DISRUPTIVE SELECTION IN CROP DEVELOPMENT

H. J DOGGETT and B. N. MAJISU
E.A.A.F.R.O., Serere, Soroti, Uganda

1. INTRODUCTION

THE cultivated and wild members of *Sorghum* section *Sorghum* sub-section *Arundinacea* (Snowden, 1936, 1955, 1961) occur together in Africa. Both groups have been divided into species and subspecies (Stapf in Prain, 1934; Snowden, *loc. cit.*), but there has been much difference of opinion on the correctness of such subdivision (Martin, 1937, 1958; Hutchinson *et al.*, 1938; Doggett, 1962, in Hutchinson, 1965; Grassl, 1962). Snowden (1936) would derive his cultivated species from certain of the wild ones. The main wild types which he suggested as progenitors of cultivated sorghums were *S. arundinaceum, S. verticilliflorum, S. aethiopicum* and *S. sudanense.*

All the African wild sorghums in the *Spontanea* series of the sub-section *Arundinacea* and all the cultivated forms are diploids ($2n = 20$). The natural occurrence of any of the series *Spontanea* outside Africa is unusual. An occasional collection has been made in India (Snowden, 1955).

S. halepense (sub-section *Halepensia*) in Africa occurs in the Mediterranean littoral. It is a tetraploid, with $2n = 40$ chromosomes, and it can sometimes cross naturally with the cultivated diploids, as it does in the U.S.A. (Hadley, 1958). The *Parasorghum* species *S. versicolor* and *S. purpureo-sericeum* ($2n = 10$) also occur in Africa. We have made repeated attempts to cross these with cultivated sorghums at both the diploid and tetraploid levels, with no success and with no indication that an embryo is ever formed. Garber (1950) reports failures of other attempts to make this cross. These species are not considered further here.

Doggett (in Hutchinson, 1965) suggested that cultivated sorghum had arisen from wild sorghum through the application of disruptive selection. Mather (1953, 1955) defined disruptive selection and deduced that its application should result in the development of polymorphism, with the production of reproductive isolation barriers within the population under the appropriate conditions. Thoday and his co-workers (Thoday, 1958, 1959, 1960, 1964; Thoday and Boam, 1959, 1961; Millicent and Thoday, 1961; Thoday and Gibson, 1962; Gibson and Thoday, 1962), working with *Drosophila*, demonstrated the correctness of Mather's deductions. They showed that: (*a*) Polymorphism could be obtained in a population under disruptive selection even with high gene flow between the diverging groups. (*b*) The divergent groups could be maintained distinct under high gene flow with negative assortative mating. (*c*) Reproductive isolation occurred between the divergent groups in spite of full opportunity for random mating.

Our results show that the behaviour of *Drosophila* in the laboratory of Thoday and his co-workers parallels the development of the sorghum crop in Africa during the past 5000 years, and it presents a model applicable to

A   1

the development of other crop plants also. We suggest that the cultivated sorghums were developed from a wild sorghum which was itself the progenitor of the wild diploid *Arundinacea* of Africa today: that the creative agency was disruptive selection arising because man was selecting in one direction and nature in another: that the populations of the cultivated and wild sorghums were maintained as distinct and continued to diverge under disruptive selection: and that some of the diversity developed by man in the cultivated crop was fed back into the wild sorghum through introgression, resulting in the diversity of the present day *Arundinacea* group.
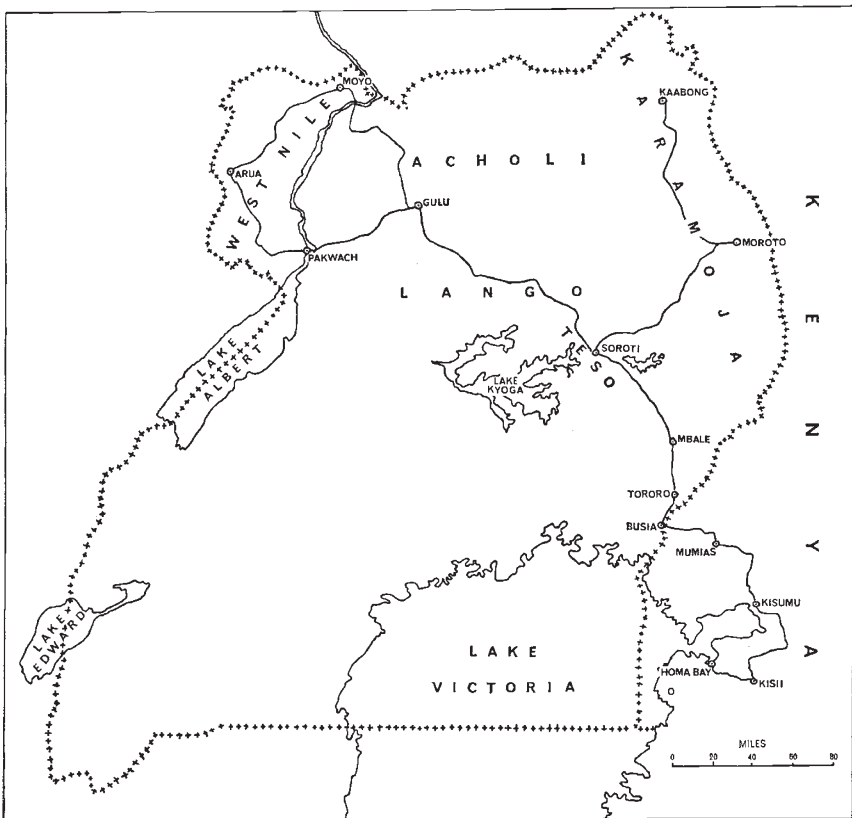
Map showing Routes along which Sorghums were collected.

———o———o——— (route)

2. MATERIALS

Sorghums. Three collections of sorghums were made: (A) In the Eastern and Northern regions of Uganda, on a route Soroti—Gulu—Moyo—Arua—Pakwach in 1958. (B) On a route Soroti—Moroto—Kaabong in 1960. (C) In Eastern Uganda and Western Kenya on a route Soroti—Mbale—Tororo—Busia—Mumias—Homa Bay—Kisii—Kisumu in 1960. (See map.) Cultivated sorghums were collected from farmers' fields and, as far as possible, wild specimens were collected within a quarter of a mile of a cultivated collection. Suspected natural wild ✕ cultivated hybrids were

labelled as such. Natural crosses between wild and cultivated sorghums may be seen occasionally in farmers' fields. Usually they are uprooted as soon as recognised, but some persist and are very evident after harvest. Vegetatively they resemble the cultivated crop, but when mature they are readily distinguished by their appearance, and by their dehiscent sessile spikelets with large jet-black glumes tightly clasping the rather small grains. We have produced plants of this type on Serere by deliberately crossing cultivated and wild sorghums and have confirmed that this is the mode of origin of these plants. In this paper, a cultivated sorghum is one grown for its grain. No fodder sorghums or sorgos are grown as such by African farmers.

The entries collected on these trips were numbered as follows:

	Entry No.	Place of collection
Wild sorghums		
S. verticilliflorum	1-8	Eastern and Northern Uganda, route A.
	9	Kenya, collected by A. V. Bogdan.
	52, 53, 57	Serere Research Station.
	58-60, 62	Karamoja border, near Mt. Nepak, route B.
	87-89	Karamoja, route B.
	105-109	E. Uganda and W. Kenya, on route C.
S. macrochaeta	10, 139, 140	Kenya, collected by A. V. Bogdan.
	12	Dry stream bed between Nairobi and Arusha.
	63	Seed from a herbarium sheet, Nairobi.
	12	Dry stream bed between Nairobi and Arusha.
	63	Seed from a herbarium sheet, Nairobi.
S. brevicarinatum	51, 74	Kenya, collected by A. V. Bogdan.
S. arundinaceum	50	Kenya, collected by A. V. Bogdan.
S. virgatum	141, 142, 145	From U.S.A., collected originally in N. Africa.
S. aethiopicum	143	From U.S.A., collected originally in Ethiopia.
S. sudanense	144	From U.S.A., collected originally in Sudan.
Cultivated sorghums		
	13-49, 64-67	E. and N. Uganda, on route A.
	68-73	Kigezi district, W. Uganda.
	90-104	Karamoja district, on route B.
	121-138	E. Uganda and W. Kenya, on route C.
Natural wild × cultivated hybrids		
	11	Near Mwanza, Tanzania, on abandoned sorghum land. Locally termed a " pungu ".

Entry No.	*Place of collection*

Natural wild × cultivated hybrids—continued

54	West Nile, Uganda, frequent on land abandoned after sorghum cultivation.
55, 56	Serere Farm, on resting land.
61	Karamoja border, near Mt. Nepak, route B.
110-120	E. Uganda and W. Kenya, on route C.

Artificial wild × cultivated hybrids

76-86	Made at Serere, as described in text.

Artificial wild × wild hybrid

146	*S. aethiopicum × S. sudanense*, produced in U.S.A.

Entry No. 75 was a deliberate wild × cultivated hybrid which was omitted as only one plant was obtained.

3. METHODS

Seed from the collected heads was grown out in progeny rows, each containing some 20-50 plants, and observations were made on a random selection of 10 plants in each row. The plant characters used in each study are indicated in the text. The row means for each character were used in calculating the hybrid index. Measurements were taken where possible, otherwise a 0, 1, 2 scoring system was used, 0 always indicating the wild type. In order to give some value to the degree of importance of a character, weightings were used, devised by Court (1963). On this system, the correlation coefficients between all characters were calculated. Any characters showing very low correlations with most other characters were omitted, as being irrelevant to the discrimination between species or groups. If any two characters showed a very high correlation, one of them was omitted, as both were likely to be governed by the same genes. From the correlation matrix the sums of the r^2 values for each variable were found, to remove problems of sign, and proportionately reduced by making $\Sigma(\Sigma r^2) = 1$. The square roots of these reduced r^2 values were then taken, the resultant values being Vj, with sign obtained by inspection of the original r values. Vj was then adjusted for scale by dividing by the sample standard deviation, giving the weighting factor Wj.

To calculate the hybrid indices, the lowest value was deducted from each set of character measurements to give a common origin, and when necessary the data for a particular character were inverted so that low values were always associated with the wild type, and high values with the cultivated type. The data were then multiplied by the appropriate value of Wj, and the result summed to give the hybrid index.

The hybrid indices so obtained showed a correlation of $r = +0.985$ with Hatheway's (1962) indices when the method was applied to his data, with the advantage that for Court's system ordinary desk calculators could be used.

4. RESULTS

Collection (A) 1959 study

The entries for this study consisted of the wild and cultivated sorghums from E. and N. Uganda, Nos. 1-8 and Nos. 13-49. Three wild collections from Kenya were also included, Nos. 9, 10 and 12, together with the natural wild ×cultivated cross No. 11, the " pungu " from Tanzania. Observations were made on 6 characters, but correlation between leaf width and stem thickness was high, and that between grain length and glume breadth was unexpectedly high ($r = 0.917$). There remained therefore only 4 characters for the hybrid index, namely: leaf width at the widest point, leaf length, glume length and grain length.

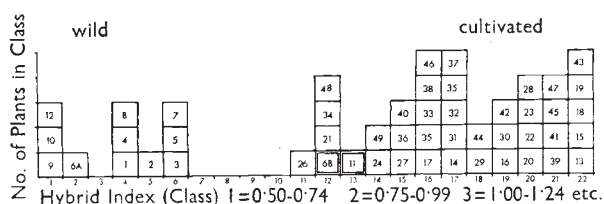The hybrid indices are shown on a block diagram in fig. 1.

FIG. 1.—Hybrid indices based on four plant characters for sorghums collected mainly along route A. Hybrids shown by double lines.

There is a clear break in the distribution, and there are evidently two populations. The three wild collections from Kenya (9, 10, 12) occupy the extreme wild end of the scale. The *S. verticilliflorum* group (1-8) occupies a place a little nearer to the cultivated end. The known hybrid (11) is central, but is together with some cultivated sorghums. With only 4 characters contributing few conclusions can be drawn.

Entry No. 6 was of particular interest. Thirty-two of the 41 plants grown were typical wild type, and the data from these are shown as 6A in fig. 1. Nine were much taller, with broad leaves and the appearance of typical F_1 plants of a wild ×cultivated cross (6B in fig. 1). It will be seen that these latter occupy an intermediate position in the figure, close to No. 11. The original plant No. 6 differed but little from the other wild sorghums collected except in the absence of an awn, although a few spikelets had short mucros (table 1).

TABLE 1

Spikelet data for entry No. 6 and the other wild sorghums of group 1-8, fig. 1 (mm.)

	Mean of wild sorghums	Range	Entry No. 6
Sessile spikelet length	5·7	5·0-6·0	4·8
Sessile spikelet breadth	2·3	2·0-2·5	2·4
Pedicelled spikelet length	5·6	5·0-6·5	4·8
Pedicelled spikelet breadth	1·1	0·8-1·2	0·9
Pedicel length	2·8	1·8-3·5	2·2
Grain length	2·8	2·2-3·3	3·0
Grain breadth	1·8	1·2-2·0	2·0

A 2

The wild-type plants produced in the progeny row of No. 6A occupied a position near the wild end of the scale in fig. 1, but all were awnless. The occurrence of 18 per cent. of F_1 hybrid plants in the progeny of this one wild plant out of only 8 collected indicates that wild and cultivated sorghums can cross naturally rather easily. The segregation data from these F_1 plants confirming their constitution is considered in a later section.

1960 Study

The material from collection (A) was augmented by wild sorghum entries 50 and 51 from Kenya, 52, 53 and 57 from Serere, with 58, 59 and 62 from the Karamoja border. The wild × cultivated cross from Arua (West Nile) No. 54 was included, together with two crosses from Serere (55 and 56) and one from the Karamoja border (61). The cultivated sorghums from Western Uganda, Nos. 68-73, were also planted in this study. These latter come from a high altitude area some 400 miles away from the cultivated group of collection (A).

Fifteen characters were chosen of those measured or scored. Stem thickness was again omitted, being too highly correlated with leaf width ($r = 0.896$). The length of pedicel on the pedicelled spikelet, and the glume length of the sessile spikelet were both highly correlated with the length of the pedicelled spikelet ($r = 0.900$, and $r = 0.896$ respectively). Glume breadth showed insignificant correlations with a lot of characters, but was related to grain length ($r = 0.743$). The final hybrid indices were calculated from the following characters:

Vegetative	*Panicle*	*Spikelet*
Waxy bloom on leaf sheath	Rhachis length	Awn length
Leaf width at widest point	Branch length	Pedicelled spikelet length
Leaf length	Node number	Hairiness of glume
Waviness of leaf margin		Grain length

The vegetative characters were observed on the fourth leaf below the panicle. The hybrid index diagram is shown in fig. 2.
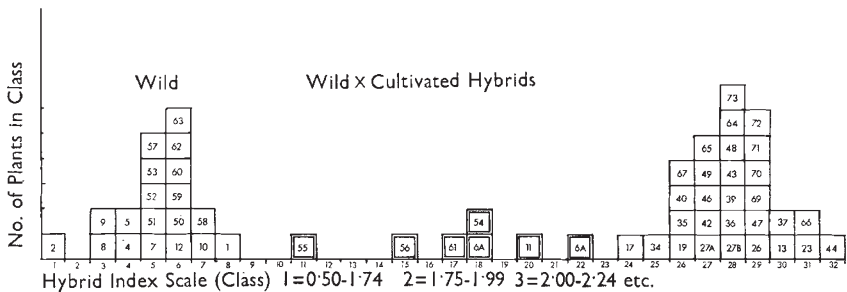

FIG. 2.—Hybrid indices of wild sorghums, cultivated sorghums, and their hybrids, based on 11 plant characters measured or scored.

In the diagram (fig. 2) the wild and the cultivated sorghums occupy very different positions on the scale. Although the wild sorghums were collected over a wide area and under a variety of names, they appear to belong to one population as far as the criteria used here are concerned. Equally, the

cultivated types form one population, into which the Kigezi sorghums apparently fit. The hybrids occupy an intermediate position. Number 6A is now intermediate, but judging from the individual plant records, it seems that a mixture of the crossed and uncrossed plants was harvested in the previous season. The F_2 generation of the natural hybrid plants, 6B has moved towards the cultivated end of the scale. Entries 11 and 54 are close together in fig. 2 though the sites where they were collected, Mwanza and Arua, are some 500 miles apart. Nos. 55 and 56, the two wild crosses from Serere, are perhaps further apart than might be expected, while 61, the cross from near Nepak, is centrally placed on the scale.

1961 Study

Nine characters were used in calculating the hybrid index, waviness of leaf margin did not score well in this season, and leaf length, panicle rhachis length, and panicle node number were omitted. Peduncle length and tiller number were included, so the characters used were: waxy bloom on leaf sheath, leaf width at the widest point, peduncle length, panicle branch length, awn length, pedicelled spikelet length, glume hairiness, grain length, and tiller count at flowering. It seemed desirable to vary the characters used, to avoid any bias due to adhering to one particular set. In the group chosen for these observations, waxy bloom, pedicelled spikelet length, hairiness of glume, peduncle length and tiller number are unlikely to have been subjected to much direct selection by man during the development of the cultivated crop. By comparison with the indices of fig. 2 the omission of leaf length diminished the influence of leaf characters, and less emphasis was placed on panicle dimensions.

In fig. 3A is shown the material from collections (B) and (C). Nos 87-89 were wild types and Nos. 90-104 cultivated varieties, collected in Karamoja along route B. Nos. 105-109 were wild types, Nos. 110-120 were natural hybrids, and Nos. 121-138 were cultivated sorghums from E. Uganda and W. Kenya collected along route C. In this diagram, the hybrids have spread into the cultivated end of the scale, and four of the Karamoja cultivated varieties, 91, 93, 94 and 97, are much nearer the centre. Only one hybrid (120) is at the wild end of the scale.

In the diagram of fig. 3B, data from some of the earlier material has been added. All the entries are from East Africa, with the exception of the wild types Nos. 141, 142, 145 (*S. virgatum*), Nos. 143, 144 (*S. aethiopicum*) and No. 146, the hybrid of *S. aethiopicum* and *S. sudanense*. Individual plants had been harvested from some rows of the 1960 study, and were grown in this group as separate progeny rows, being distinguished by a letter following the number. Entries 76 to 86 are the F_1 generations of deliberate hybrids made at Serere, as follows:

76	5×68	80	19×4	84	37×4
77	5×37	81	19×5	85	68×2
78	4×68	82	37×5	86	68×5
79	2×37	83	37×4		

The normal hot-water emasculation technique (Doggett, 1958) was used to make these crosses, and a good seed-set was obtained after pollination regardless of whether wild or cultivated sorghum was used as the female

parent. All the entries in fig. 3B were as usual grown and recorded simultaneously. The wild and the cultivated groups of fig. 3B are clearly distinct, but show a considerable spread. Where several separate progeny rows from the same entry were grown, there is a spread over several classes, *e.g.* 5A-5H at the wild end, 68A-68C at the cultivated end, and such variation would
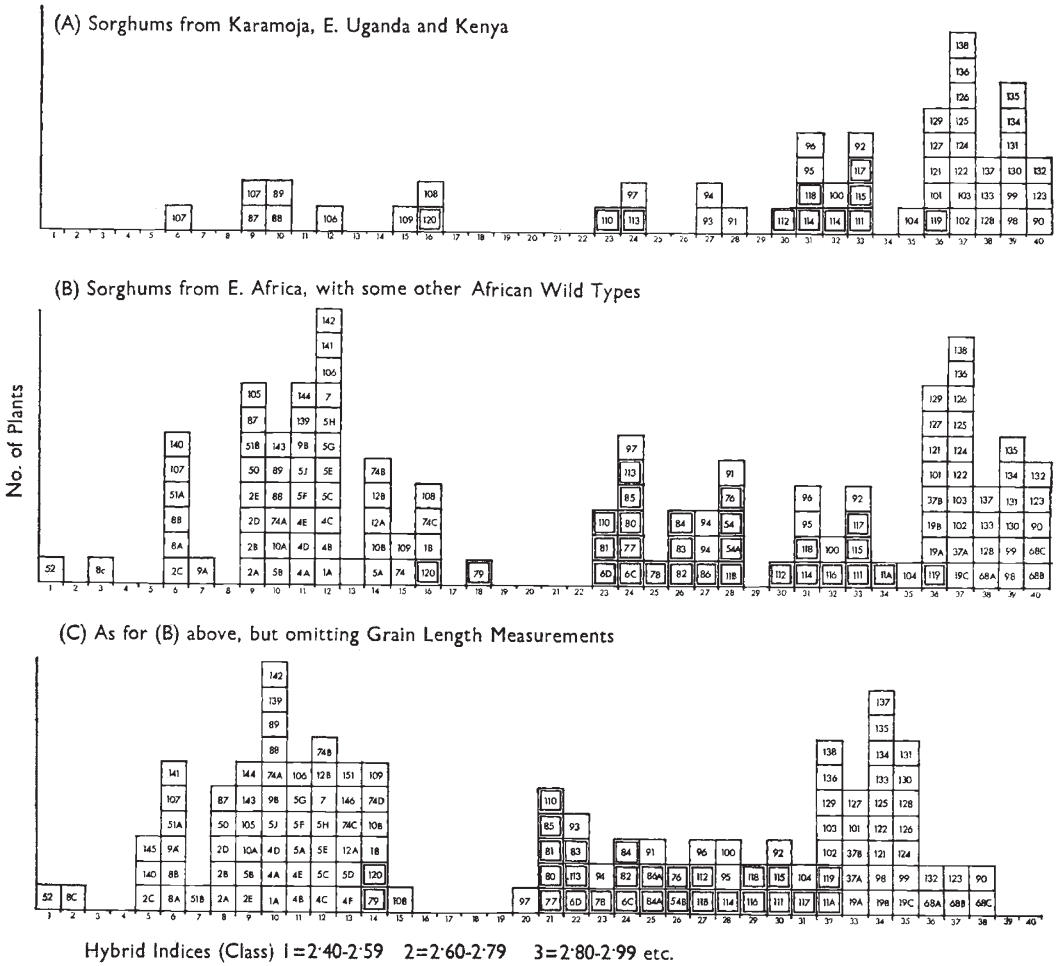
(A) Sorghums from Karamoja, E. Uganda and Kenya

(B) Sorghums from E. Africa, with some other African Wild Types

No. of Plants

(C) As for (B) above, but omitting Grain Length Measurements

Hybrid Indices (Class) 1 = 2·40-2·59   2 = 2·60-2·79   3 = 2·80-2·99 etc.

Fig. 3.—Hybrid indices for sorghum based on 9 plant characters. Hybrids are shown by double lines.

be expected. The deliberate crosses occupy quite a broad spectrum, not evidently related to the positions of the parents. Reciprocal crosses are fairly close together. The various wild sorghums all seem to fit into one population, in fact the two on the extreme end, Nos. 8C and 52, were both definite *S. verticilliflorum* collections, one from Nebbi in the West Nile district of Uganda, the other from near Serere.

Fig. 3C shows data from the same entries as in fig. 3B, but with the omission of grain length measurements. This character will have been subjected to strong direct human selection and could be suspected of having

Fig. 4.—Pictorial Scatter Diagram Relating African Wild And Cultivated Sorghums

an undue influence on the results. However, the two diagrams in fig. 3B and 3C are substantially the same, and evidently grain length is only one factor contributing to these results. The pattern is a clear one of hybrids lying between the wild and cultivated groups but overlapping with both. The presence of undoubted hybrids on the shoulders of both the wild and cultivated distribution curves does imply that introgression is occurring between them.

Fig. 4 shows a pictorial scatter diagram (Anderson, 1949) for the entries of fig. 3 which brings out rather clearly the occurrence of this introgression between the wild and the cultivated sorghums.

5. THE HYBRIDS

(a) *Segregation from the hybrids*

Deliberate crosses

Some of the deliberate hybrids (76 to 86 in fig. 3B above) were continued on to the F_2 generation. Unfortunately very few parent plants were grown, but in fig. 5 are shown the hybrid indices for parents and F_2 generations in
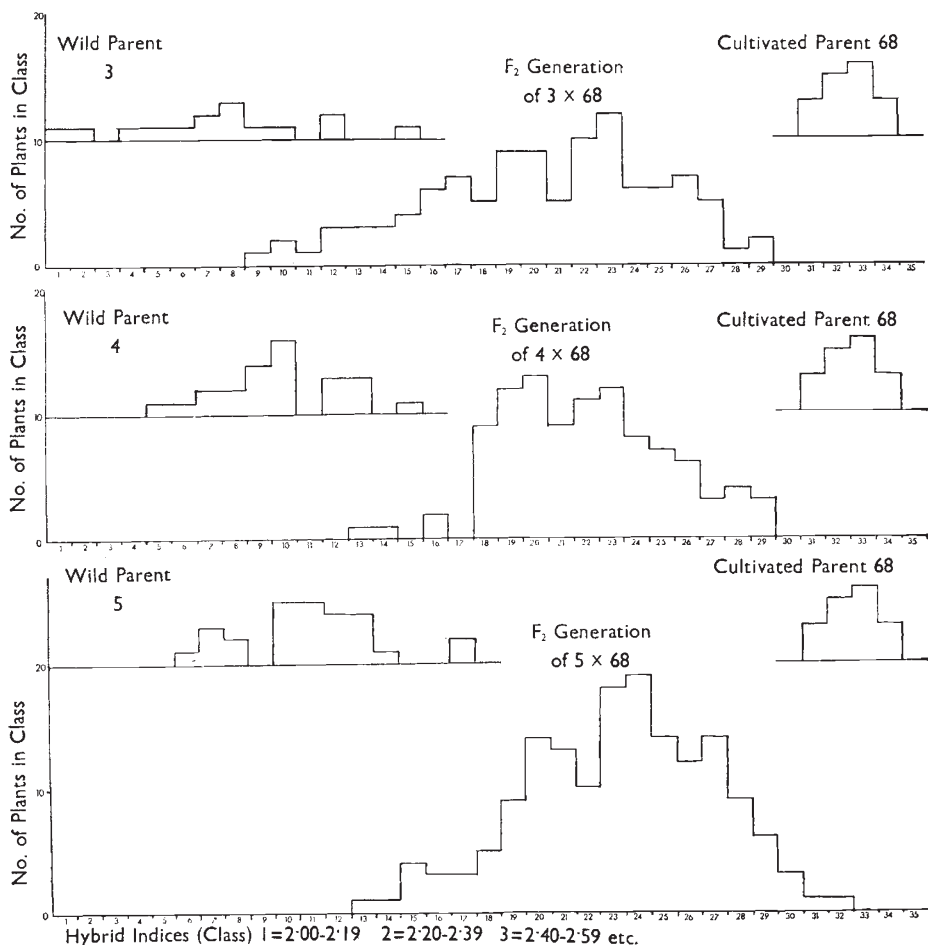

FIG. 5.—Inheritance in wild cultivated crosses, as estimated by hybrid indices based on 7 plant characters.
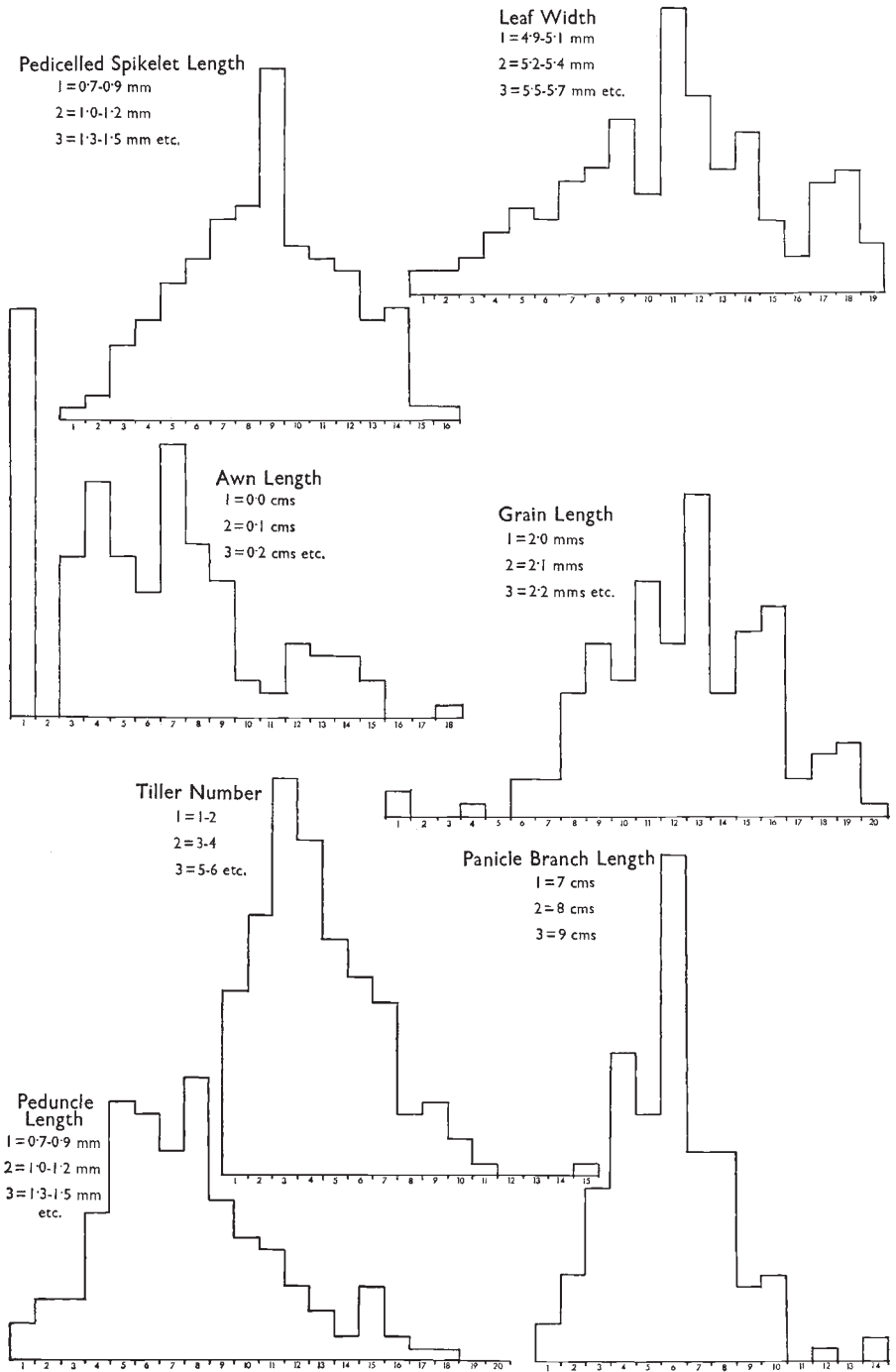
FIG. 6.—Inheritance of the 7 characters used in the hybrid indices for the cross of wild cultivated sorghum, entry 5 × entry 68.

three of the crosses, all having the same cultivated parent in common.   The
three F_2 generations lie midway between the parents, and the spread tends
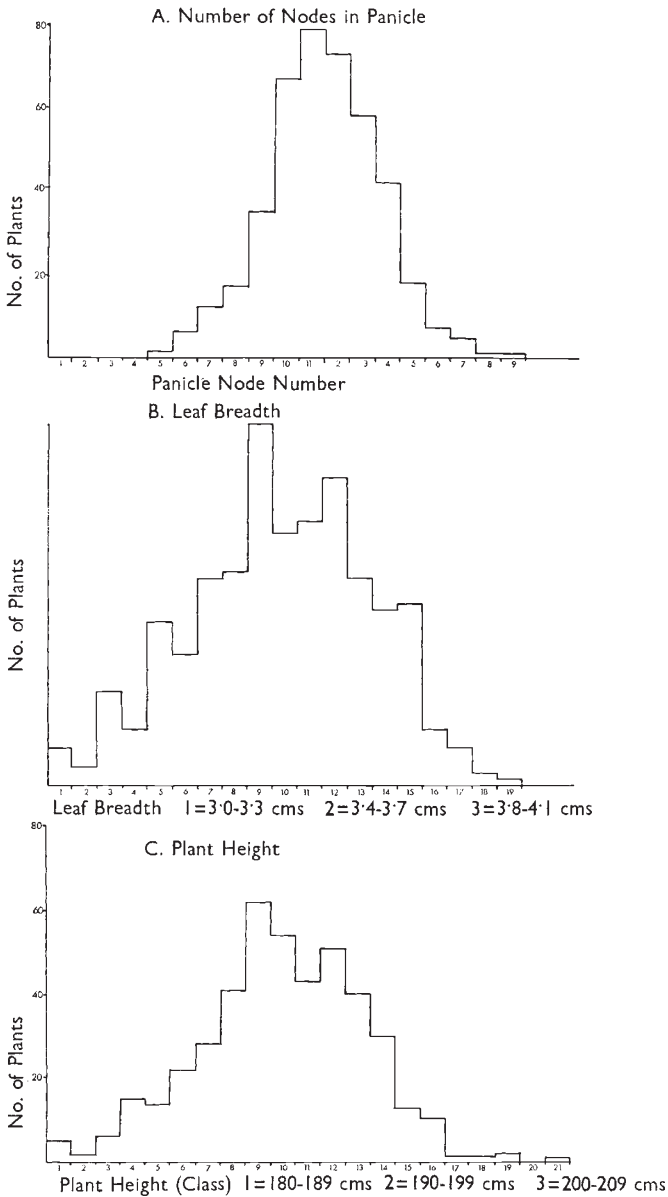to be related to the spread of the wild parent.   There is a suggestion of a

FIG. 7.—Distribution of 3 plant characters in a natural wild cultivated sorghum hybrid,
No. 6B.

dip in the centre of the F_2 diagrams, perhaps tending to form the wild and
cultivated type populations.   This cannot be shown to be real statistically
on the data presented, but the dip does occur in all three F_2 diagrams.

In fig. 6 are shown histograms for the F_2 segregations of the individual characters used in the hybrid index calculations, for the cross No. 76 and its reciprocal No. 86. Panicle branch length, pedicelled spikelet length, tiller number and peduncle length show polygenic inheritance. There is a suggestion in both grain length and leaf width of some segregation into distinct groups: and the segregation of awn length resembles that found by Jowett (1962) in crosses between cultivated sorghums, except that there is a clear break between the awned and awnless classes.

Natural cross

The 9 hybrid plants from entry No. 6 (fig. 1, above) derived from a natural wild × cultivated sorghum cross were bulked and grown as an F_2. The ratio of plants with shedding sessile spikelets to non-shedding was 320:105, almost exactly a 3:1 ratio. This character is controlled by a single gene (Ayyanger *et al.*, 1936; Karper and Quinby, 1947) so this population was clearly an F_2. Other characters in the bulk measured or scored gave no indications of simple gene differences. The segregation of height, leaf breadth and panicle node number are shown in fig. 7. The general resemblance between the patterns of fig. 7 and those of the deliberate hybrids in fig. 6 is good, and it seems certain that the hybrid plants obtained when collection 6 was first grown represented the F_1 generation of a wild × cultivated sorghum cross which had occurred naturally.

The 105 non-shedding plants obtained from the F_2 of entry No. 6 were grown out as F_3 rows, and 74 of these (70 per cent.) yielded one or more sterile plants, 23 rows showing at least 20 per cent. of sterile plants. There had been no indication of sterility in either the F_1 or the F_2 generations grown from No. 6, but its occurrence in the F_3 suggests that the wild × cultivated sorghum cross is a fairly wide one.

Local women were asked to select the cultivated heads from the F_3 progeny rows of the 105 non-shedding F_2 plants. They chose 149 heads, 57 of which were confidently given local names (see appendix) as varieties in cultivation. The remainder were considered suitable to grow as grain sorghums, though not at present in use. These 149 heads were then separated on Snowden's (1936) key, yielding the following of his species:

S. caudatum	111
S. caffrorum	7
S. guineense	24
S. roxburghii	2
Indeterminate	5
	——
	149
	——

It seems that acceptable grain sorghum types can segregate from the F_3 of a wild × cultivated sorghum cross, and that several of Snowden's species can be obtained from such an F_3.

(b) *The natural wild × cultivated hybrid population*

The entries in the intermediate hybrid zone of the hybrid index diagrams might well have consisted of F_2 or early generation hybrids, but observation indicated that there was also a proportion of uniform types which showed

little or no segregation when grown out as progeny rows. Entry Nos. 11 and 54 were conspicuous in this respect. The data from fig. 3 were examined to estimate differences between the variability within the wild, cultivated and hybrid groups. The comparison was made between 10 wild and 10 cultivated entries from the model classes of fig. 3B, the 11 artificial hybrids, and 9 collected hybrids. Of the 13 collected natural hybrids, Nos. 119 and 120 were omitted as back-crossed types, and Nos. 6, 11 and 54 because they had been grown on Serere for at least two generations previously. Figures were available from 10 plants of each entry, and in table 2 (A) is shown the range of the measurements for the main characters expressed as a percentage of the mean. In table 2 (B) is shown the range of the 10 plant means.

TABLE 2

Range of percentage variation in some entries of fig. 3, (a) estimated by expressing the range as a percentage of the mean, and (b) the range of the means. (Ten plants measured in each entry.)

Characters	No. of entries	Leaf breadth	Panicle length	Panicle branch length	Glume length	Pedicelled spikelet length	Grain length	Grain breadth
(a) *Range of percentage variation*								
Wild	10	16-81	7-52	19-60	6-44	24-52	14-55	5-78
Cultivated	10	13-52	13-82	18-58	14-43	25-71	9-30	10-40
Artificial hybrid, F_1	11	14-38	17-66	14-65	11-70	22-54	11-28	9-32
Collected hybrids	9	21-51	24-70	33-88	8-54	12-60	8-41	16-45
(b) *Range of 10 plant means*								
Wild	10	28-61	420-530	19-25	5·3-7·0	4·6-6·6	2·4-3·6	1·5-2·4
Cultivated	10	81-103	140-260	52-106	3·8-4·4	2·6-3·6	3·4-4·5	3·0-4·0
Artificial hybrids, F_1	11	64-94	330-620	14-28	4·4-5·3	3·7-4·7	3·4-3·9	2·2-2·4
Collected hybrids	9	59-99	240-290	80-109	3·7-5·9	2·8-5·3	3·0-3·8	2·1-2·7

In table 2 (*a*), there is considerable variation in all groups, as might be expected from the hybrid index diagrams. The variation within entries is as great as that between entries, thus in No. 135 of the cultivated group, the range of grain length measurement was 11 per cent. of the mean, but panicle length range was 82 per cent. of the mean. Similarly for No. 121, panicle length range was 13 per cent. of the mean, but the pedicelled spikelet length range was 71 per cent. of the mean. The collected hybrids in table 2 (*a*) are no more variable than the modal representatives of the wild or cultivated groups.

Table 2 (*b*) shows that for leaf breadth, the range of means was similar in the collected hybrids and the wild or cultivated groups. The range of panicle length was substantially lower in the collected hybrids, while for grain dimensions the range of the collected hybrids tended to be similar or lower. The collected hybrids showed a much greater range of panicle branch length than the wild sorghums, but a lesser ranger than the cultivated types. For both glume length and pedicelled spikelet length the collected hybrids were similar to, or slightly greater in range than the wild types, but substantially greater than the cultivated entries. If entries 6, 11 and 54 are

included, they fall within similar limits except that the lower limit of leaf breadth becomes 53 mm.

In 1965 remnant seed of the available natural hybrid entries was grown as progeny rows, and the first 20 plants in each row were harvested. Photographs of the heads from these plants are shown in plates I-III. It will be seen that 54A (plate I, B and D) and 54B (plate II, A) and 111 (plate II, B and C) are fairly uniform, and so is No. 112 (plate III, D) although of a different panicle type. The remaining entries (Nos. 116, 117 and 120, plate III, A, B and C) are all obviously segregating, especially No. 120.

6. DISCUSSION

The results from these studies show that the wild and cultivated sorghums form very distinct populations. When only 4 plant characters were used for calculating the hybrid indices, separation between the wild and cultivated populations was good (fig. 1), and when 11 plant charcters were used the degree of separation was increased (fig. 2). Only when cultivated sorghums from Karamoja district were included in the study was there a " tail " in the direction of the wild type at the lower end of the cultivated sorghum frequency distribution (fig. 3). This is considered later. The intermediate position on the frequency diagrams is occupied by hybrids between the wild and cultivated sorghums. There is a clear resemblance between our first three text-figures and those obtained for *Drosophila* by Thoday and Gibson (1962) and by Thoday (1964, fig. 6). All these diagrams show two distinct populations, with hybrids occupying intermediate positions, and we suggest that the sorghum populations have diverged from a common origin through the operation of disruptive selection as did the *Drosophila* populations of Thoday and Gibson.

A situation in which directional selection alone could have resulted in the development of the cultivated from the wild sorghum is difficult to imagine. With both natural selection and human selection favouring different phenotypes in the population a disruptive selection situation must have existed. That directional selection may well have operated from time to time in local areas in the course of the crop's development is not in doubt, but the initiation and main course of the crop's development must surely have been under disruptive selection.

Thoday and Gibson gave full opportunity for random mating during the course of the disruptive selection which resulted in the production of their two populations. In sorghum also there has been, and still is, every opportunity for gene flow between the wild and cultivated types. Wild sorghums are often to be found adjacent to cultivated fields, or as weeds in these fields. The amount of outcrossing in cultivated sorghum is often around 5-10 per cent. (*e.g.* Sieglinger, 1921; Hsu, 1934; Jones and Sieglinger, 1951). In the wild sorghums, higher figures of 18-30 per cent. are reported (Burton, 1951). Hybrids can be made readily between the cultivated and wild forms, and occur naturally rather frequently. We collected one wild plant which gave 18 per cent. of F_1 hybrids in its progeny (entry No. 6). Since the selection pressures applied by man and by nature result in a disruptive selection situation, then the results from *Drosophila* obtained by Thoday and his co-workers demonstrate how the enoblement of sorghum could have occurred even in the presence of abundant crossing with the unimproved wild type. Secondly, when Millicent and Thoday (1961) subjected their

divergent populations to negative assortative mating with 25 per cent. gene flow, most of the difference between their divergent populations was maintained. We have demonstrated that gene flow is occurring between the wild and cultivated sorghums, although we have no estimate of the amount of such gene flow. However, even if this gene flow was considerable, as it could well have been in the early days of cultivated sorghum development, the results of Millicent and Thoday (1961) show that differences developed under disruptive selection between the wild and cultivated sorghums would still be maintained. Thirdly, divergence in *Drosophila* had occurred after only 12 generations in one trial, and after only 7 generations in another, under a regime of disruptive selection with opportunity for random mating (Thoday and Gibson, 1962; Thoday, 1964). This demonstrates that the time required for the development of the sorghum crop from the wild type by disruptive selection need not have been great. The crop probably originated about 3000 B.C. (Doggett in Hutchinson, 1965) and the great differences between the cultivated crop and its wild progenitor evident today could well have been developed in this short period of time through the operation of disruptive selection.

A feature of much interest is the central position of the intermediate populations of hybrids in the diagrams. Thoday concluded that mating preference could account for a substantial part of the reproductive isolation which he observed between his divergent *Drosophila* lines. There was also some evidence for slower development of the hybrids, and poor competition between the hybrids and one of the divergent populations. In sorghum, there is preferential mating within the groups in the sense that there is a substantially greater chance of the plants being self-pollinated rather than cross-pollinated. Today, there is also a greater likelihood of a cultivated sorghum in a field being pollinated by another cultivated type than by a wild type, but in the initial stages of crop enoblement the converse will have been true. Competition is evidently also important, as well as the ecological conditions under which the hybrids might persist.

Large hybrid swarms might be expected as a result of natural crossing between wild and cultivated sorghum. In fact, these do not occur. Forms intermediate between the two main populations have been demonstrated in the hybrid index diagrams, but their frequency of occurrence is low relative to the size of the wild and cultivated populations. When F_2 generations are deliberately grown under good cultivation the bulk of these populations in fact occupy the region intermediate between the wild and the cultivated parents (figs. 5 and 6). In nature, most of these intermediates are eliminated, mainly through natural and human selection, although sterility in the F_3 may play a small part (*cf.* Clausen and Hiesey, 1958). There are two sharply distinct environments: there is the niche successfully occupied by the wild sorghum and here natural selection will eliminate plants whose characters lie outside the wild range. At the other extreme, there is the cultivated field with man exercising a rather strong selection pressure against all but the cultivated forms. Most hybrid derivatives lacking the broad leaves and stout stems of the cultivars will be uprooted early on: and any which show signs of the tight black glumes and dehiscent sessile spikelets are uprooted when recognised. Such forms are frequent enough to be named in certain of the African languages, *e.g.* " pungu " in Kisukuma. It is clear from fig. 6 that when hybrid indices are based on 7 plant characters, few of

the F_2 segregates from wild × cultivated crosses fall within the range of either the wild or the cultivated populations. With only these two extreme environments, very low survival rates for hybrid segregates showing inter-mediate characters would be expected.

There is, however, a third ecological niche. Anderson (1949) pointed out that if hybrids are to survive, there must be intermediate habitats for them. In sorghum, the great majority of intermediates occur in field margins and on recently abandoned cultivation. Over much of Africa, it has long been customary to cultivate land for a period of years, then to abandon it. For security reasons in the past, fields were grouped close together, and this still tends to be the case. Abandoned land reverts to natural grassland and bush, but the process takes several seasons. Even today, cultivated fields are mainly a patchwork of small plots, with all stages of cultivation and abandoned cultivation contiguous. In any year there are field margins and plots of land abandoned for one or more years within pollinating distance of each other where the rigours of natural selection are somewhat ameliorated by the residual effects of cultivation. Although any one plot of land shows conditions of recently abandoned cultivation for only a short time, in terms of the locality it is a rather stable environment through constant renewal, and it persists as long as man is cultivating in the area. The wild × cultivated sorghum hybrids survive in this third ecological zone of recently abandoned cultivation and field margins. Given some movement of seed through birds, man and animals, coupled with free movement of pollen, the survival of the hybrids should result in the development of a third sorghum population, adapted to the conditions of this intermediate ecological niche. We were impressed by the number of our wild × cultivated hybrid collections which were not actively segregating early generation hybrids, in fact, these were in a minority. The majority of our collections showed rather little segregation, and fell into a few main types. Some showed great uniformity, such as entries 11, 54, 111 and 112. The illustrations in plates I-III attempt to demonstrate this. The data of table 2 support the suggestion that a definite intermediate sorghum popula-tion does exist, and indicate that the variability in it is no greater than that within the wild and cultivated populations. It seems that natural selection defines a population which can survive in the wild, and also a population which can survive in the intermediate niche of recently abandoned cultiva-tion, while man selects the population of the cultivated land.

The " black amber " type weed sorghums in the U.S.A. are relevant here. In Kansas a number of these weed sorghums persist, and have been known to survive in a field through a wheat crop followed by a lucerne crop. They can be classified into a few main types, two of which resemble plate I, B and D, and plate III, D (Casady, 1959, 1965). These weeds are reputed to have come from " black amber ", a Chinese forage sorghum, but it is probable that they in fact represent the surviving intermediate types from sudan grass (wild sorghum) × cultivated crosses, establishing rather more strongly under Kansas conditions than they do in East Africa.

The existence of an intermediate population facilitates introgression between the wild and cultivated groups. A great mixture of types occurs in cultivated fields, and any plant showing cultivated characters would survive among the crop so long as it had persistent sessile spikelets and threshed easily. Figs. 1-3 and the scatter diagram in fig. 4 indicate that
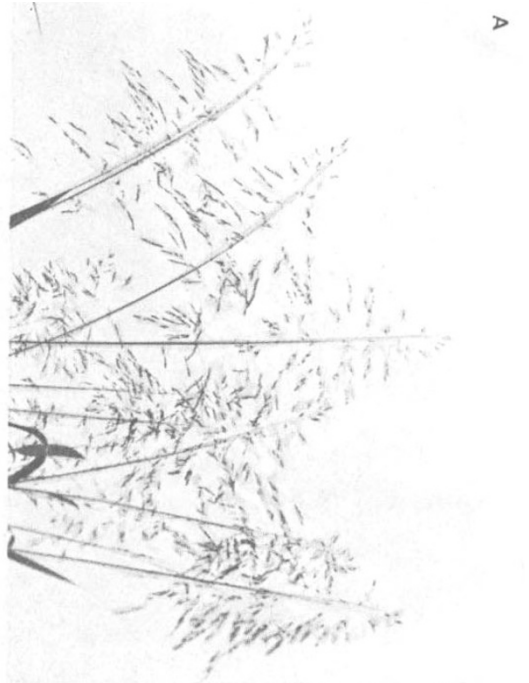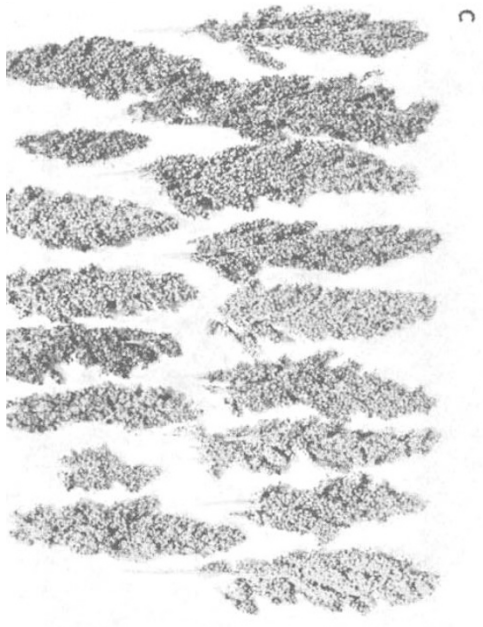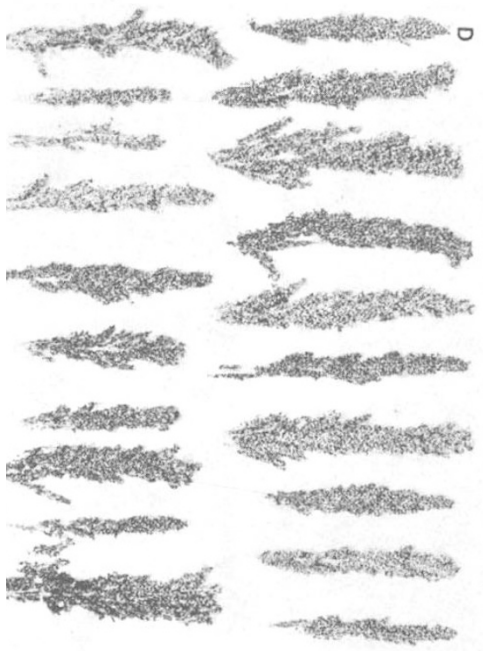
Plate I

(A) The wild sorghum *S. verticilliflorum.*

(B) No. 54A, the natural hybrid collected in the West Nile district of Uganda.

(C) No. 138, a cultivated entry collected in West Kenya on route C.

(D) Heads of No. 54A.

Plate II

Natural hybrids, from fig. 3.

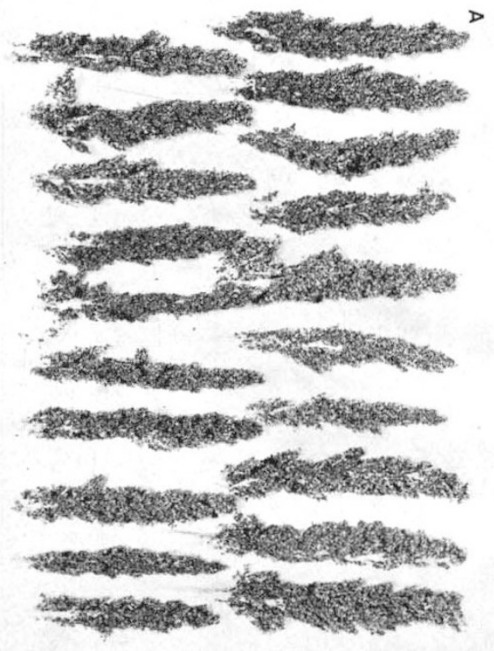(A) No. 54B.   (B) No. 114.   (C) No. 111.   (D) No. 118.

Plate III

Natural hybrids from fig. 3.

(A) No. 116⎫
(B) No. 117⎬ Segregation is evident in all of them, especially No. 120.
(C) No. 120⎭
(D) No. 112.   Quite uniform, but a distinctly different type from No. 54, the length of panicle branch being the main contrast.
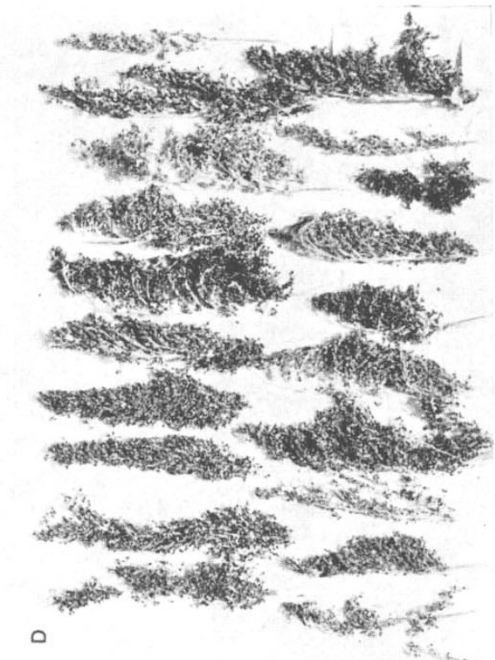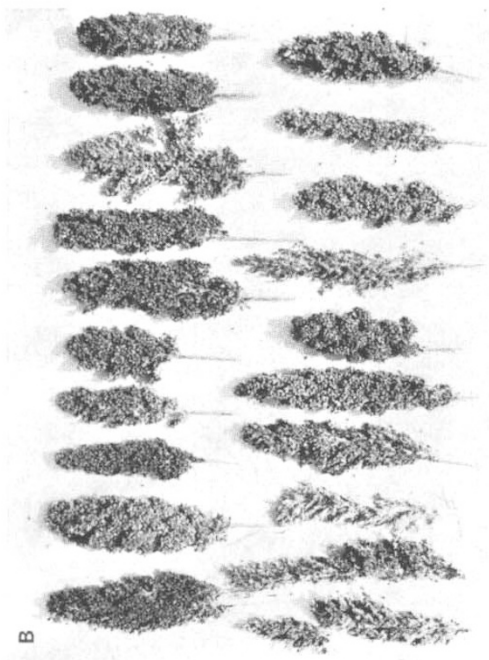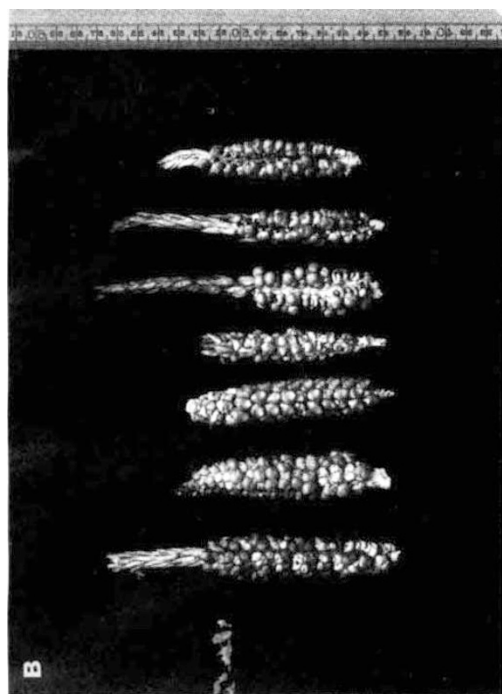
Plate IV

(A) Tetraploid maize.   (B) *4n* Maize × *Zea perennis.*

(C) 1st Nackcross of *4n* Maize × *Zea perennis.*   (D) 2nd Backcross of *4n* Maize × *Zea perennis.*

introgression between the wild and cultivated sorghums in fact occurs. The chance collection of No. 6, giving a natural hybrid population when grown out, was fortunate in this connection. The fact that local women* would accept and name as cultivated types a number of the F_3 plants derived from No. 6 indicates both that wild × cultivated crosses are still playing a part in the development of the local cultivated races, and also that by the F_3 generation a number of derivatives of such a cross could survive in the cultivated field without being uprooted. It is possible that entry No. 6 was itself a product of introgression between the wild and cultivated types. It is also significant that in fig. 3 the cultivated varieties which occur in the hybrid zone of the diagram all came from Karamoja (Nos. 91-97 and 100) where agriculture is still primitive. Under such conditions the wild and cultivated types might be expected to resemble each other more closely.

These population studies clarify the species relationships within the *Sorghum* sub-section *Arundinaceae* group. The character measurements used to calculate hybrid indices gave a fairly full description of the plant, and no evidence was obtained to suggest that there are different species within either the wild or the cultivated populations examined, although a wide range of wild types was included. There is, however, good reason to treat the wild and cultivated groups as distinct species. Their populations are sharply separated on the hybrid index diagrams, and a substantial measure of sterility was noticed in the F_3 of a cross between the wild and cultivated types (derivatives of entry No. 6). The F_2 populations from such a cross showed a median dip in the histograms of the segregation of the majority of characters studied, tending to separate into wild and cultivated populations. Clayton (1961) has shown that *Sorghum bicolor* (Linn) Moench is the appropriate name for the cultivated sorghums. Grassl (1962) and Doggett (1962 in Hutchinson, 1965) have suggested that *S. arundinaceum* be considered for the wild sorghums.

Snowden (1936, 1955) subdivided the wild and cultivated sorghums of the sub-section *Arundinaceae* into numerous species. That some classification of these very varied groups is a practical necessity is not in doubt, but Hutchinson *et al.* (1938) have pointed out the objections to treating the divisions as separate species. Snowden noted the resemblances between his wild and cultivated species and these resemblances coincided with similarity of geographical distribution. This led Snowden to suggest that his cultivated species were derived from the corresponding wild species. Thus, *S. guinëense* was thought to have come from *S. arundinaceum* in West Africa; *S. caudatum* and *S. caffrorum* from *S. verticilliflorum* in East and Central Africa; and *S. durra* from *S. aethiopicum* in North-East Africa. It seems clear from our studies that these resemblances observed by Snowden are in fact due to introgression between the wild and cultivated types. As the wild sorghum was carried along in the crop, man induced changes in the crop by selection, these changes were fed back to the wild type through introgression, and some survived in the wild population. The variability in the wild sorghums of the sub-section *Arundinacea* is therefore only a pale reflection of the great variation induced by man in the cultivated crop. The wild population also acts as a reservoir for certain characteristics of the cultivated crop in the area,

* Among the Iteso, the women have prime responsibility for the grain crops, both in the field and in the granary, and have a most thorough and detailed knowledge of the various cultivated forms.

B

although this may not be apparent. Thus, the hybrids from entry 6B produced a large number of recognised local cultivated forms and 4 Snowden species. A cross on Serere between entry No. 143 (*S. aethiopicum*) and combine kafir 60, both less than a metre tall, produced plants 6 ft tall with the characteristics of several Snowden cultivated species typical of North-East Africa.

The pattern of development in the sorghum crop appears to have consisted basically of a disruptive selection situation resulting in the production and maintenance of a polymorphic population. The divergent populations hybridised, and because of the existence of the habitat of recently abandoned cultivation and field margins, an intermediate population became established. It would be a great oversimplification to regard disruptive selection as the only agency in the development and diversification of this crop. The persistence of intermediates permitting introgression will have contributed greatly to the variability in which man worked. With population movements there must have been separation, isolation and recombination all playing their part in diversification. Indeed, the situation for the diversification of sorghum in Africa must often have been close to the ideal for rapid evolution, with a large population divided and subdivided into partially isolated local races of small size (Wright, 1931). Nevertheless, this basic pattern of disruptive selection for crop development seems a most likely one for sorghum and for many other crops, unless completely separated from their wild progenitors through transportation to a new area without the wild type being carried along as a crop weed, or by some other isolating mechanism such as polyploidy.

The development of the maize crop

The possible parallel with maize has already been noticed (Doggett, 1965). Maize outcrosses, and it is likely that the original wild and improved *Zea* crossed freely. Under such circumstances disruptive selection must have occurred. Mangelsdorf (1960) has shown that a very early maize could be classified as an annual form of *Tripsacum*, though the name *Zea* had priority.

Reeves and Mangelsdorf (1959) demonstrated that teosinte is a *Tripsacum* × maize hybrid. It seems unlikely that such hybridisation is only recent, it must surely also have occurred when the early cultivated *Zea* and the wild *Tripsacum*-like *Zea* were more similar. Teosinte occurs as a weed in the maize fields of Guatamala and Mexico, and it is often confined to fence rows and the margins of rice and corn fields. Anderson questioned whether it was ever truly wild (Mangelsdorf, 1947). This is just the kind of habitat occupied today by the intermediate sorghum population. Certainly teosinte hybridises freely with maize, and Mangelsdorf (1961) writes: " Introgression of teosinte into maize, which now is virtually an established fact, may actually represent a secondary introgression of *Tripsacum* into maize with teosinte serving principally as a bridge over which there is a flow of genes between the distantly related genera, *Zea* and *Tripsacum* ". Wellhausen *et al.* (1952) show that in some maize races, such as Olotillo and Tepecintle, there has been introgression with teosinte, while Celaya has received teosinte genes from three different sources. Mangelsdorf (1961) also draws attention to the work of Farquharson (1957) and Maguire (1957) which indicates that even today some South American maize varieties hybridise with *Tripsacum* and that some crossing over between

chromosomes occurs. Mangelsdorf (in Hutchinson, 1965) remarks that " It is doubtful whether among varieties of maize now in existence there is any that is completely free of introgression from teosinte or *Tripsacum* ".

Thus, the pattern outlined by Doggett (1965) of a wild *Tripsacum*-like *Zea* from which cultivated maize was derived by disruptive selection with teosinte forming the intermediate population would fit the above observations. It seems most likely that the *Tripsacum*-teosinte-maize situation is parallel with but further advanced than the wild-intermediate-cultivated sorghum situation of today. The fact that present-day *Tripsacum* has a basic chromosome number of $n = 9$ compared with the $n = 10$ of maize or teosinte need not represent a serious objection to this pattern. The original wild *Tripsacum*-like *Zea* may well have been lost, but some of the present-day *Tripsacums* will have been derived from a common source, and they still show affinity and hybridise with maize. Mangelsdorf (1947) has pointed out that the introduction of cattle and other grazing animals could have led to the decimation of wild maize in many of the places where it occurred. Even if the annual derivatives of the primitive *Tripsacum*-like *Zea* have in fact disappeared, some of their germ-plasm is available in teosinte, and it seems that the modern *Tripsacum* is still contributing some genetic variability to the teosinte-maize system.

Polyploidy and the intermediate population

An intermediate population is both an additional source of variability and a channel for gene flow between the wild and the cultivated types. It may also be important in relation to polyploidy in crop plants. The chance of a polyploid arising and persisting within a cultivated grain crop itself is rather small. If autoploid, it may be rejected because of reduced seed set: if alloploid, it will show undesirable wild characters. There is a better chance of a polyploid surviving in the wild population, and the intermediate population could act as a bridge in conveying the polyploidy to the cultivated crop. Certainly this could happen in sorghum. *S. halepense* is regarded as an alloploid consisting of 2 genomes which is believed to have arisen as a segmental alloploid between two 20-chromosome species (Duara and Stebbins, 1952; Endrizzi, 1957). In this century it has crossed in the Argentine with a cultivated sorghum to give the very successful tetraploid *S. almum* (Parodi, 1943; Endrizzi, 1957). Crosses between tetraploid and diploid sorghum occur naturally and the hybrids are sometimes tetraploid (Hadley, 1958). *S. almum* thus represents the intermediate population between wild *S. halepense* and cultivated diploid sorghum. From the first cross between *S. almum* and cultivated sorghum, cultivated types with good seed set have been selected at Serere. If such types survived on recently abandoned cultivation, they might be brought into cultivation, or cross further with the cultivated sorghums to yield progeny with a greater chance of being acceptable in cultivation. It has proved easy to transfer the fertility and balance of *S. halepense* to cultivated sorghum via *S. almum* and so to produce a tetraploid cultivated crop plant. Autotetraploid cultivated sorghum was in fact used as the recurrent parent instead of the diploid, to speed up the process (Doggett, 1964).

Polyploidy might arise intially in the intermediate population itself, and the presence of a persisting intermediate population would increase the chances of such polyploidy surviving. There is the same possibility of later

transfer to the cultivated crop as noticed above for sorghum. *Zea perennis*, which arose in the wild, crosses and back-crosses to autotetraploid maize very readily at Serere, and it is difficult to avoid contamination of one by the other (plate IV). It is significant that, in both sorghum and maize, tetraploid wild forms and tetraploid intermediates (*S. almum* and *Zea perennis*) have arisen. These could represent the first step towards the later development of these crops at the tetraploid level, a step perhaps already taken by some of the existing polyploid crops.

The powerful nature of the disruptive selection forces is impressive: the wild and cultivated sorghums differ at perhaps the species level after the rather short period of around 5000 years. The wild and cultivated derivatives of the maize progenitors are separated at the genetic level after only about 8000 years. The rapidity with which the cultivated crops developed in the presence of their wild progenitors has always been difficult to explain. Disruptive selection seems to provide the key, and the development of wild, intermediate and cultivated populations with gene flow between them ensures the production and increase of the very large amount of variability needed for the development of a cultivated crop. The existence of the intermediate population facilitates the transfer of polyploidy to the crop plant from the wild type in which it may have arisen. This under the influence of disruptive selection could lead to a further advance in the development of the crop plant.

7. SUMMARY

1. Hybrid indices based on a wide range of plant characters were calculated for wild and cultivated sorghums, and for natural and artificial hybrids between them.

2. The wild and cultivated sorghums represent two distinct populations, with the hybrids occupying an intermediate position. There was a strong resemblance between our diagrams and those found by Thoday and his co-workers when they applied disruptive selection to *Drosophila*. Cultivated sorghum was developed from a single wild species of the sub-section *Arundinacea* through disruptive selection. It was also maintained in the presence of the wild type under disruptive selection, in spite of considerable gene flow between the two groups.

3. The wild and cultivated sorghum groups differ at the species level, but there was no evidence for subdividing either the wild or cultivated populations of our study into species.

4. An intermediate population has established from the natural wild and cultivated hybrids. This does not consist only of early generation hybrids, but also contains a good proportion of rather homozygous lines. The existence of the ecological habitat of recently abandoned cultivations and field margins has enabled this intermediate population to establish and persist.

5. The presence of this intermediate population ensures continued introgression between the wild and cultivated sorghums. In addition to enhancing the variability of the cultivated crop in which man selects, introgression results in the wild type being somewhat modified in the direction of the cultivated forms. This accounts for the similarities observed by Snowden (1936) between the wild and cultivated sorghums of the same geographical area.

6. The development of the maize crop can be explained along the same lines as those set out for sorghum, except that the crop is of greater antiquity so divergence has continued further. The pattern *Tripsacum*-teosinte-maize parallels the wild-intermediate-cultivated sorghums of our study.

7. The established intermediate population could act as a bridge to transfer polyploidy from the wild type to the cultivated crop, or polyploidy might arise within the intermediate population. Examples are furnished by *Sorghum almum* and *Zea perennis*.

8. REFERENCES

ANDERSON, E. 1949. *Introgressive Hybridization.* Wiley, New York.

AYYANGAR, G. N. R., RAO, V. P., AND PONNAIYA, B. W. X. 1936. Deciduous sessile spikelets in sorghum. *Curr. Sci., 5,* 299.

BURTON, G. W. 1951. The adaptability and breeding of suitable grasses for the South Eastern States. *Advanc. Agron., 3,* 197.

CASADY, A. J. 1959 and 1965. Personal communication from Kansas State University, Manhattan.

CLAUSEN, J., AND HIESEY, W. M. 1958. *Experimental Studies in the Nature of Species,* IV. Carnegie Institute, Washington.

CLAYTON, W. D. 1961. (79) Proposal to conserve the generic name Sorghum Moench. (*Gramineae*) versus Sorgum Adans. (*Gramineae*). *Taxon, 10(8),* 242.

COURT, M. N. 1963. Personal communication.

DOGGETT, H. 1958. The breeding of sorghum in East Africa. *Emp. J. Exper. Agric., 26,* 37.

DOGGETT, H. 1964. Fertility improvement in autotetraploid sorghum. II. *Sorghum almum* derivatives. *Heredity, 19,* 543.

DOGGETT, H., in HUTCHINSON, J. B. (Editor). 1965. The development of the cultivated sorghums. *Essays on Crop Plant Evolution,* p. 50. Cambridge University Press.

DOGGETT, H. 1965. Disruptive selection in crop development. *Nature, Lond., 206,* 279.

DUARA, B. N., AND STEBBINS, G. L. 1952. A polyhaploid obtained from a hybrid derivative of *Sorghum halepense* × *S. vulgare* var *Sudanense. Genetics, 37,* 369.

ENDRIZZI, J. E. 1957. Cytological studies of some species and hybrids in the Eu-sorghums. *Bot. Gaz., 119,* 1.

FARQUHARSON, L. I. 1957. Hybridisation in *Tripsacum* and *Zea. J. Hered., 48,* 295.

GARBER, E. D. 1950. Cytotaxanomic studies in the genus *Sorghum. Univ. Calf. Pub. Bot., 23,* 283.

GIBSON, J. B., AND THODAY, J. M. 1962. Effects of disruptive selection. VI. A second chromosome polymorphism. *Heredity, 17,* 1.

GRASSL, C. O. 1962. Classification of *Sorghum* Section *Sorghum. Sorghum Newsletter, 5,* 85. Sorghum Research Committee, U.S.A.

HADLEY, H. H. 1958. Chromosome numbers, fertility, and rhizome expression of hybrids between grain sorghum and Johnson grass. *Agron. J., 50,* 278.

HATHEWAY, W. H. 1962. A weighted hybrid index. *Evolution, 16,* 1.

HSU, T. S. 1934. A study of natural crossing in Kaoliang. *Bull. Coll. Agric. For. Nanking,* No. 25 (n.s.).

HUTCHINSON, J. B., PANSE, V. B., APTE, N. S., AND PUGH, B. M. 1938. Studies in plant breeding technique. IV. Crop analysis and varietal improvement in Malvi *Jowar. Ind. J. Agric. Sci., 8,* 131.

JONES, M. D., AND SIEGLINGER, J. B. 1951. Effect of wind direction on natural crossing in sorghum, *Sorghum vulgare* Pers. *Agron. J., 43,* 571.

JOWETT, D. J. 1962. The inheritance of awnless. *Record of Research, Ann. Rept. E.A.A.F.R.O. Kenya,* for 1961.

KARPER, R. E., AND QUINBY, J. R. 1947. The inheritance of callus formation and seed shedding in sorghum. *J. Hered., 38,* 211.

MAGUIRE, M. P. 1957. Cytogenetic studies of *Zea* hyperploid for a chromosome derived from *Tripsacum. Genetics, 42,* 473.

MANGELSDORF, P. C. 1947. The origin and evolution of maize. *Advanc. Gen., 1,* 161.

MANGELSDORF, P. C. 1960. Reconstructing the ancestor of corn. *Rept. Smithsonian Inst., Washington, 1959,* 495.

MANGELSDORF, P. C. 1961. Introgression in maize. *Euphytica, 10,* 157.

MANGELSDORF, P. C., in HUTCHINSON, J. B. (Editor). 1965. The evolution of maize. *Essays on Crop Plant Evolution,* p. 23. Cambridge University Press.

MATHER, K. 1953. The genetical structure of populations. *Symp. Soc. Exp. Biol., 7,* 66.

MATHER, K. 1955. Polymorphism as an outcome of disruptive selection. *Evolution, 9,* 52.

MILLICENT, E., AND THODAY, J. M. 1961. Effects of disruptive selection. IV. Gene-flow and divergence. *Heredity, 16,* 199.

PARODI, L. R. 1943. Una neuva especie de *sorghum* cultivada en las Argentina. *Rev. Argentina de Agron., 10,* 361.

REEVES, R. G., AND MANGELSDORF, P. C. 1959. The origin of corn. II. Teosinte a hybrid of corn and *Tripsacum. Bot. Mus. Leafl. Harvard Univ., 18,* 357.

SIEGLINGER, J. B. 1921. Cross-pollination of milo in adjoining rows. *J. Amer. Soc. Agron., 13,* 280.

SNOWDEN, J. D. 1936. *The Cultivated Races of Sorghum.* Adlard, London.

SNOWDEN, J. D. 1955. The wild fodder sorghums of the section Eu-sorghum. *J. Linn. Soc. Lond., 55,* 191.

SNOWDEN, J. D. 1961. The classification and nomenclature of *Sorghum,* Section *Sorghum. Sorghum Newsletter, 4,* 67. Sorghum Research Committee, U.S.A.

STAPF, O., in PRAIN, D. (Editor). 1934. *Flora of Tropical Africa, 9,* 104. Reeve, Ashford, England.

THODAY, J. M. 1958. Effects of disruptive selection: the experimental production of a polymorphic population. *Nature, 181,* 1124.

THODAY, J. M. 1959. Effects of disruptive selection. I. Genetic flexibility. *Heredity, 13,* 187.

THODAY, J. M. 1960. Effects of disruptive selection. III. Coupling and repulsion. *Heredity, 14,* 35.

THODAY, J. M. 1964. Effects of selection for genetic diversity. *Genetics To-day,* pp. 533-540. Pergamon Press.

THODAY, J. M., AND BOAM, T. E. 1959. Effects of disruptive selection. II. Polymorphism and divergence without isolation. *Heredity, 13,* 205.

THODAY, J. M., AND BOAM, T. E. 1961. Effects of disruptive selection. V. Quasi-random mating. *Heredity, 16,* 219.

THODAY, J. M., AND GIBSON, J. B. 1962. Isolation by disruptive selection. *Nature, 193,* 1964.

WELLHAUSEN, E. J., ROBERTS, L. M., AND HERNANDEZ, X., in collaboration with MANGELSDORF, P. C. 1952. Races of maize in Central America. *Bussey Institution, Harvard University.*

WRIGHT, SEWALL. 1931. Evolution in Mendelian populations. *Genetics, 16,* 97.

APPENDIX

Comments by Iteso women on cultivated type plants from the F_3 generation of a naturally occurring hybrid derived from entry 6

There were 105 F_3 rows, of which 54 rows yielded 149 " cultivated " plants. Fifty-seven of these F_3 plants were immediately recognised, named with confidence, and their grain uses explained to us.

The names given were as follows:

Iteso name	Number of plants
Edeidei	3
Egaat	8
Emocat	15
Edyama	1
Okinei	8
Okwaras	4
Oyara	18
	57

The remaining 92 plants were not regarded as varieties already in cultivation, but were considered quite suitable to grow. The women in fact asked for some of the heads to take and plant in their own gardens.