf{B}_2$ modifiers. 514 contains no major blackarm-resistance factors and shows the grade '10' symptoms typical of 'fully susceptible' American types.

In the same paper it was stated that '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..."'. Subsequent results, obtained during the present investigation into the genetics of Dwarf-bunched, have shown that the partially resistant and susceptible classes usually overlap, so that $\mathbf{B}_1\mathbf{b}_1$ and $\mathbf{b}_1\mathbf{b}_1$ are not distinguishable with certainty on the genotypic background of the F_1.

Description of strains

514 is a vigorous American Upland (*G. hirsutum* L.) type which grows to an average height of over 4 ft. at Shambat.* It was derived, by selection, from the Sudan 'Pump Scheme Strain' which itself originated as an importation of Nyasaland Upland.†

XA129, like 514, was obtained by selection from Pump Scheme Strain.

Uganda B31 is an American Upland type which was imported from Uganda. B31, at Shambat, shows somewhat stunted growth and does not usually average more than 2–2½ ft. in height.

Uganda SP84 is a bulk introduction from Uganda.

511D was bred in the Sudan by selection from Uganda SG85.

Deltapine is a bulk introduction from the Delta and Pineland Co., U.S.A.

513 was bred from an introduction of Punjab Early Strain, an American Upland type from India.

Sakel (*G. barbadense* L.) is a commercial type introduced from Egypt. Three types were used, viz. NT2, a tall 'leggy' variety, X1730, a shorter more 'bushy' type, and Domains Sakel proper. All three types though very distinct commercially are of Sakel origin, and for the purposes of this paper have been indiscriminately called Sakel.

Description of Dwarf-bunched

Pl. 5, fig. 1*a*, shows typical Dwarf-bunched plants and Pl. 5, fig. 1*b*, illustrates the appearance of such plants after removing all leaves. The leaves are only slightly reduced in size, whilst flowers and bolls are more or less normal. The stems and branches show excessively short inter-nodes so that the plants have a rounded, bunched-up appearance. Dwarfs grow to a height of about 8 or 10 in., whereas the normal height for 514 at Shambat is over 4 ft.

The genetics of Dwarf-bunched

Crosses between 514 *and Uganda* B31

F_1 *of* 514 × *Uganda* B31

The F_1 showed normal growth, the plants averaging about the same height as 514.

F_2 *of* 514 × *Uganda* B31

In the F_2 of 514 × B31 a number of dwarfed plants appeared. These were difficult to classify with certainty, as the F_2, in general, showed considerable variation in height and the dwarfs themselves also varied. The number of normal plants as compared with dwarfs

* Shambat is in the immediate vicinity of Khartoum, in the Northern Sudan.

† The origin of Nyasaland Upland and also of Uganda varieties is given in greater detail by Nye & Hosking in Tothill (1940).

approximated to a 13 : 3 ratio (Table 1), suggesting that normality is dependent on the presence of either of two duplicate factors, one giving an intermediate heterozygote and the other dominant.

If it be assumed that the Dwarf-bunched phenotype comprises the double recessive $\mathbf{d_a d_a d_b d_b}$ genotype with the addition of the heterozygous class $\mathbf{d_a d_a D_b d_b}$, then the F_2 of 514 and B 31 (Table 1) would give the following ratio:

$1\mathbf{d_a d_a d_b d_b}$ $2\mathbf{d_a d_a D_b d_b}$	3 Dwarf-bunched plants
$1\mathbf{D_a D_a d_b d_b}$ $2\mathbf{D_a d_a d_b d_b}$ $4\mathbf{D_a d_a D_b d_b}$ $2\mathbf{D_a D_a D_b d_b}$ $1\mathbf{d_a d_a D_b D_b}$ $2\mathbf{D_a d_a D_b D_b}$ $1\mathbf{D_a D_a D_b D_b}$	13 Normal plants

The rather poor agreement between the ratio obtained and the 13 : 3 ratio expected on this basis may be ascribed to the variability of the $\mathbf{d_a d_a D_b d_b}$ plants of the F_2.

Table 1. *F_2 of 514 × Uganda B 31*

Family no.	Actual		Expected (13 : 3)		χ^2
	Normal	Dwarf	Normal	Dwarf	
XHA 1434	626	151	631·3	145·7	0·24
XHA 1634	401	96	403·8	93·2	0·10
XHA 1734	73	15	71·5	16·5	0·17
XHA 1834	306	69	304·7	70·3	0·03
XHA 1934	181	57	193·4	44·6	4·22
XHA 2034	72	25	78·8	18·2	3·14
XHA 2134	142	34	143·0	33·0	0·04
XHA 2234	166	58	182·0	42·0	7·50
Totals	1967	505	2008·5	463·5	15·44

$P = 0{\cdot}05$ (approx.).

In three subsequent sowings of this F_2 it was found to be impossible to grade the plants into Normals and Dwarfs with any accuracy owing to the very wide variation of the intermediate group. The most one could say was that in each of these F_2's about a quarter of the population was of intermediate or dwarf type and the remainder normal.

Dwarf-bunched × 514

A pure-breeding Dwarf-bunched family originally obtained from the F_2 of the backcross 514 × (B 31 × 514) was crossed with 514. The F_1 of this cross showed normal growth and the F_2 could be classified, with no possibility of confusion, into two clear-cut groups, viz. Normal growth and Dwarf-bunched (Table 2).

Table 2. *Classification of F_2 of Dwarf-bunched* × 514

Family no.	Actual		Expected (3 : 1)		χ^2
	Normal	Dwarf	Normal	Dwarf	
BA 431/40	353	100	339¾	113¼	2·07
BA 432/40	324	105	321¾	107¼	0·06
BA 433/40	189	59	186	62	0·19
Totals	866	264	847½	282½	2·32

P lies between 0·5 and 0·6.

Self-bred seed of these Dwarf-bunched plants yielded dwarfs only, showing that these plants were all homozygous for the character, i.e. $\mathbf{d_a d_a d_b d_b}$.

The 3 : 1 ratio of Normals to Dwarfs obtained in the F_2 of Dwarf-bunched × 514 shows that Dwarf-bunched differs from 514 in a single recessive factor, $\mathbf{d_a}$. Thus B31 would be of $\mathbf{d_a d_a D_b D_b}$ genotype and 514 would be $\mathbf{D_a D_a d_b d_b}$. A Dwarf-bunched plant ($\mathbf{d_a d_a d_b d_b}$) crossed with 514 would give $\mathbf{D_a d_a d_b d_b}$ which would show normal growth. In F_2 the ratio 1 $\mathbf{d_a d_a d_b d_b}$: 2 $\mathbf{D_a d_a d_b d_b}$ + 1 $\mathbf{D_a D_a d_b d_b}$ would be obtained, i.e. one Dwarf-bunched to three Normals.

Dwarf-bunched × Uganda B31

The F_1 of Dwarf-bunched × B31 was mainly of intermediate habit but ranged from plants almost indistinguishable from the Dwarf-bunched parent to plants approaching the height of Uganda B31. It is evident, therefore, that this heterozygote, which, on a two-factor hypothesis, must be $\mathbf{d_a d_a D_b d_b}$, lacks dominance.

In F_2, although the presence of dwarfs was obvious, it was impossible to count them and to classify the families into Dwarf-bunched, Intermediate and Normal. This difficulty was not due solely to the variability of the Intermediate group, since, apart from variation, which was considerable, the families were grown late on very poor soil with the result that B31, never a robust type at Shambat, was itself very stunted.

The cross Uganda B31 × 513

Uganda B31 crossed with 513 gave a normal F_1 and no dwarf types in F_2.

The cross Uganda B31 × Gambia Native (G. hirsutum *var.* punctatum)

Uganda B31 crossed with Gambia Native gave a normal F_1, but Dwarf-bunched plants appeared in F_2.—Again no clear-cut ratio was observed owing to the variability of the intermediate group, and the most one could say was that in a total F_2 progeny of 406 plants, not less than 19 true dwarfs were present. A repeat of this, next season, gave an F_2 progeny consisting of 13 true dwarfs to 103 plants ranging from normal to nearly dwarf. Adding these two seasons' results together gives 490 normal to 32 true dwarfs, in excellent agreement with the ratio of 489·4 : 32·6 expected on a 15 : 1 basis.

Crosses between $\mathbf{B_1 B_1}$ *Sakel and* 514

Crosses were made between Sakel containing $\mathbf{B_1}$ and 514. This blackarm-resistant Sakel was obtained from the fifth Sakel backcross of Uganda B31 × Sakel.

The F_1 of $\mathbf{B_1 B_1}$ Sakel × 514 showed normal growth, but in F_2 a number of typical Dwarf-bunched plants appeared. The F_2 could not be classified into definite groups because of the great variation in height commonly found in such *barbadense* × *hirsutum* F_2's, and, although typical Dwarf-bunched plants were present, there was a more or less complete gradation from dwarfs to the shorter 'normals'. As a check, however, crosses had been made between $\mathbf{b_1 b_1}$ Sakel (also of fifth backcross origin) and 514 and, though these also showed great variation in height in F_2, no Dwarf-bunched plants were present.

In the following seasons this experiment was repeated, using first $\mathbf{B_1 B_1}$ Sakel derived from the seventh Sakel backcross of Uganda B31 × Sakel and, later, ninth, eleventh and twelfth backcross material. In the F_2's of all these $\mathbf{B_1 B_1}$ Sakel × 514 hybrids, a number of Dwarf-bunched plants again appeared.

Since, even after thirteen crosses of $\mathbf{d_a B_1}$ with Sakel $\mathbf{D_a b_1}$, the two genes $\mathbf{d_a}$ and $\mathbf{B_1}$ had not been separated, it is evident that they must be closely linked. Indeed, it might well

be argued that they are identical, and that the action of $\mathbf{d}_a$ in producing Dwarf-bunched in conjunction with $\mathbf{d}_b$ is merely a pleiotropic effect of $\mathbf{B}_1$.

Crosses between $\mathbf{B}_1\mathbf{B}_1$ *Sakel and various cotton varieties*

In the following crosses the male parent was, in each case, BAR 2/8. This variety is a Sakel type homozygous for $\mathbf{B}_1$. It was obtained by selfing out $\mathbf{B}_1\mathbf{B}_1$ plants from seventh Sakel backcross material of Uganda B 31 × Sakel origin.

BAR 2/8 was crossed with a number of American Upland strains with the following results:

G. hirsutum parent	F_1	F_2
Uganda SP 84	Normal	One progeny contained Dwarf-bunched plants, a second contained none
511 D	,,	No Dwarf-bunched
XA 129	,,	Contained Dwarf-bunched
514	,,	Contained Dwarf-bunched
Deltapine	,,	One progeny contained Dwarf-bunched, a second contained none

From these crosses, and those reported earlier, it is clear that the gene $\mathbf{d}_b$ is present in Gambia Native (*G. hirsutum* var. *punctatum*), 514, Uganda SP 84, XA 129 and Deltapine, but that it is not present in all *hirsutum* cottons. It is absent, also, from the three Sakel (*barbadense*) varieties: Domains Sakel, NT 2 and X 1730, since transferences of $\mathbf{B}_1$ to these varieties have been made with complete success and have produced no sign of dwarfing.

Transference of Dwarf-bunched from G. hirsutum *to* G. barbadense

When the close connexion between the character Dwarf-bunched and the blackarm-resistance gene $\mathbf{B}_1$ was realized it seemed probable that the knowledge could be utilized in checking the genotype of Sakel strains to which $\mathbf{B}_1$ had been transferred. Clearly this check would be superfluous in a Sakel containing $\mathbf{B}_1$ alone, since spraying with blackarm disease would at once disclose the presence of this factor. Where, however, $\mathbf{B}_1$ was combined with $\mathbf{B}_2$ in a single strain, the grade of resistance, alone, proved to be no certain test of the presence of $\mathbf{B}_1$ since this gene does not greatly add to the resistance of $\mathbf{B}_2$ and there is a considerable overlap between the $\mathbf{B}_1\mathbf{B}_2$ and $\mathbf{b}_1\mathbf{B}_2$ phenotypes in a Sakel background.

As a test for the presence of $\mathbf{B}_1$ in a variety, crosses could be made with Dwarf-bunched. Plants homozygous for $\mathbf{B}_1$ would then yield F_1 seed from which intermediate Dwarf-bunched plants would grow.

It was felt that, for such check-crossing, the clearest results would be obtained if the character Dwarf-bunched were first transferred to a Sakel background.

Accordingly, a start was made using homozygous dwarfs selfed out from an F_2 progeny of 514 × $\mathbf{B}_1\mathbf{B}_1$ Sakel. One of these dwarfs was backcrossed to $\mathbf{B}_1\mathbf{B}_1$ Sakel yielding a progeny of semi-dwarfs which showed considerable variation.

In such a transference, clear segregation would not be expected, since the $\mathbf{D}_b$ heterozygote has been shown to be intermediate and to overlap the normal and the homozygous dwarf classes. In fact, although in each backcross generation it was possible to choose, with confidence, semi-dwarfs as parents for the next generation, it was never possible to be certain of the upper limit of the semi-dwarf class. Approximate classifications were made and gave the distributions shown in Table 3. There was a similar uncertainty in the classification of progenies obtained on selfing intermediate plants in the second, third and fourth backcrosses. Samples of the data obtained are given in Tables 4 and 5.

One noticeable thing in these various backcrosses to $\mathbf{B_1B_1}$ Sakel strains was that the intermediate Dwarf-bunched ($\mathbf{d_a d_a D_b d_b}$) lost much of its similarity to Dwarf-bunched and became more 'normal' in appearance, though still ranging in odd plants almost down to

Table 3. *Summary of results obtained by backcrossing* 514 *to* $\mathbf{B_1B_1}$ *Sakel*

	Normal	Intermediate
2nd backcross	47	48
3rd backcross	20	18
4th backcross	10	8
Totals	77	74

the full Dwarf-bunched. The main difference in the later 'Sakel' backcrosses between intermediates and normals was that intermediate plants were much more monopodial and 'bushy' than the normals.

Eight intermediate plants selfed in the second 'Sakel' backcross gave the distributions shown in Table 4.

Table 4. F_2 *of* 514 *backcrossed twice to* $\mathbf{B_1B_1}$ *Sakel*

Family no.	Dwarf + Intermediate	Normal	Expected 3 : 1	Totals	χ^2
BA271/43	207	60	200¼ : 66¾	267	0·91
BA272/43	93	26	89¼ : 29¾	119	0·63
BA274/43	33	18	38¼ : 12¾	51	2·88
BA275/43	62	37	74¼ : 24¾	99	8·08
BA276/43	196	97	219¾ : 73¼	293	10·27
BA278/43	44	27	53¼ : 17¾	71	6·43
BA280/43	157	70	170¼ : 56¾	227	4·13
Totals	792	335	845¼ : 281¾	1127	33·33

P is less than 0·001.

In the F_2 of the fourth backcross to $\mathbf{B_1B_1}$ Sakel the progenies were classified into three groups 'Normal', 'Doubtful' and 'Dwarf plus Intermediate' (Table 5).

Table 5. F_2 *of* 514 *backcrossed four times to* $\mathbf{B_1B_1}$ *Sakel*

Family no.	Dwarf + Intermediate	Doubtful	Normal
BA641/45	225	40	44
BA642/45	86	8	52
BA643/45	91	13	80
BA644/45	106	6	38
BA645/45	159	8	119
BA646/45	166	12	62
Totals	833	87	395
Expected (3 : 1)	936·25	—	328·75

That the uncertainty of the classification is due to the variability of a single heterozygous class ($\mathbf{d_a d_a D_b d_b}$) is shown by the results of the detailed examination of family BA646/45. The data in Table 5 were taken early in the season: this family was later re-examined by two observers, and the distinction between the classes was found to have improved with age. It was found that the family could be grouped with some certainty into 60 Dwarfs, 106 Intermediates, 12 Doubtfuls and 62 Normals. Adding the Doubtfuls to the Intermediates gives 60 : 118 : 62—a close approximation to expectation on a 1 : 2 : 1 basis.

The relationship between $\mathbf{d_a}$ *and the blackarm-resistance gene* $\mathbf{B_1}$

A Dwarf-bunched plant in the F_2 of a second Sakel backcross was crossed with $\mathbf{b_1b_1}$ Sakel. All the F_1 plants showed normal growth; progenies of nine of these plants gave the distributions shown in Table 6.

Table 6. *F_2 of third Sakel backcross*

Family no.	Normal		Doubtful		Dwarf + Intermediate	
	Resistant	Susceptible	Resistant	Susceptible	Resistant	Susceptible
BA647/45	86	28	13	2	27	—
BA648/45	115	59	20	1	22	—
BA649/45	90	41	12	2	26	—
BA650/45	131	46	9	—	30	—
BA651/45	89	56	10	—	24	—
BA653/45	119	45	7	2	36	—
BA654/45	130	56	18	1	38	—
BA655/45	156	91	14	1	61	—
BA656/45	85	62	13	1	28	—
Totals	1001	484	116	10	292	—

The close linkage of $\mathbf{B_1}$ and $\mathbf{d_a}$ is amply demonstrated in this material. Among 292 plants classified as Dwarf or Intermediate there was not a single susceptible plant.

DISCUSSION

From the standpoint of the applied geneticist, the importance of the character Dwarf-bunched lies in the close linkage which obtains between the blackarm-resistance gene $\mathbf{B_1}$ and the factor $\mathbf{d_a}$. In the first place it would obviously be of value to free $\mathbf{B_1}$ from its deleterious component $\mathbf{d_a}$ in order to render this resistance gene 'safe' for use in all crosses. There appears to be little hope of doing this, since linkage of $\mathbf{d_a}$ and $\mathbf{B_1}$ has been shown to be close. Indeed, during the course of a large programme of crossing Dwarf-bunched with blackarm-susceptible types no susceptible Dwarf-bunched or susceptible Intermediate plant ever appeared.

To the pure geneticist the main point of interest about Dwarf-bunched is that the duplicate genes $\mathbf{D_a}$ and $\mathbf{D_b}$ have different dominance reactions. On Fisher's (1930) theory, dominance is dependent on the genotypic background rather than on the gene itself. These duplicate factors do not conform to this theory in that, on the one genetic background, $\mathbf{D_a}$ is fully dominant whilst $\mathbf{D_b}$ lacks dominance. In the case of $\mathbf{D_a}$, therefore, dominance is a function of the gene itself.

SUMMARY

In the F_2 of a cross between two American Upland (*G. hirsutum*) types, Uganda B31 and the Sudan variety 514, a number of markedly dwarfed, 'bunched-up' plants appeared. Investigation showed that normality as opposed to 'Dwarf-bunched' depends on the presence of either of two duplicate genes, one dominant and the other giving an intermediate heterozygote. These genes have been called $\mathbf{D_a}$ and $\mathbf{D_b}$, the former deriving from 514 and the latter from Uganda B31. 514 is of $\mathbf{D_aD_ad_bd_b}$ genotype, Uganda B31 is $\mathbf{d_ad_aD_bD_b}$, Dwarf-bunched is $\mathbf{d_ad_ad_bd_b}$, and the heterozygote $\mathbf{d_ad_aD_bd_b}$ shows considerable variability with a range from dwarf to normal.

The gene $\mathbf{d_b}$ occurs in Gambia Native (*G. hirsutum* var. *punctatum*) and in the American Upland varieties Uganda SP84, XA129 and Deltapine, but it was not present in all Upland varieties examined.

The gene d_a is closely linked with (or possibly identical with) the blackarm-resistance gene B_1. Since *G. barbadense* types are of $D_aD_aD_bD_b$ composition, B_1 can be utilized in conferring blackarm resistance on this group. Its use within the *G. hirsutum* group is fraught with the danger of producing Dwarf-bunched types as the end-product.

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EXPLANATION OF PLATE 5

Fig. 1*a*

Two fully developed Dwarf-bunched plants.

Fig. 1*b*

Two fully developed Dwarf-bunched plants from which all leaves have been removed.

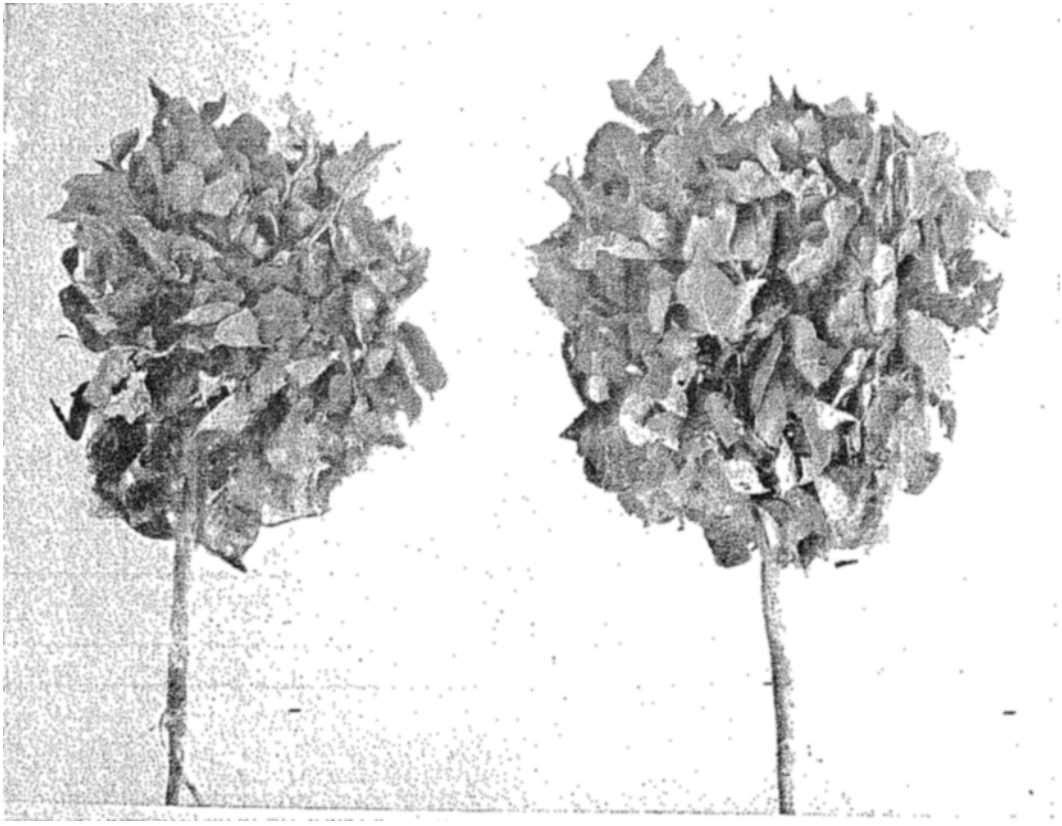

Fig. 1*a*.