FERTILITY IMPROVEMENT IN AUTOTETRAPLOID SORGHUM

I. CULTIVATED AUTOTETRAPLOIDS

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1. INTRODUCTION

THE development of autotetraploid crop varieties when the harvest required is the seed has not been generally successful, usually because of reduced fertility, although Muntzing (1948, 1951) has had good results with autotetraploid rye. The temperate cereals have been actively developed for a long time, and polypoidy has already been utilised in wheat, and oats. The tropical grains of Africa have not been subjected to such intensive development, and it may be possible to utilise polypoidy profitably in some of them.

The potential advantages of tetraploid cultivated sorghums have been outlined by Doggett (1957, 1962) and Bhatti (1959). The possibility that tetraploid sorghum hybrids may show a slower decline in hybrid vigour on inbreeding than the corresponding diploids could be of importance in underdeveloped countries. The variability available in tetraploid populations based on a wide range of diploid material will also be of much value. Randolph (1935, 1941) working with tetraploid maize found that hybrids between certain inbred tetraploid lines were fertile and showed pronounced hybrid vigour. Tetraploid maize work has continued (*e.g.* Alexander, 1960; Cavanah and Alexander, 1963) but as yet maize tetraploids have not proved generally useful. The prospects for sorghum are better, as the naturally occurring tetraploids *S. halepense* and *S. alnum* are both successful plants, and are interfertile with autotetraploid cultivated sorghum. *S. alnum* arose perhaps 30-40 years ago from a natural cross between diploid sorghum and *S. halepense* (Parodi, 1943; Endrizzi, 1957).

Chin (1946) found that in colchicine-induced autotetraploid sorghum 19 per cent. of the pollen grains were defective, and the tetraploids were later maturing than the diploids. Casady and Anderson (1952) found 83 per cent. seed set in the F_1 of the cross (autotetraploid Sudan grass $\times$ *S. halepense*). The latter parent showed 80 per cent. seed set and diploid Sudan 86 per cent. The tetraploid Sudan parent seed set was recorded as very low; these authors' table 1A suggests it was about 37 per cent. Endrizzi (1957) recorded one 30 per cent. and two 80 per cent. seed sets on 40 chromosome plants of Sudan grass $\times$ *S. halepense*, while two such plants in Sudan grass $\times$ *S. alnum* gave 78 and 92 per cent. seed sets. Hadley (1958) found 90 to

98 per cent. of stainable pollen, and over 75 per cent. seed set, in 40 chromosome plants obtained from pollinating diploid genetic male-sterile stocks ms_2/ms_2 with *S. halepense*. Bhatti (1959) crossed cultivated sorghum $\times$ *S. virgatum*, then doubled with colchicine. The single tetraploid F_1 plant had a 73 per cent. seed set, and the F_2 seed sets ranged from below 5 per cent. to above 75 per cent., with the mode in the 26-40 per cent. class. A single tetraploid plant from the backcross to cultivated sorghum showed 93 per cent. seed set, but its progeny showed the same range and mode value as the first F_2 . Schertz (1962) found 35 per cent. of stainable pollen in colchicine-induced auto-tetraploids of cultivated sorghum, and a mean seed set of 10 per cent.

Cytological observations agree that in tetraploid sorghum univalents and trivalents are few. Figures are summarised in table 1.

TABLE 1
Cytological observations on tetraploid sorghums

Authors	Material	No. of cells	Configurations—average per cell				Notes
			I	II	III	IV	
Butany in Endrizzi (1957)	Auto. Sudan grass	66	0.20	10.50	0.02	4.40	0.10 VI+ 0.03 VIII
Schertz (1962)	Auto. cultivated	70	0.0-0.2	14.0-18.0	0.0-0.8	1.3-3.0	
Endrizzi (1957)	Kafir $\times$ <i>S. alnum</i>	72	0.35	10.69	0.12	4.47	
Endrizzi (1957)	Kafir $\times$ <i>S. alnum</i>	81	0.81	12.69	0.15	3.32	0.01 VI
Endrizzi (1957)	Sudan $\times$ <i>S. alnum</i>	94	0.36	10.61	0.08	5.50	
Endrizzi (1957)	Kafir $\times$ <i>S. halepense</i>	75	0.69	10.18	0.21	3.64	
Endrizzi (1957)	Kafir $\times$ <i>S. halepense</i>	68	1.26	11.43	0.41	3.81	

The quadrivalent frequency is much below that recorded in tetraploid maize, where modes of 8 (Kadam, 1944) and 7 to 9 (Randolph, 1935) have been reported. Kadam (1944) found 35 to 42 per cent. aneuploids, and Catcheside (1956) found 32 per cent. aneuploids, in the progeny of autotetraploid maize plants. Schertz (1962) found a figure of 36 per cent. aneuploids in his autotetraploid sorghum. In F_1 tetraploids developed from hybridisation with *S. halepense*, aneuploids were nil in 21 plants (Hadley, 1958) and in an F_2 , 34 per cent. of the plants had 38 or 39 chromosomes (Hadley, 1953). In a similar cross Endrizzi reported no aneuploids in 10 F_1 plants: from *S. alnum* crosses with Kafir and Sudan with Kafir and Sudan grass there were 18 per cent. aneuploids: from *S. alnum $\times$ *S. halepense*, 25 per cent., aneuploids (Endrizzi, 1957).*

2. MATERIALS AND METHODS

Cultivated sorghums. The diploid stock of line A was derived from the first backcross of a Congo Hegari type (27 U.T.) by a tall Tanganyika type (Wiru) which occurs to the south of Lake Victoria. The Hegari was the recurrent parent. The

origin of the diploid stock of line B was similar, except that the non-recurrent parent was Msumbiji, which grows near the coast of Southern Tanganyika, some 600 miles from the region where Wiru is cultivated. Lines A and B had both been selected for the grain and glume characters of the Shallu type parent, and the vegetative characters of the Hegari parent. Selection and inbreeding had continued for four and three generations respectively before the lines were made autotetraploid with colchicine.

Colchicine treatment. Sorghum seeds surface-sterilised with mercuric chloride were germinated on filter paper in sterile Petri dishes for 4 days. The coleoptile tips were sliced off about 0.5 mm. above the node, and the seedlings were then inverted into 0.1 to 0.2 per cent. aqueous colchicine for 4 to 6 hours in a humidity chamber. The roots were not in contact with the colchicine. After treatment, seedlings were well washed in sterile water, allowed to recover for 48 hours in Petri dishes, then planted out. On the average, a half to three-quarters of the seedlings showed marked swelling and checked growth, and 10 to 20 per cent. of the original seedlings survived to give tetraploid plants. It was sometimes necessary to cut back the main shoot to stimulate tillering, one or more such tillers often being tetraploid. Sectorial diploid-tetraploid panicles occurred in some plants.

Seed set counts. Counts were made in the field on at least 200 sessile spikelets from each plant, and the percentage seed set represents the number of grains per 100 spikelets. The sampling was done on branches from the middle nodes of the panicle.

Cytological preparations. Chromosomes were examined in aceto-carmin p.m.c. smears, or in aceto-orcin root-tip squashes.

Sites. In 1958 the work was transferred from Ukiriguru, Lake Province, Tanganyika, to Serere, Eastern Province, Uganda.

3. FERTILITY IMPROVEMENT ON HYBRIDISATION OF AUTOTETRAPLOID LINES

Lines A and B were doubled with colchicine, and showed seed sets of 31 per cent. They were then crossed together; the F_1 showed a 68 per cent. seed set and the F_2 74 per cent., while the diploid grown simultaneously with parent B and the F_1 showed 88 per cent. seed set (Doggett, 1957).

The low seed sets of these early autotetraploids precluded their being of practical value, but the large increase in fertility resulting from the hybridisation of A and B was of interest. The parents, F_1 , F_2 and F_3 generations were grown at Ukiriguru simultaneously, without replication. Variances were calculated from the angular transformation of the data. Up to this stage, no selection had been practised, but the heads from which the seed was derived had been self-pollinated. Table 1 gives a summary of the observations made, and figure 1 gives a histogram of the F_3 seed set to illustrate the type of distribution obtained.

The changes in seed set resemble those reported earlier (Doggett, 1957). There is the same pronounced increase in the F_1 , which is maintained in the F_2 . It falls somewhat in the unselected F_3 . The diploid mean is decidedly low for sorghum—but that was a seasonal effect. The diploid line was not identical with that from which the tetraploids A and B were developed, but was of similar origin. There was a relationship between F_3 row mean seed set, and the seed set on the F_2 heads from which they came, the regression value being $b = 1.244$, S.E. = 0.092, significant beyond the $P = 0.001$ point.

The seed set data in table 2 and figure 1 are consistent with the pattern to be expected were high seed set controlled by complementary genes. The variances figures cannot carry much weight, as there was no replication. The data from table 8, however, indicate that seed set is not influenced by block effects in the field. The variances in table 2 from the F_1 onwards are consistent. The F_1 has a similar variance to the inbred diploid, and the two F_2 variance estimates, made from the F_2 heads and from simultaneously grown F_3 rows, are virtually identical. From these figures, variance above a value of about 38 is largely genetic, and the F_2 and F_3 show increasing levels of genetic variance as might be expected for the segregation of inherited characters

TABLE 2

Percentage seed sets, and variances of parents and 3 hybrids generations of the autotetraploid sorghum cross $A \times B$ (1957)

	Parent A	Parent B	$A \times B$ F_1	$A \times B$ F_2	$A \times B$ F_3 , individual plants	$A \times B$ F_3 , means of rows from individual F_2 heads	Diploid
Percentage seed set—							
Mode (class) (per cent.)	20-24	20-29	65-69	70-74	55-59	55-59	75-79
Mean (per cent.)	19	33	66	67	56	55	81
Range, low (class) (per cent.)	0-4	5-9	30-34	30-34	0-4	35-39	55-59
Range, high (class) (per cent.)	35-39	60-64	80-84	90-94	85-89	70-74	95-99
Number of plants counted	27	66	33	139	1758	27 average in 58 rows	72
Variance (on angular transformation . . . . .)	56.12	72.78	37.43	66.54	81.12	65.41	38.18

in an autotetraploid. Unfortunately, the high variance figures for the autotetraploid parent lines A and B spoil this picture.

Selection for high seed set was begun in the F_3 , and was continued in subsequent generations. The selected F_4 to F_7 generations were grown simultaneously, without replication, with the results shown in table 3.

In table 3, mean seed set has held steady at about the 70 per cent. level, although the selection pressure for high seed set was strong, and neither the lower nor upper end of the range appears to have changed.

The variance for the diploid was obtained from a random scatter of 19 diploid lines (actually inbreds from a varietal collection), so should be a maximum figure, including the environmental and available genetic variance in the diploid collection. It is therefore unlikely that the genetic variance in the tetraploids of table 3 was different from that of the diploid collection. Absence of replication precludes any

comparison with the table 1 group, but the F_4 - F_7 variances are much below that of the F_3 in table 2.

FIG. 1.—Distribution of the seed-set in tetraploid hybrid $A \times B$ and in parents.

The covariances of seed set between progeny row and parental head from generation to generation should indicate whether there was much genetic variance present (table 4).

These covariances support the impression formed from the variances in tables 1 and 2, that selection for high seed set in the F_3 brought about an immediate and large reduction in the genetic

variance. It seems that from the F_4 onwards but little genetic variance remained.

The few plants taken as selections from the F_3 (25 in all) were able to transmit to their progeny the ability to give a seed set rather similar in value and distribution to that of the original ($A \times B$) F_1 , and this

TABLE 3

Percentage seed set and variances of F_4 to F_7 generation of $A \times B$ tetraploid hybrid, selected for high seed set in each generation (1960)

	F_4	F_5	F_6	F_7	Diploid
Mode (class %)	70-74	70-74	70-74	70-74	90-94
Mean (%)	71.4	70.5	70.7	70.1	89.9
Range, low (class %)	50-54	35-39	40-44	40-44	75-79
Range, high (class %)	85-89	85-89	90-94	90-94	95-99
Number of plants counted	69	257	367	1476	68
Variance (on angular transformation)	26.29	28.99	23.52	23.68	30.57

TABLE 4

Covariances of seed set in successive generations of autotetraploid hybrid $A \times B$. Generations were grown in diverse environments, including greenhouse, wet season and dry season plantings

Generation	F_3/F_2	F_4/F_3	F_5/F_4	F_6/F_5	F_7/F_6	F_8/F_7
Covariance	+30.51	-0.39	-0.77	+3.62	+0.55	+2.03
n	61	24	24	17	95	55

situation persisted for the selected heads from F_4 onwards. The very low seed set classes present in F_3 were eliminated and did not occur again.

4. CYTOLOGICAL OBSERVATIONS

Some plants from the F_6 generation grown in the dry season were examined. Unfortunately the parents were not available. The 28 plants analysed had 40 chromosomes, and configurations are shown in table 5, with 5 per cent. confidence limits.

TABLE 5

Cytological analysis of F_6 generation of hybrid $A \times B$. Means of 28 plants, 10-20 cells analysed per plant

	Configurations per cell			
	I	II	III	IV
Mean	0.15	7.46 $\pm$ 0.44	0.09	6.17 $\pm$ 0.22

Three hundred and eighteen cells were analysed in all, and although there was variation in cells within plants, the mean number of configurations per plant was very similar. The number of quadrivalents is somewhat higher than that found by other workers, but univalent and trivalent frequencies are of a similar order to others reported. The figures suggest a fairly consistent chromosome pattern in the F_6 generation.

Another indication of stability comes from the rate of diploid reversions. The selection of plants with the best seed sets meant that any diploids present were noticed. Two diploids were found in the F_3 (1760 plants), and four in an F_4 of 218 plants. None was found in F_5 , but one F_6 planting showed two in 145 plants. Another F_6 planting of different lines showed no diploids in 367 plants while none was found in the F_7 (1476 plants) and F_8 (579 plants).

5. SEGREGATION FOR PLANT COLOUR

The cross $A \times B$ was segregating for the factor pair Pp . Four separate F_2 plantings were used to obtain estimates of the segregation ratio. The data were homogeneous ($P = 0.90-0.95$) and gave the following pooled estimate:—

P	p	Ratio	χ^2 for 20:78:1	P value for χ^2	α^*	S.E. of α^*
2924	128	22:8:1	1.102	0.2-0.3	0.11437	0.02658

* α is here taken as the proportion of gametes produced by double reduction, and was calculated from the relation $\alpha = 3\sqrt{Z - \frac{1}{2}}$, with standard error of $\frac{3}{2}\sqrt{\frac{1-Z}{n}}$. These formulæ were derived from the gametic output of $\frac{1}{2}(1+2\alpha)$ for PP and pp gametes, and $\frac{1}{2}(4-4\alpha)$ for Pp gametes (Fisher and Mather, 1943). I am much indebted to D. Jowett for their derivation. The formulæ quoted by Little (1945) based on the original definition of α by Mather (1936) give double the above values.

The maximum probable value of α can be taken as 0.1429 ($\frac{1}{7}$), so the value found here is high, and not significantly below $\frac{1}{7}$. This is compatible with the rather high level of quadrivalent formation observed (60 per cent. in table 5). It also implies that the P locus is not located near the centromere, and that the $DRsP$ chromosome (Stephens and Quinby, 1939) is often involved in quadrivalent formation.

6. THE PROGRESS OF SELECTION FOR HIGH SEED SET

In table 6 is set out the percentage seed sets of selected heads and their progeny rows for the first three generations. From an F_2 of 62 plants, 58 yielded seed. All of these were counted and planted to give the F_3 , without selection for seed set.

Up to F_4 , the progress seemed promising, but the F_4 seed setting conditions were excellent (in a greenhouse in the dry season), and the diploids ranged from 93 to 99 per cent. seed set. The subsequent behaviour of these families is seen in table 7, where the mean of the

TABLE 6

Percentage seed sets of selections and their progeny rows from the cross ($A \times B$)

No.	F_2 Head	F_3 Row mean	No.	F_3 Selection	F_4 Row mean	No.	F_4 Selection
3	87.4	62	3/8	84	79.4	3/8/1	91.8
9	61.7	59	9/3	81	78.1	9/3/2	90.6
26	85.8	70	26/6	81	83.7	26/6/2	92.1
			26/10	83	76.0	26/10/2	88.0
						26/10/4	89.9
34	82.3	62	34/12	82	79.6	34/12/1	90.6
39	82.8	65	39/37	87	74.4	39/37/1	82.8

TABLE 7

Mean percentage seed set, angles and confidence limits of families derived from autotetraploid cross $A \times B$

	3/8/1	9/3/2	26/6/2	26/10/2	26/10/4	34/12/1	39/37/1
F_5 (per cent.) .	82.7	71.3	70.6	77.1	75.9	74.0	60.1
Angle . . .	65.5 $\pm$ 7.7	57.9 $\pm$ 4.3	57.7 $\pm$ 5.8	63.2 $\pm$ 6.5	61.6 $\pm$ 5.9	59.6 $\pm$ 3.6	51.0 $\pm$ 7.0
F_6 (per cent.) .	—	—	81.9	80.4	78.3	74.0	—
Angle . . .	—	—	64.8 $\pm$ 4.7	63.6 $\pm$ 0.9	62.6 $\pm$ 1.2	59.4 $\pm$ 1.7	—
F_7 (per cent.) .	69.5	75.3	72.5	66.8	68.9	69.6	71.5
Angle . . .	56.7 $\pm$ 1.2	60.7 $\pm$ 1.0	58.6 $\pm$ 0.6	54.9 $\pm$ 0.5	56.4 $\pm$ 0.5	56.6 $\pm$ 1.2	58.0 $\pm$ 0.8
F_8 (per cent.) .	76.1	81.0	77.8	69.8	78.6	79.3	78.9
Angle . . .	60.8 $\pm$ 1.6	64.4 $\pm$ 0.6	62.1 $\pm$ 0.7	56.7 $\pm$ 1.4	62.7 $\pm$ 0.6	63.1 $\pm$ 0.8	63.1 $\pm$ 1.7

progeny rows for each family in each generation is given, together with the angular transformation and 0.05 per cent. confidence limits.

There is no reason to suppose from tables 6 and 7 that selection from F_5 to F_8 made any progress towards improving seed set, and this conclusion accords with the covariance values recorded earlier. Selection is being continued.

7. SEED SETS ON OTHER AUTOTETRAPLOID CULTIVATED SORGHUMS

Well over 100 cultivated sorghum varieties have been doubled with colchicine. Individual heads have shown seed set variations between

5 and 80 per cent. There appear to be differences between varieties. Table 8 shows the seed sets of cultivated autotetraploid sorghum varieties. Lines within varieties are indicated by letters following the varietal name. Seed set estimates were from 21 heads of each entry in three replications of a randomised block design.

TABLE 8

Differences in percentage seed set between cultivated autotetraploid sorghum lines and two diploids (1961)

Variety	Percentage seed set	Angle	Variety	Percentage seed set	Angle
N 1 (diploid) .	91.9	73.6	Natal Red. A .	60.4	51.0
SA 2 (diploid) .	90.4	72.1	SA 2 A .	60.1	50.8
T 32 A .	76.7	61.2	Redlan D .	59.8	50.6
Redlan A .	67.0	55.0	R 1 B .	59.7	50.6
N 1 A .	66.2	54.5	R 1 C .	58.8	50.1
Rhod. Rs. A .	64.1	53.2	R 1 D .	57.7	49.4
N 1 B .	63.9	53.1	B 9 A .	57.5	49.3
N 1 C .	63.5	52.9	B 9 B .	56.5	48.8
Rhod. Rs. B .	63.3	52.7	B 5 A .	53.4	47.0
Redlan B .	62.2	52.1	SA 2 B .	51.9	46.1
R 1 A .	62.1	52.0	B 5 B .	45.7	42.5
Redlan C .	61.2	51.5	B 5 C .	42.1	40.4
P. Baker A .	60.7	51.2	B 5 D .	41.1	39.9

Differences for significance at $P = 0.05$, angular values, Duncan's multiple range test (Harter, 1960).

$P = 2$	4	6	8	10	16	20	25
5.2	5.6	5.8	6.0	6.1	6.3	6.4	6.4

In this trial, the C.V. was 5.5 per cent., and the F value for replication was 0.3, so position in the field did not influence seed set. The trial formed part of a larger one including 15 lines of *S. alnum*, of which details will be reported later. There was ample tetraploid pollen shed by the *S. alnum*, and seed set was not limited by pollen shortage. Any interference between diploid and tetraploid pollen must have been slight, as the seed set of the diploids and of some of the *S. alnum* lines was at the 90 per cent. level, a figure often obtained at Serere. The heritability estimate was $h^2 = 73$ per cent. for that part of the trial in table 8. The results show that there were differences between the seed-sets of these autotetraploid varieties at $P = 0.05$, but not between lines within varieties, excepting in the case of B 5. The diploid seed sets were well ahead of the tetraploid sets, and the fertility of T 32 was similar to that found earlier in the A $\times$ B cross. Supporting evidence for the inheritance of seed set in some of the table 8 varieties is given by unreplicated data available from a later planting in 1961, and from a 1960 planting, as shown in table 9.

The general trend in each planting is similar. There was no significant difference between B 9 and N 1 in table 8, so only T 32 is anomalous in the (B) 1961 planting. N 1 is low in 1960.

TABLE 9

Percentage seed sets of autotetraploid sorghum varieties. The number of plants in each sample is shown in brackets

Variety	(A) Mean in 1961 trial (Table 8)	(B) 1961, later planting	(C) 1960
T 32 . .	76.7	64.3 (17)	65.9 (7)
N 1 . .	64.5	72.5 (22)	41.1 (5)
Redlan . .	62.6	67.0 (37)	51.7 (8)
P. Baker . .	60.7	63.0 (15)	53.0 (9)
R 1 . .	58.5	70.0 (32)	49.1 (9)
B 9 . .	57.0	70.3 (40)	49.4 (4)
SA 2 . .	56.0	55.3 (34)	45.6 (12)
B 5 . .	45.6	51.9 (44)	40.6 (23)

There was insufficient seed available of really low seed-set types to permit their inclusion in the trial of table 8. Some would certainly have shown means well below 40 per cent.

8. DIPLOID SEED SETS

In 1963 conditions for seed set were exceptionally good, and it was possible to demonstrate differences in diploid seed set on a large variety trial. (table 10). The layout was a Youden square of 31 varieties and hybrids in six replications. Seed set was counted on six heads of each entry in each replication.

Differences required for significance (arcsine figures):—

P	p = 2	4	6	8	10	20	30
0.05	2.1	2.3	2.4	2.5	2.5	2.6	2.7
0.01	2.8	3.0	3.1	3.2	3.2	3.4	3.5

The C.V. for the trial was 2.4 per cent., and the heritability estimate was $h^2 = 77$ per cent. The variances for replications and for blocks were similar to the error variance, so again position in the field did not influence seed set, which was also wholly independent of flowering date. A mean seed set of 95.2 per cent. based on 1116 randomly chosen heads is unusually high.

It is of interest to note that there were no differences between the kafirs of S. African origin whether received direct or after being worked on in the U.S.A. (Pearl Kafir, Combine 2, Grohoma, Combine kafir 60 Birdproof). The two definite Hegari types, B.C. 27 and Early Hegari,

TABLE 10
Seed set differences between diploid varieties and hybrids

Variety	Percentage set	Arcsine	Variety	Percentage set	Arcsine	Variety	Percentage set	Arcsine
Dobbs	97.3	81.1	SB 68	95.7	78.6	Hybrid 726	94.5	76.9
Hybrid H×61	97.1	80.8	E. Hegari	95.5	78.3	Combine 2	94.4	77.0
Hybrid H×57	97.1	80.7	L. 28	95.4	78.2	Grohoma	94.4	76.7
SB 79	97.0	80.6	Hybrid H×58	95.3	78.3	CK 60	94.1	76.8
Hybrid H×76	96.8	80.4	Hybrid H×60	95.3	78.2	SB 65	93.9	76.4
Hybrid H×78	96.7	80.3	Pearl Kafir	95.2	78.0	S. Durra Milo	93.8	76.4
Hybrid H×37	96.1	79.4	SB 77	95.0	77.6	C 1	93.6	76.3
S.R.D. 30	96.0	78.8	BC 27	94.9	77.3	Framida	93.6	76.0
Wheatland	95.9	78.7	SB 62	94.7	77.2	Hybrid 610	93.5	76.0
Tada	95.8	79.0	SB 75	94.6	77.2	Birdproof	93.5	76.0
			L 17	94.6	77.0			

are similar in seed set though one comes direct from the Congo and the other, much earlier maturing, from the U.S.A. The varieties L 17 and L 28 are both local types from the Lango district of Uganda, and their seed set does not differ. The variety C 1 came from Chad, and Framida from S. Africa. The latter originated in the then French Equatorial Africa, and these two varieties are very similar.

The hybrids with "Hx" numbers were produced at Serere, and are crosses of CK 60, or White Wheatland, with one of the "SB" numbers in the trial, Early Hegari, or B.C. 27. They occupy the upper part of the table, and if this is an expression of heterosis, it was not shown by the U.S.A. hybrid 610 nor by the Israel Hybrid 726. The SB numbers are locally bred sorghums of hybrid origin, and SRD 30 is a Sudanese variety. Sooner Durra Milo is from the U.S.A.

9. DISCUSSION

There is much evidence that fertility in annual plants is under close genotypic control. Genotypic control of chromosome behaviour in rye has been shown by Rees (1955, 1957), Thompson (1956), Rees and Thompson (1956, 1958). Rees (1955) gives references to work on other crops. Riley and Chapman (1958) showed that chromosome pairing is gene controlled in hexaploid wheat.

Sorghum has diversified throughout Africa and southern Asia, and shows a wealth of variability in morphological characters, as has been demonstrated by Snowden (1936). It is likely that the gene systems which control seed set have diversified also, and varietal differences are to be expected.

The data presented here (table 10) confirm that differences between the seed sets of diploid sorghum varieties exist and are highly heritable, though the differences themselves are small. Any mutation affecting seed set adversely would be eliminated if its effect was large, so only small differences would be expected.

Differences in the genotypic control systems of seed set which pass unnoticed at the diploid level might well become apparent in autotetraploids. The data in tables 8 and 9 show that there are large differences in autotetraploid seed set. The heritability values were similar to those found in the diploid trial (77 and 73 per cent), and although differences between varieties were significant, in only one instance were differences between lines of a variety significant. We conclude that the existence of differences in the genotypic fertility control systems of sorghum varieties has been proved.

The behaviour of the autotetraploid cross $A \times B$ is entirely consistent with this view. Two low seed-set autotetraploid lines gave much higher seed set (some 65 per cent.) in the F_1 of the cross between them. The F_2 showed a similar mean fertility to the F_1 , but the range was greater. This behaviour was repeated in two separate seasons (Doggett, 1957, and the data reported here). The F_3 generation showed a lower mean

set and a still wider spread at the low end of the scale. Selection for high seed-set in the F_3 resulted in the complete elimination of the low seed set classes, which would surely have been noticed in the 1476 plants of the F_7 had they been present. It proved possible to maintain the seed set at about the 70 per cent. level in subsequent generations, and to develop stable lines. The variance estimates and the practical results showed that once selection was begun, genetic variance fell rapidly to a low figure, and it did not prove possible to increase seed-set significantly above the F_1 value. These results are clearly consistent with complementary gene action with high seed set dominant. The rapid elimination of the low seed-set classes on the application of selection indicates that only few genes were involved.

It is quite reasonable to assume that the parental types A and B did differ in their genotypic fertility control systems. Although both had been backcrossed once to the common parent 21 U.T., both had been intensively selected for the grain and glume type of the non-recurrent parents. The Wiru type, the progenitor of A, would fall into Snowden's (1936) *S. conspicuum*, with W. African affinities. The Shallu type from which B was derived belongs to *S. roxburghii*, which occurs mainly on the E. African Coast with affinities in India and Burma. The Wiru and Shallu involved could well have been isolated from each other for a very long period, so the presumption of differences in their genotypic fertility control systems is a legitimate one.

There is no information on how the fertility systems operate. The slight cytological evidence available suggests that the number of quadrivalents at meiosis is consistent, and to this extent chromosome behaviour is "regular". The inheritance data confirm that one chromosome at least is often involved in quadrivalent formation. Possibly types giving rise to aneuploids were responsible for the low seed set classes, and selection has favoured the types which transmit a pattern of orderly chromosome behaviour.

Increased seed set resulting from the intercrossing of autotetraploids has been recorded for other plants, including antirrhinum (Sparrow, Ruttle and Nebel, 1942), rye (Müntzing, 1948, 1951) and rice (Morinaga and Kuniyama, 1946; Masima and Uchiyamada, 1955). These last authors concluded that the increased fertility in rice could largely be accounted for by a decrease in the number of quadrivalents in the hybrids when compared with the parental lines. Whatever may be discovered about the operation of the genotypic fertility control systems in sorghum, the clear demonstration of the existence of differences suggests that fully fertile autotetraploid sorghum is an objective attainable by the plant breeder. It also sheds a little more light on the development of fertile autotetraploids during evolution.

10. SUMMARY

1. The autotetraploid sorghum lines A and B of low seed set were intercrossed. Fertility was doubled in the F_1 (66 per cent. seed set), and

the F_2 showed a similar mean set with wider range. The F_3 seed set was lower and the range was further increased.

2. Selection in the F_3 for high seed set resulted in a sharp fall in genetic variance, which was extremely low in subsequent generations. Selection was continued to F_8 , and stable lines with seed sets similar to that of the F_1 were obtained, but it was not possible to obtain lines of higher fertility.

3. Plants of the F_6 generation showed 6.2 ± 0.22 IV and 7.5 ± 0.44 II per cell, with a very low frequency of I and III.

4. The segregation of Pp showed that the proportion of gametes formed by double reduction did not differ from one-seventh, thus confirming that the DRsP chromosome at least is frequently involved in quadrivalent formation.

5. Rather large differences in seed sets between autotetraploid sorghum varieties were observed, but in only one case was there a difference between lines within a variety. The heritability estimate was 73 per cent.

6. Very small real differences between the seed sets of diploid varieties were detected. The heritability estimate was 77 per cent.

7. It was concluded that there are differences in the genotypic fertility control systems of sorghum, which result in slight differences in seed set at the diploid level, but which may show up as much larger differences at the tetraploid level. The genotypic fertility control systems of A and B differed, and complementary gene action accounted for the higher seed set of the F_1 of $(A \times B)$, and for the subsequent behaviour of the cross under selection. The genes concerned must impose a consistent pattern of chromosome behaviour to account for the observed results.

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