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MULTIVARIATE ANALYSIS OF GENETIC DIVERGENCE IN *EU-SORGHUMS*

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A study of the nature of genetic divergence in *Sorghum* by multivariate analysis was undertaken to examine the nature of differentiation within this genus and to improve the existing criteria of its classification. Forty-six populations of *Eu-Sorghum* representing its different series and sub-series were selected. Based on Mahalanobis' D^2-statistic, the population could be grouped into 15 clusters. The spatial disposition of the clusters and their relative divergence was in broad agreement with that of Snowden in seven clusters, but only in partial agreement in the other cases with the phylogenetic relations indicated by him. The grouping was confirmed by canonical analysis. After a comparison of the present results with those reported by others, the sub-genus *Eu-Sorghum* could be divided into nine species.

INTRODUCTION

The genus *Sorghum* has considerable genetic diversity among its numerous cultivated forms which are grown for diverse purposes and are capable of growing under wide agro-climatical conditions. The classification of this genus has been controversial since pre-Linnean times with confusion even about its genetic rank and the nature of taxonomic differences between the species. The classification of *Sorghum* still used is that by Snowden (1936) which is based mostly on herbarium specimens using morphological characters, mainly of the panicle and spikelets and has not satisfactorily resolved the difficulties due to overlapping of several quantitative and qualitative characters and the free exchange of genes between the so-called species. For the same reason, the cytogenetic studies have also not helped to overcome the difficulties in classifying this material. Multivariate analysis in classifying biological populations (Blackith 1960, Nair *et al.* 1960, Rao 1960, Murty *et al.* 1962, Cassie 1963) has proved to be useful and will be appropriate for a material like *Sorghum*.

Hence an attempt was made to utilize such techniques and Mahalanobis' D^2, in particular, to re-examine this genus *Sorghum* on the basis of quantitative characters related to fitness.

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Material and Methods

The material comprised of 46 populations representing 22 species of the section, *Eu-Sorghum* (Snowden, 1936) which included cultivated fodder and grain types. The experiment was laid out in a randomized complete block design with three replications conducted over two years, 1962 and 1963, at Delhi. The net individual plot size was a single row of three metres.

Observations were recorded on each of the ten plants selected at random per plot, excluding the borders on ten characters as detailed below:

$$\textit{Growth rate per day} = \frac{\text{Height on the day of panicle emergence—height on the 30th day}}{\text{Number of days between the 30th day from sowing and the day of panicle emergence}}$$

Transformation of the data to another scale was not found necessary since the error variances for this character were found to be stable over seasons (Smith and Robson 1959).

Days to flower.—The number of days taken from sowing date to the day of anthesis in the middle of the panicle on the main axis.

Panicle length.—The length of that portion of the panicle bearing spikelets measured in centimetres.

Number of primaries in the panicle.—The number of primary branches of the panicle per node, counted at three equidistant places representing the bottom, the middle and the top one-third portions respectively, of the panicle.

Length of primaries of the panicle.—Length of the primary branches measured in millimetres at three places at the positions mentioned above.

Angle of primaries of the panicle.—The angle of divergence of a representative primary branch of the panicle from the main rachis measured in degrees at the three places mentioned above.

Number of secondaries in the panicle.—The numbers of secondary branches on each primary branch, counted at the three points indicated above.

Distance between whorls of the panicle.—The distance between the successive whorls of primary branches of the panicle measured in millimetres at the bottom, middle and top one-third parts of the panicle.

Distance within whorls of the panicle.—The distances between primary branches within each whorl were found to vary. This distance was measured in millimetres at the same three places as indicated above.

Number of seed-bearing spikelets.—The number of fertile spikelets per primary branch counted in the same three places as indicated above.

The significance of the differences between the populations for the aggregate of the ten characters was tested by Wilks' Λ -criterion. Mahalanobis' D^2-statistic was utilized to assess the divergence between the populations. The character means (x's) were transformed into uncorrelated variables

(y's) by Dwyer's square root method and the grouping was done by Tocher's method as outlined by Rao (1952).

Experimental Methods

Analysis of means

The means of the 46 populations for the ten characters are presented in Table I. Growth rate was the highest in one of the two *arundinaceums* and one of the two *nervosums*. However, they were not the earliest to flower indicating that earliness and growth rate were not directly related. Both the *virgatums* and one of the *nervosums* which were the earliest to flower had only intermediate growth rates. Among the panicle characters, there were wide differences between the species and also populations within the same species such as *S. roxburghii*, *S. caffrorum*, *S. subglabrescens* and *S. nervosum* for most of the characters. *S. halepense* had the longest panicle whereas *S. splendidum* exhibited comparatively higher means for a majority of the panicle characters. The number of primaries were the highest in *caffrorums* and the lowest in *virgatum* and *sudanense*. The angle of primaries was large in fodder types like *S. halepense*, *S. sudanense* and *S. splendidum*. The compact head types, such as *durras*, had close whorls while lax-head types such as *S. sudanense* and one of the populations of *S. roxburghii* had widely separated whorls. Some populations of *Hegari*, *S. roxburghii* and *S. cernuum* had large number of spikelets, whereas M 35–1 from Maharashtra and one population of *S. cernuum* had fewer spikelets.

The analysis of variance of means for the ten characters (Table II) indicated that the populations differed significantly for each character.

Test by Wilks' Λ-criterion showed that the differences in the mean values of the populations with regard to the pooled effect of the ten characters were highly significant (χ^2 for 450 d.f. = 12493·09).

The common dispersion matrix is presented in Table III and the uncorrelated linear combinations (y's) are obtained by Dwyer's square root method (Table IV).

The 1035 D^2 values between all possible pair combinations were calculated.

The populations included in each cluster are listed in Table VII. Intra- and inter-cluster D^2 are represented diagrammatically in Table V (*see also* Fig. 1).

An examination of the D^2 values revealed that *S. halepense* was the most divergent from the rest of the populations. The D^2 values involving populations 7 (*S. sudanense*), 14 (*S. roxburghii*), 15 (*S. roxburghii*) and 42 (*S. splendidum*) were also large. Population 35 (*S. subglabrescens*) was unique in having high values of D^2 with others. Populations within each of the same species of *S. arundinaceum*, *S. virgatum*, *S. dochna*, *S. cernuum* and

TABLE I

Means of the 46 populations of Sorghum *for ten characters*

Population	Growth rate cm/day	Days to flower	Panicle length (cm)	No. of primaries	Length of primaries (mm)	Angle of primaries	No. of secondaries	Distance between whorls (mm)	Distance within whorls (mm)	No. of seed-bearing spikelets
1	2	3	4	5	6	7	8	9	10	11
1. *S. halepense*	7·3	57·3	38·4	4·2	35·9	80·7	6·7	33·1	1·2	37·0
3. *S. arundinaceum* ..	7·9	62·0	24·3	6·7	62·0	31·7	6·2	22·6	1·4	16·2
4. *S. arundinaceum* ..	9·3	53·2	25·4	6·8	69·4	32·7	6·3	25·5	1·3	15·5
5. *S. virgatum*	4·2	43·4	19·5	2·1	41·6	21·1	4·4	18·7	1·4	18·4
6. ,, ...	4·3	48·0	22·6	3·1	61·5	31·8	5·4	27·7	1·3	13·8
7. *S. sudanense*	6·4	54·1	41·5	2·9	111·4	45·1	6·1	35·2	1·5	25·0
8. ,, ..	3·8	54·0	22·5	2·4	70·2	36·6	5·4	26·0	1·3	19·1
9. *S. drummondii* ..	5·5	62·0	23·7	6·9	75·3	24·6	6·4	27·9	0·9	13·3
10. *S. guineense*	2·5	118·7	22·9	6·0	62·8	29·5	5·4	27·0	1·2	12·8
11. *S. conspicuum* ..	3·1	126·8	21·1	5·2	63·1	30·6	6·4	24·0	1·2	21·3
12. *S. roxburghii* ..	5·1	64·3	30·0	6·9	107·0	22·8	6·4	32·6	1·0	29·3
13. ,, ..	7·4	50·9	24·8	9·7	94·9	31·1	6·9	34·3	0·8	19·8
14. ,, ..	3·1	51·0	24·9	9·0	97·0	20·7	5·7	32·8	0·7	21·4
15. ,, ..	3·3	105·1	21·4	6·7	98·6	21·5	8·6	18·5	0·6	41·9
16. *S. nigricans*	2·9	52·5	15·9	7·3	46·7	41·7	5·6	15·1	1·2	12·7
18. *S. caudatum*	5·6	60·0	16·2	7·5	57·8	23·7	6·0	18·2	1·3	22·3
20. *S. caffrorum*	6·4	53·3	17·0	6·9	50·9	33·4	6·3	24·1	1·0	17·3
21. ,, ..	2·1	60·6	21·8	13·5	75·3	27·2	7·7	31·8	0·7	23·7
22. ,, ..	2·1	62·7	21·3	14·0	75·0	22·4	6·9	24·4	0·8	25·0

TABLE I—(*contd.*)

Means of the 46 populations of Sorghum *for ten characters*

Population	Growth rate cm/day	Days to flower	Panicle length (cm)	No. of primaries	Length of primaries (mm)	Angle of primaries	No. of secondaries	Distance between whorls (mm)	Distance within whorls (mm)	No. of seed-bearing spikelets
1	2	3	4	5	6	7	8	9	10	11
23. *S. caffrorum*	4·4	63·3	23·3	7·2	61·0	24·7	7·3	30·9	1·2	27·3
24. *S. dochna*	4·0	91·2	23·3	8·0	58·9	21·9	7·1	25·7	0·5	29·4
25. ,, ..	4·9	84·4	21·6	6·4	53·6	20·3	6·2	22·1	0·8	23·8
26. *S. bicolor*	2·6	104·9	18·1	5·6	66·0	20·7	5·9	21·1	1·0	16·0
27. *S. milliiforme* ..	7·3	51·1	19·3	6·9	56·1	40·0	6·3	18·1	1·6	16·4
28. *S. cernuum*	4·2	107·5	15·5	5·9	47·2	29·6	6·9	15·6	0·9	39·2
29. ,, ..	5·2	84·3	9·4	6·5	28·9	21·6	6·5	9·7	0·7	4·9
30. *S. durra*	4·0	117·9	20·3	7·4	57·4	30·8	6·1	21·5	0·9	25·6
31. ,, ...	6·1	57·9	10·6	9·3	37·0	42·5	6·0	6·6	0·9	21·1
32. ,, ..	7·4	53·7	10·6	9·0	34·7	40·1	6·2	6·4	1·0	25·3
33. ,, ..	6·0	68·8	9·9	7·2	33·4	27·6	6·0	7·9	0·7	12·1
34. *S. membranaceum* ..	4·4	94·2	16·3	8·2	54·4	31·2	7·2	20·0	0·5	32·7
35. *S. subglabrescens* ..	3·6	116·1	8·2	7·7	27·7	30·2	6·0	6·7	0·6	17·1
36. ,, ..	4·4	96·1	14·6	6·6	39·3	25·1	6·4	12·0	0·6	31·6
37. *S. membranaceum* ..	4·4	92·6	15·5	7·5	51·7	33·1	7·1	16·3	0·5	38·6
38. *S. basutorum* ..	6·8	57·8	26·2	9·6	76·8	23·2	6·2	33·3	0·6	22·3
39. *S. nervosum*	5·6	49·4	20·1	6·5	67·3	19·0	6·4	25·1	1·6	15·4
40. ,, ..	10·1	55·8	24·4	6·4	71·1	20·0	6·0	19·9	1·8	27·4
41. ,, ..	3·5	53·9	19·2	9·0	57·2	19·8	5·8	20·0	1·0	15·4

TABLE I—(*concld.*)

Means of the 46 populations of Sorghum *for ten characters*

Population	Growth rate cm/day	Days to flower	Panicle length (cm)	No. of primaries	Length of primaries (mm)	Angle of primaries	No. of secondaries	Distance between whorls (mm)	Distance within whorls (mm)	No. of seed-bearing spikelets
1	2	3	4	5	6	7	8	9	10	11
42. *S. splendidum*	6·7	55·3	37·8	6·3	140·4	43·5	8·2	48·4	0·9	15·8
43. *S. caffrorum*	2·1	62·3	21·5	11·4	71·2	20·7	6·9	26·1	0·9	25·8
44. „ ..	2·1	60·8	22·2	8·7	74·7	23·8	7·7	31·6	1·0	32·2
*45. *Hegari*	4·1	55·0	21·1	5·6	52·1	90·6	6·1	17·3	1·9	39·6
*46. „ ..	3·5	60·6	16·5	5·4	37·8	26·8	5·3	14·8	1·7	28·4
*47. Milo	6·2	58·4	14·1	6·7	40·8	30·8	5·0	15·1	1·1	13·0
*48. „ ..	6·9	56·1	14·8	6·5	39·2	29·7	4·5	15·2	1·4	16·6
50. M 35–1	6·0	67·5	17·1	7·0	54·6	24·3	6·0	20·7	1·2	7·9
Plot mean	50·0	699·3	200·6	212·9	1896·5	877·8	188·9	670·3	31·0	676·2
Grand mean	5·0	69·9	20·6	7·1	63·2	29·3	6·3	22·3	1·0	22·5
S.E. (experimental) ..	4·3	27·9	13·5	20·2	193·1	66·8	17·1	73·8	5·7	152·6
C.V.	8·7	4·0	6·5	9·5	10·2	7·6	9·0	11·0	18·2	22·6

Population numbers 2, 17, 19 and 49 did not flower

* Populations 45 to 48 are commercial types from the U.S.A.

S. membranaceum and within Milos showed low D^2 values which were not significant. However, the D^2 values between the populations, *S. roxburghii*, *S. caffrorum*, *S. durra*, *S. subglabrescens*, *S. sudanense* and *S. nervosum* were significant.

TABLE II

Analysis of variance of means for ten characters in 46 populations of Eu-Sorghum *based on plot totals (M.S.S.)*

Source of variation	Blocks	Populations	Error
Degrees of freedom	2	45	90
Growth rate	35·57 n.s.	1124·75*	18·01
Days to flower	711·07 n.s.	154723·13*	776·19
Panicle length	23·84 n.s.	14485·93*	180·79
Number of primaries	1195·88 n.s.	15581·57*	407·28
Length of primaries	208·74 n.s.	1476475·46*	37282·99
Angle of primaries	5365·79 n.s.	299976·76*	4455·74
Number of secondaries	34·24 n.s.	1931·97*	291·59
Distance between whorls	9407·86	207516·60*	5450·29
Distance within whorls	45·66 n.s.	358·27*	32·06
Number of seed-bearing spikelets ..	47108·16 n.s.	213294·02*	23278·00

n.s.—not significant
* Significant at 1 per cent level

From the relative positions in Fig. 1, it could be seen that clusters II, VI, VIII and IX were close together while clusters, X, XI and XIII were close to each other. The position of cluster IX indicated its affinity with clusters

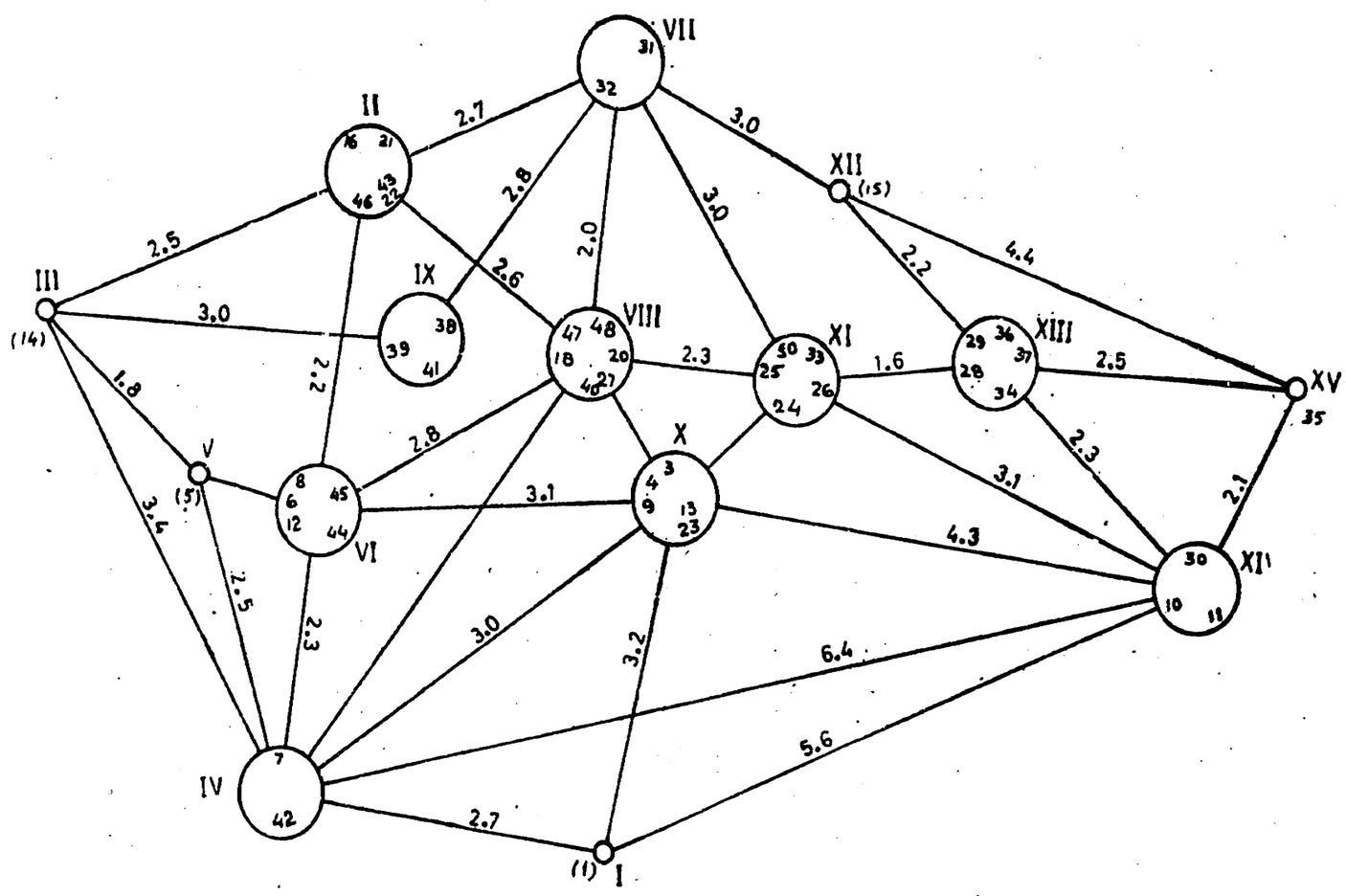

FIG. 1. Genetic divergence in some species of *Eu-Sorghum*

TABLE III

Common dispersion matrix of the ten characters in Sorghum

	Growth rate	Days to flower	Panicle length	Number of primaries	Length of primaries	Angle of primaries	No. of secon-daries	Distance between whorls	Distance within whorls	Number of fertile spikelets
1	18·0	−50·4	+12·1	+12·0	+230·4	+40·6	+5·0	+45·0	−0·5	+177·1
2	—	776·2	+103·5	−16·0	+1806·0	−40·5	+43·5	+14·9	+18·3	+1439·3
3	—	—	180·8	+90·3	+1968·0	+126·3	+107·2	+486·4	+21·7	++679·6
4	—	—	—	407·3	+1652·4	−30·5	+102·9	+1173·9	−20·4	+670·6
5	—	—	—	—	37283·0	+2317·9	+1927·7	+7569·2	+173·2	+9023·3
6	—	—	—	—	—	4455·7	+104·0	+894·6	+39·4	+2324·3
7	—	—	—	—	—	—	291·6	+573·4	+21·5	+1472·5
8	—	—	—	—	—	—	—	5450·3	−53·1	+4274·9
9	—	—	—	—	—	—	—	—	32·1	+109·9
10	—	—	—	—	—	—	—	—	—	23278·0

TABLE IV

Mean values uncorrelated standardized variables of the 46 populations for ten characters in Sorghum

	y_1	y_2	y_3	y_4	y_5	y_6	y_7	y_8	y_9	y_{10}
1	+17·14	+30·81	+13·98	−1·89	−22·72	+34·98	+12·53	−2·81	−11·82	−85·65
3	+18·60	+33·37	+0·65	+6·44	−24·92	+14·39	+17·94	−4·53	+4·03	−97·59
4	+21·95	+21·45	+1·59	+5·86	−23·56	+14·10	+16·82	−3·00	+2·98	−95·99
5	+9·78	+21·84	+4·02	−0·33	−16·76	+9·22	+11·70	+3·30	+1·31	−60·01
6	+10·03	+23·77	+5·63	+0·57	−15·02	+13·73	+11·52	+5·67	−0·55	−68·36
7	+15·04	+28·60	+18·03	−4·90	−18·36	+17·59	+7·62	+5·15	−5·05	−70·35
8	+8·85	+25·58	+5·05	−0·17	−12·82	+15·72	+10·80	+5·10	−0·85	−65·39
9	+12·85	+30·68	+2·74	+5·44	−18·58	+10·88	+14·94	+1.38	−0·89	−84·97
10	+5·84	+49·83	−5·03	+8·51	−28·15	+14·22	+18·60	+3·24	+0·72	−117·74
11	+7·55	+53·76	−8·69	+8·23	−28·63	+16·30	+22·58	+2·52	+0·34	−126·45
12	+12·06	+31·21	+7·99	+5·16	−14·15	+8·93	+9·63	+1·62	+0·98	−66·14
13	+17·43	+28·40	+3·58	+10·49	−15·18	+13·21	+18·39	−3·70	+1·04	−87·03
14	+7·32	+23·67	+8·23	+9·52	−9·56	+8·70	+6·56	−1·61	+0·40	−49·77
15	+7·65	+45·29	−4·61	+9·41	−15·89	+10·30	+19·99	−6·17	−0·51	−89·45
16	+6·73	+24·00	+0·69	+9·50	−15·96	+20·20	+14·01	−12·13	+6·41	−68·71
18	+13·09	+29·97	−3·28	+10·08	−17·69	+11·39	+16·24	−6·93	+6·98	−77·60
20	+15·04	+28·23	−2·24	+8·39	−19·44	+15·66	+10·81	−1·23	+3·90	−75·68
21	+4·92	+26·36	+5·01	+18·02	−16·56	+14·00	+14·65	−11·78	+4·61	−62·32
22	+5·05	+27·25	+4·12	+19·07	−17·00	+11·96	+13·20	−17·27	+7·38	−68·29
23	+10·25	+29·95	+3·38	+7·64	−21·08	+11·82	+17·86	+0·85	+0·15	−81·97
24	+9·35	+40·59	−1·28	+10·35	−24·39	+11·37	+19·35	−3·21	−1·12	−96·58
25	+11·54	+38·92	−2·43	+7·79	−26·10	+10·52	+19·53	−1·54	−0·04	−98·79
26	+6·10	+44·49	−6·65	+8·63	−21·07	+11·07	+18·02	+0·43	+1·35	−101·88
27	+17·21	+28·38	−0·95	+7·74	−20·26	+18·29	+17·34	−8·95	+7·41	−86·74
28	+9·96	+47·35	−11·04	+9·92	−26·87	+15·88	+24·67	−4·69	+0·31	−110·22
29	+12·94	+39·26	−13·04	+11·53	−24·48	+12·21	+22·53	−7·81	+3·67	−110·81
30	+9·30	+51·14	−8·63	+11·48	−30·03	+16·70	+22·13	−3·73	+1·55	−120·71
31	+14·33	+29·71	−8·11	+14·34	−20·57	+21·22	+19·75	−20·26	+9·37	−85·72

Population numbers 2, 17, 19 and 49 did not flower

TABLE IV—(*concld.*)

Mean values uncorrelated standardized variables of the 46 populations for ten characters in Sorghum

	y_1	y_2	y_3	y_4	y_5	y_6	y_7	y_8	y_9	y_{10}
32	+17·42	+29·52	−8·79	+13·75	−21·70	+19·82	+14·18	−18·08	+10·49	−76·43
33	+14·03	+33·90	−10·55	+11·79	−21·84	+14·37	+21·41	−12·46	+5·63	−97·71
34	+10·33	+42·25	−8·16	+12·71	−24·33	+16·41	+22·84	−6·99	+1·26	−103·74
35	+8·46	+50·03	−18·00	+15·31	−28·94	+17·78	+26·50	−12·45	+5·08	−125·73
36	+10·39	+43·02	−9·94	+10·78	−26·78	+13·90	+23·50	−8·27	+2·32	−104·47
37	+10·40	+41·64	−8·54	+11·79	−23·87	+17·20	+23·75	−8·78	+1·15	−100·50
38	+16·06	+30·48	+4·14	+10·28	−21·79	+10·50	+14·10	−1·69	−0·31	−82·99
39	+13·13	+25·77	+1·86	+6·72	−14·92	+8·18	+14·21	−0·64	+5·44	−71·97
40	+23·73	+33·31	−0·44	+5·53	−23·50	+8·05	+16·86	−4·04	+7·07	−88·93
41	+8·20	+25·23	+2·60	+11·33	−17·43	+9·97	+13·28	−9·49	+5·06	−66·43
42	+15·77	+29·37	+14·46	+1·52	−10·20	+16·50	+8·87	+8·92	−6·77	−78·07
43	+4·87	+27·02	+4·43	+16·68	−17·21	+11·01	+13·49	−12·89	+4·71	−62·89
44	+5·01	+26·49	+5·24	+10·33	−14·41	+11·41	+14·74	−2·27	+1·88	−62·63
45	+9·59	+26·34	+3·30	+5·38	−19·10	+9·25	+15·28	−2·83	+6·97	−60·56
46	+8·13	+27·89	−0·84	+6·65	−20·06	+13·43	+15·89	−6·00	+7·08	−69·29
47	+14·54	+30·03	−5·37	+9·26	−20·81	+14·26	+16·90	−7·18	+5·67	−86·83
48	+16·19	+29·87	−5·12	+8·59	−21·95	+14·37	+16·18	−6·60	+7·47	−85·13
50	+14·15	+33·45	−4·32	+9·32	−20·91	+11·85	+17·98	−3·79	+4·33	−96·09

Population numbers 2, 17, 19 and 49 did not flower

TABLE V

Intra- and inter-cluster average D^2 values

Cluster No.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
I	—	18·88	26·48	7·36	18·04	15·00	17·89	12·77	14·31	10·12	15·97	16·39	21·14	31·01	42·80
		(4·35)	(5·15)	(2·71)	(4·24)	(3·87)	(4·23)	(3·57)	(3·78)	(3·18)	(4.00)	(4·05)	(4·60)	(5·57)	(6·54)
II		1·78	6·34	12·45	6·29	4·76	7·22	6·76	4·04	10·71	16·27	13·88	24·65	44·37	50·36
		(1·38)	(2·52)	(3·52)	(2·51)	(2·18)	(2·69)	(2·60)	(2·01)	(3·27)	(4·03)	(3·73)	(4·97)	(6·66)	(7·10)
III				11·41	3·33	4·27	22·03	17·45	8·85	20·85	31·85	24·52	39·15	68·69	81·83
				(3·38)	(1·82)	(2·07)	(4·69)	(4·18)	(2·98)	(4·57)	(5·64)	(4·95)	(6·26)	(8·29)	(9·26)
IV				2·01	6·32	5·42	22·15	10·98	7·75	9·01	17·99	15·57	27·92	40·63	56·78
				(1·41)	(2·51)	(2·23)	(4·71)	(3·31)	(2·78)	(3·00)	(4·24)	(3·97)	(5·41)	(6·37)	(7·54)
V						1·49	16·93	10·18	4·84	12·22	21·66	17·55	32·79	52·38	65·50
						(1·22)	(4·11)	(3·19)	(2·20)	(3·50)	(4·65)	(4·19)	(5·73)	(7·24)	(8·09)
VI						2·05	13·56	7·79	3·53	9·35	16·92	11·60	26·94	44·60	55·51
						(1·43)	(3·68)	(2·79)	(1·88)	(3·06)	(4·11)	(3·41)	(5·19)	(6·68)	(7·45)
VII							1·37	4·16	7·69	7·92	9·08	8·73	11·93	28·70	28·21
							(1·17)	(2·04)	(2·77)	(2·82)	(3·01)	(2·96)	(3·45)	(5·36)	(5·31)
VIII								1·70	3·65	2·77	5·16	5·27	9·56	23·07	30·19
								(1·30)	(1·91)	(1·66)	(2·27)	(2·30)	(3·09)	(4·79)	(5·50)
IX									3·00	5·04	10·28	8·16	17·35	33·11	41·28
									(1·73)	(2·25)	(3·21)	(2·86)	(4·17)	(5·75)	(6·42)
X										2·19	3·97	4·86	8·31	18·67	26·19
										(1·48)	(1·99)	(2·20)	(2·85)	(4·32)	(5·12)
XI											1·70	2·77	2·64	9·39	14·24
											(1·30)	(1·66)	(1·63)	(3·07)	(3·77)
XII													4·91	14·06	18·93
													(2·22)	(3·75)	(4·35)
XIII													0·91	5·04	6·02
													(0·95)	(2·25)	(2·45)
XIV														1·14	4·28
														(1·06)	(2·07)
XV															—
															—

Figures in parentheses are the square roots of the average D^2 values

TABLE VI

Values of the first two canonical vectors in Eu-Sorghum

Canonical vector	Growth rate	Days to flower	Panicle length (cm)	Number of primary branches in panicle	Length of primaries of the panicle (cm)	Angle of primaries of the panicle (°)	Number of secondaries in panicle	Distance between whorls of panicle (cm)	Distance within whorls of panicle (cm)	Number of fertile spikelets
	1	2	3	4	5	6	7	8	9	10
I	−0·0108	−0·3534	0·2642	−0·0623	0·1949	−0·0435	−0·1857	0·0353	0·0022	0·8518
II	0·1035	0·0919	0·4213	−0·4395	0·0297	0·0536	−0·1529	0·6319	−0·3857	−0·1862

VIII and X. Cluster II consisted of the populations belonging to the subseries *Caffra*, while cluster IX had only the species belonging to the subseries *nervosa*. The three species with close resemblance, *S. cernuum*, *S. subglabrescens* and *S. membranaceum*, entered cluster XIII. Populations 1, 14 and 35 appeared to be distinct and occurred in different clusters, I, III and XV respectively which contained one population each and diverged in different directions. The derived *S. virgatum* (population 6) and derived

TABLE VII

Grouping of 46 populations of Sorghum *into 15 clusters*

Cluster	Populations included
I	1, *S. halapense*
II	16, *S. nigricans*; 21, *S. caffrorum*; 22, *S. caffrorum*; 43, *S. caffrorum*; 46, Hegari
III	14, *S. roxburghii*
IV	7, *S. sudanense*; 42, *S. splendidum*
V	5, *S. virgatum*
VI	6, *S. virgatum* (derived); 8, *S. sudanense* (derived); 12, *S. roxburghii*; 44, *S. caffrorum*; 45, Hegari
VII	31, *S. durra*; 32, *S. durra*
VIII	18, *S. caudatum*; 20, *S. caffrorum* (derived); 27, *S. milliforme*; 40, *S. nervosum*; 47, Milo; 48, Milo
IX	38, *S. basutorum*; 39, *S. nervosum*; 41, *S. nervosum*
X	3, *S. arundinaceum*; 4, *S. arundinaceum*; 9, *S. drummondii*; 13, *S. roxburghii*; 23, *S. caffrorum*
XI	24, *S. dochna*; 25, *S. dochna*; 26, *S. bicolor*; 33, *S. durra*; 50, M 35–1
XII	15, *S. roxburghii*
XIII	28, *S. cernuum*; 29, *S. cernuum*; 34, *S. membranaceum*; 36, *S. subglabrascens*; 37, *S. membranaceum*
XIV	10, *S. guineense*; 11, *S. conspicuum*; 30, *S. durra*
XV	35, *S. subglabrascens*

S. sudanense entered cluster VI while their parental species, populations 5 and 7, were found in different clusters, V and IV, respectively. Thus the method was potent enough to separate clearly the derived types from their corresponding parental species. Populations 7 and 42 belonging to two different species, *spontanea* and *sativa* (*nervosa*) respectively, were found together in cluster IV, whereas populations 12, 13, 14 and 15 which are

considered to belong to the same species, *S. roxburghii*, were found distributed among divergent clusters indicating the inadequacy of the criteria used in the previous classifications.

Canonical analysis.—The grouping obtained using D^2-statistic was also confirmed by canonical analysis (Fig. 2). It was significant that the clusters I, III, IV, VII, XIV and XV were distinctly delineated in their positions in the canonical analysis (Fig. 2) similar to their positions in the D^2 analysis (Fig. 1).

A study of the first two canonical vectors revealed that the number of fertile spikelets, flowering time, panicle length and length of primaries of the panicle were important in that order in the major axis of differentiation, while distance between whorls followed by number of primaries, panicle length and distance within whorls were important in the secondary axis of differentiation (Table VI).

The value of the first canonical root was 21737·42, the second 3863·19, while the sum of the remaining eight canonical roots was 3734·48, showing thereby that the first two roots accounted for 87·2 per cent of the total variation, the first root alone accounting for 74·1 per cent. Thus a two-dimensional representation of the varieties in a λ_1-λ_2 graph (Fig. 2) was found adequate.

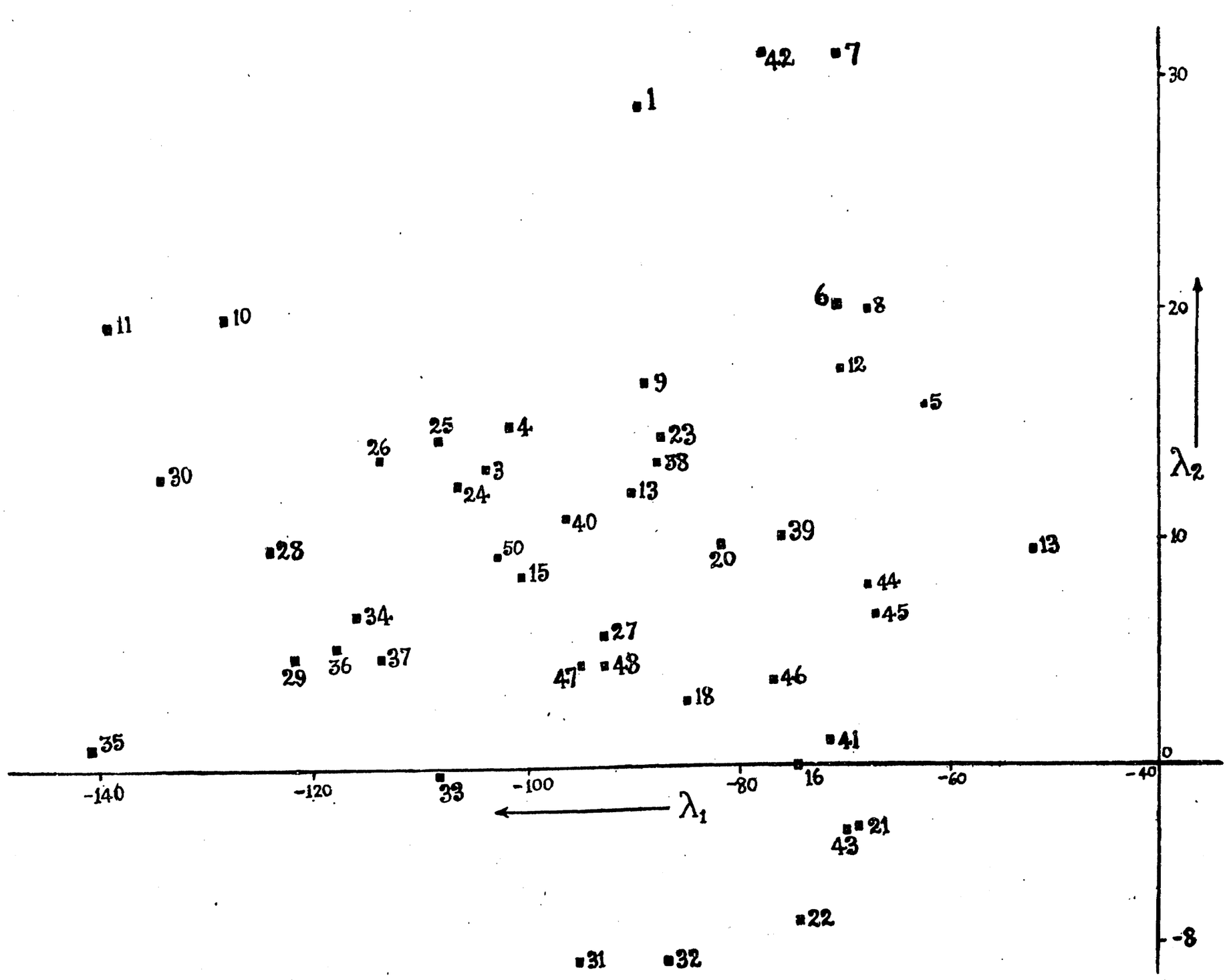

FIG. 2. Canonical analysis of divergence in *Eu-Sorghums*

Discussion

The polyphyletic origin of the genus *Sorghum* (Vavilov 1935) and its varying habit from rhizomatic perennial to annual, lacking root stock, had enriched its variability under natural selection. Superimposed on this, the adaptive capacity of *Sorghums* to the stresses of moisture and temperature under different agro-ecological conditions had further contributed to its genetic diversity under human selection. However, the wide range of races grown by man for the same end production, the diverse agronomical practices (Schwanitz 1959, Darlington 1963) to suit different regions and the mixed cropping pattern (Anderson 1961) associated with cultivated *Sorghum* had kept the so-called species in a flux instead of allowing them to evolve in a direction.

The extent of outbreeding in cultivated *Sorghum* varies from 0·6 to 50 per cent. Consequently, in the absence of well-defined crossability barriers between species, there are innumerable forms in *Eu-Sorghum* ($2n = 20$). Therefore, the classification of the genus has been difficult and controversial (Damon 1962, Grassl 1962, Snowden 1963, Chandrasekhariah and Murty 1964).

Reports about the regular meiosis in the hybrids between species of *Eu-Sorghum* (Garber 1944 and Celarier 1958), lack of any data on the basic species with $n = 5$, which might have given rise to cultivated *Sorghums* (Garber 1950), inadequate knowledge about the role of incomplete gene exchange (Laubscher 1945) and limited information on the role of polyploidy in the evolution of the genus (Magoon and Shambulingappa 1961) had prevented the formulation of an acceptable classification. Recent data on the inheritance of blocks of characters (Damon 1962), the role of structural differences and accumulation of gene mutations (Shambulingappa and Magoon 1963) have not adequately explained the mechanisms responsible for speciation in this sub-genus. The small size of the chromosomes, particularly in *Eu-Sorghums*, had made a study of the chromosomal differentiation very difficult. Moreover, superficial resemblances between chromosomes might not indicate the genetic affinity between species as revealed in *Quercus* and *Crepis* (Stebbins 1950).

The available classifications of *Eu-Sorghum* (Ball 1910, Snowden 1936, 1955 and Webster, personal communication) were based mainly on morphological characters without an indication of the type of their variability and overlapping of characters within species. The classification of Snowden (1936) was based on 2,347 herbarium specimens with differences in sessile spikelet characters as primary criteria. For example, the character spikelet shape was considered to be important in distinguishing primitive types with lanceolate shape from the advanced ones with rhomboid shape. This character was not consistent between populations of the same species. For example,

the shape tended to ovate from lanceolate in *S. virgatum* and *S. sudanense* while they should have been only lanceolate. The lower glume of the sessile spikelet, supposed to be characterized by a transverse wrinkle and depression in *S. cernuum*, was not met with in all its populations. Similar instances, pertaining to other characters used in Snowden's classification, such as panicle density, grain exposure and awning within each species, could be given. Such a variability existing for monogenic or digenic characters (Ayyangar *et al.* 1942) could be due to the free exchange of genes between species.

Moreover, these characters have been described without any quantitative specificity for each class and were subject to different interpretations. Therefore they could not be used to compare data of different workers. The role of these characters in the evolution in the genus has also not been analysed. While reproductive parts could be used as major criteria for classification, there is a possibility to improve such classifications based on herbarium specimens after having an idea of the selection forces in the ecological conditions of the living material and subjecting the material to a quantitative analysis. As stated by Grassl (1962), a majority of workers in *Sorghum* consider *S. vulgare* as the botanical name for all the grain forms. Commercial classifications (Ball 1910 and Webster, personal communication) had also been based on morphological characters like panicle density and seed exposure with the same limitations enumerated above, particularly when considerable variability could be found within species and overlapping between species with respect to such characters. Hence many workers in *Sorghum* (Grassl 1962, Damon 1962, Chandrasekhariah and Murty 1964) including Snowden (1963) have felt the need for reconsideration of *Sorghum* classification. No classification would be satisfactory in such inter-breeding groups unless genetic variability for components of fitness and the response of the populations to natural and human selection had been taken into account.

The broad phylogenetic basis of Snowden's classification was confirmed in this study to some extent in seven out of the 15 clusters, namely I, II, IV, VII, IX, X and XIII. In these seven clusters, grouping was parallel to the relationship within each of the sub-series. For instance, cluster II consisted of populations belonging to sub-series *caffra* and cluster IX consisted of populations belonging to sub-series *nervosa*. Likewise, the cluster XIII comprised *S. cernuum* and *S. subglabrescens* of sub-series *durra* in addition to *S. membranaceum* of sub-series *nervosa*, both closely related.

In the case of the four clusters (IV, VIII, XI and XIV) showing partial agreement, one or two members of the clusters belonged to different series of Snowden. Thus in cluster VI, while *S. caffrorum* and *S. roxburghii* belonged to series *sativa*, the other members were derived from series *spontanea*. However, the series were found to be related although the extent of affinity between them could not be assessed from the diagram by Snowden.

In the other four clusters, there was dispersion of members of the same sub-series into different clusters. For example, the population of *S. roxburghii* occurred in two distinct clusters III and XIII. In cluster XV, one population of *S. subglabrescens* was found separated from its related species.

Although the intra-cluster membership was parallel to that of Snowden's grouping in a majority of the cases, the inter-cluster distances could not be compared with his scheme, since there was no indication of the degree of divergence between species in the diagram postulated by him and only the paths of phylogeny were outlined in his report.

The major differences between Snowden's results and the present study were as follows: The wide divergence among the members within *S. roxburghii*, *S. durra* and *S. subglabrescens* was expected, since they had been cultivated in widely different environments ranging from 14° lat. to 34° lat. in India and probably in similar regions in East Africa. There could be wide differences in the altitudes as in valleys and mountain regions at which *S. roxburghii* has been cultivated. It has been grown for fodder, grain and country beer as a pure crop or in mixture with other crops. It was found to have some genes introgressed from *S. durra* and *S. conspicuum* as revealed by the several intergradations of the panicle characters in its populations found in the tribal areas of Orissa, Madhya Pradesh and Andhra Pradesh and East African regions (Snowden 1936). These factors might have been responsible for the extensive divergence found in this species.

The variation among the populations of *S. durra* was also quite high in both Indian, Ethiopian and other North African collections (Damon 1962). This species could be grown in summer or winter for fodder or grain under irrigated as well as arid conditions as in Rajasthan. It had been subjected to extensive human and natural selection as in the case of *S. roxburghii*. As pointed out by Snowden (1936) himself, there was so much intercrossing in this species that it would be difficult to classify it properly. Damon (1962) found extensive variation in this species in the panicle form from dense-compact to very loose and elongated to very short main axis (3 cm to 30 cm). The situation in *S. subglabrescens* was quite similar to that found in the two species, *S. durra* and *S. roxburghii*. Thus human selection as well as natural selection might have been responsible for the wide divergence within each of the species (Chandrasekhariah and Murty 1964). Introgression between these species and *S. cernuum* would appear to have contributed quite considerably to the high variability within these species. Moreover, the extensive hybridization carried in the U.S.A. between stocks of diverse cultivated species was bound to cause further confusion in the classification of the derived types which were included in one or the other species for simplicity.

The divergence between the forms of *S. caffrorum* was not as large as in the above three species, as revealed by the occurrence of its populations in closely

related clusters. This species was not as widely cultivated in the major *Sorghum* growing tracts of the world as *S. roxburghii*, *S. durra* or *S. subglabrescens*.

The presence of derived *sudanense* and *virgatum* along with *roxburghii* and *Hegari* in the same cluster pointed to the latter being involved in their origin. However, multivariate analysis was potent enough to distinguish them from their parental species, *S. virgatum* and *S. sudanense* respectively. *Hegari*, which was considered to be intermediate between *S. caffrorum* and *S. caudatum*, did not occur in any of the clusters where the two latter species were represented. On the other hand, it occurred with derived fodder types and *S. roxburghii*. This would point to the incongruity of the commercial classification based on empirical criteria.

The position of population 35 (*S. subglabrescens*) in cluster XV was unique. It possessed compact earhead, highly condensed rachis, short primary branches and very closely spaced spikelets resembling *S. durra*. It was also late in flowering, but robust in development. Although its head resembled that of *durra* considerably, its distance from *durra* cluster (VII) was quite large. According to Snowden's scheme, it should belong to *S. subglabrescens* but for its short compact head. It belonged, in the present grouping, to a cluster which was the farthest apart from all the other clusters. Although it appeared to have some panicle characters similar to those of *S. cernuum*, it was slightly apart from that species also. Therefore its origin could be complex.

In cluster VIII, *S. milliforme*, *S. nervosum* and *S. caudatum* were expected together according to the phylogenetic diagram by Snowden (1936). However, the presence of Milo and derived *caffrorum* in this cluster was not expected. The affinity between *S. caudatum* and *S. caffrorum* of sub-series *caffra* might have been responsible for this grouping. The possibility of introgression between *S. durra* and *S. caudatum* in the origin of some Ethiopian types was discussed by Damon (1962). A similar introgression might be responsible for the affinity of members within this cluster.

The two species of *bicoloria* sub-series, *S. bicolor* and *S. dochna*, have occurred in cluster IX along with *S. durra* indicating some affinity between them. However, population 33 of *S. durra* and M 35–1 (population 50) of *S. cernuum* entered the same cluster, although they were not close to *bicoloria* group. Actually these populations did not tally with Snowden's descriptions of *S. durra*, *S. subglabrescens* and *S. cernuum*. Possibly the wide range of variation in these species was not available to Snowden.

The relationship was also indicated between *S. durra*, *S. guineense* and *S. conspicuum*. Introgression could be a potent cause for the presence of *S. durra* in cluster XIV along with *S. conspicuum* and *S. guineense* of *guineensia* sub-series.

The clusters I, III, V, XII and XV contained only one population each. *S. halepense* (cluster I) and *S. virgatum* (cluster V) are wild types distinct

from the rest of the clusters. The other two clusters III and XIII with *roxburghii* represented the diversity of this species as described earlier. The population in cluster III agreed with Snowden's description in having hairs on rachis and spikelets, while the population in cluster XII did not.

Clusters II and IX included populations from sub-series *caffra* and *nervosa* respectively. Clusters XI, XIII and XIV each consisted of populations coming from two different sub-series, *bicoloria* and *durra*, *durra* and *nervosa*, *durra* and *guineensia* respectively. Cluster IV included two populations belonging to different series altogether, namely, *sativa* and *spontanea*. The clusters VI, VIII and X each had populations coming from two sub-series. Cluster VI appeared to consist of only derived types of *S. virgatum*, *S. sudanense*, *S. roxburghii*, *S. caffrorum* and *S. caudatum*. This would mean that some clusters consisted of single species, while others consisted of members belonging to different sub-series or even different series indicating the lack of barriers for gene exchange. Cluster VI, in particular, appeared to give a clear indication of a gene complex derived from different sources.

The role of fodder species in the evolution of grain forms was also evident from this analysis. *S. virgatum* in cluster V occurred close to cluster VI having derived types, cluster III having *S. roxburghii* and cluster VII including *S. sudanense*. The morphology of this population agreed well with Snowden's description and its position was in agreement with Piper's (1915) observation that *S. virgatum* crossed freely with *S. sudanense* and with other cultivated types. However, its relative position (Fig. 1) appeared to be in contradiction with the views of both Piper and Snowden who felt that *S. virgatum* had no affinity with the grain types of cultivated *Sorghum*. The present study had indicated that *S. virgatum* might have played a role in the evolution of grain types, such as those belonging to *S. roxburghii*, as could be seen from the similarity between the earheads of one of the populations of *S. roxburghii* and of the derived *S. virgatum*.

The position of *S. sudanense* (population 7) in cluster IV was in agreement with that of Snowden's phylogenetic diagram which indicated that it was distantly related to *nervosa* group in cluster IX and *bicoloria* group in cluster XI.

The populations 3 and 4 belonging to *S. arundinaceum* were found in cluster X along with populations of *S. drummondii*, *S. roxburghii* and *S. caffrorum*, but not close to cluster XIV having populations of *guineensia* as pointed out by Snowden. The reason for their being not close to *guineensia* might be the fact that these populations under study did not appear to be identical with the representatives of wild *S. arundinaceum*, described by Snowden.

The position of *S. halepense* (cluster I), a rhizomatous type with 40 somatic chromosomes, in not being far away from the other groups, appeared to support the view of other workers (Snowden 1936, Krishnaswamy 1951,

Duara and Stebbins 1952, Bhatti *et al.* 1960) that it contained one genome from *arundinacea* group.

The configuration of clusters obtained in the present investigation would reveal that Snowden's classification could be only partially acceptable even if there were to be barriers of gene exchange between species since the characters chosen by him were simply inherited with parallel variation in different species. The differences between species was not reflected in the reproductive parts only, since the vegetative characters also contributed to population fitness. However, with introgression reported in the subsequent studies on this genus (Celarier 1958 and Damon 1962) and confirmed by the present study, the choice of characters for classification by Snowden does not appear to be adequate. For example, in some of the *cernuums* in the present collection, there was no depression on glumes of sessile spikelets which was considered to be one of the distinguishing features of this species. In the subseries *nervosa* also, the presence of prominent nerves on the lower glume of the sessile spikelet was considered to be an important distinguishing character. Moreover, populations of *S. nervosa* with obscure nerves could also be found. These characters, chosen by Snowden, have been useful in the taxonomy of higher plants with distinct barriers to gene exchange, but would need modification to delineate boundaries of populations with free gene exchange. In such cases, differences between populations have been due to changes in the frequencies of alleles, influencing the reproductive and biological fitness (Dobzhansky 1955). Changes in such gene frequencies would result in changes in the genetic variance in fitness, as measured by the number of successful offspring left by an individual in the next generation. Racial differences have been the compounded effects of such differences between individuals of each population and therefore should be the products of differences in gene frequencies between the populations (Fisher 1930, Crow 1955). Therefore variability for such characters influenced by the genetic system mentioned above should be taken as the major criterion for grouping different populations.

Among the ten characters chosen for the present study, flowering time was an important component of fitness, since photo-periodic sensitivity as found in *Sorghum* and the variable weather conditions such as high rainfall or very dry weather which would reduce the amount of available pollen, could limit the reproductive potential of a population. Growth rate had been an essential contributor for fitness and survival in mixed cropping and different agro-climatological conditions. Characters such as panicle length, number of panicle branches and spikelets directly contributed to the number of offspring. Angle of primaries and condensation of rachis would be important in relation to the extent of damage by the fauna of the area.

Proposed phylogenetic relationship in Eu-Sorghum.—On the basis of available evidence, it would appear that the classification problems encountered

in this group have been mostly due to the inadequate understanding of the evolutionary forces and clear delineation of species boundaries in *Eu-Sorghums*. The proposed interrelationship of the species of *Eu-Sorghum* present in Fig. 4 can be summarized as follows:

S. sudanense considered by Snowden (Fig. 3) to be one of the four primary species in the evolution of the cultivated *Sorghums* would not appear to be so as revealed by its divergence from other species. *S. halepense*, *S. sudanense* and *S. virgatum* appeared quite close together along the boundary of the phylogenetic diagram. The contention of Snowden that *S. virgatum* was not involved in the evolution of cultivated types might not be true, since it was closer to *S. roxburghii* as compared to *S. sudanense* and *S. arundinaceum* which also happened to be grassy species. *S. sudanense* and *S. halepense* were much closer to each other than to *S. arundinaceum* or grain types.

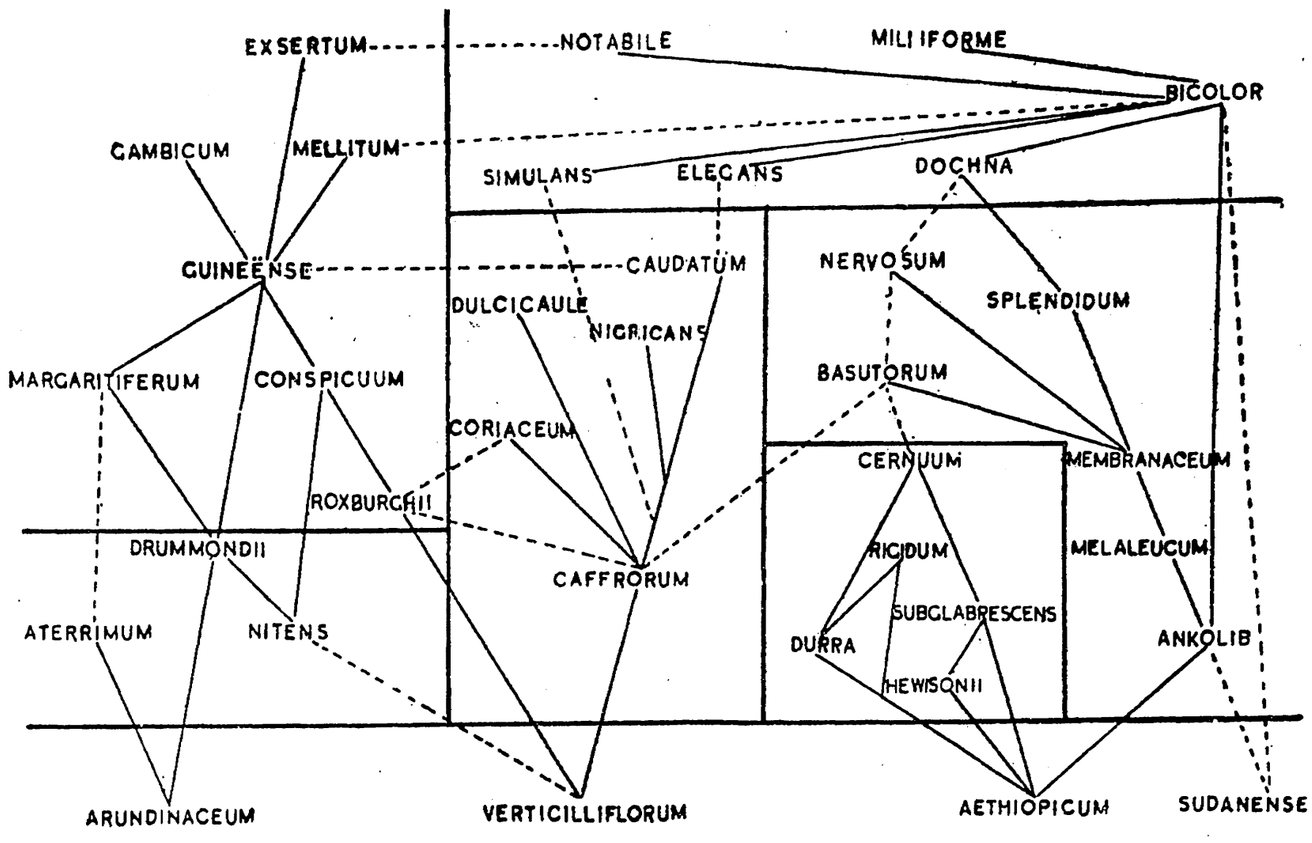

FIG. 3. Diagram illustrating the probable relationships of the wild and cultivated races, Snowden (1936).

The proximity of Milo group with *S. arundinaceum* was another interesting feature. Among the cultivated grain types, Milos, *nervosums* and *caffrorums* were close to each other and different from *S. roxburghii*, *S. durra*, *S. subglabrescens* and *S. conspicuum*. The major cultivated species, *S. roxburghii*, *S. durra*, *S. subglabrescens* and *S. cernuum* occupied four different corners of the diagram, while the grassy types occupied distinctly different positions from these species. *S. caffrorum* occupied intermediate position between *S. roxburghii* and *S. durra*. *S. nervosum* appeared in a similar position in another direction, but closer to Milo and *Feterita*. It is likely that *S. caffrorum* and *S. nervosum* might have developed parallel features, particularly in panicle characters.

S. roxburghii and *S. conspicuum* were the farthest apart and most divergent from each other. Next in the order of divergence are the pairs *S. durra*

and *S. subglabrescens*, *S. durra* and *S. cernuum*, and *S. nervosum* and *S. cernuum*. *S. subglabrescens* and *S. conspicuum*, although distinct in appearance, appeared quite close to each other. *S. cernuum* occupied an intermediate position between *S. durra* and *S. conspicuum*, and *S. durra* and *S. subglabrescens*.

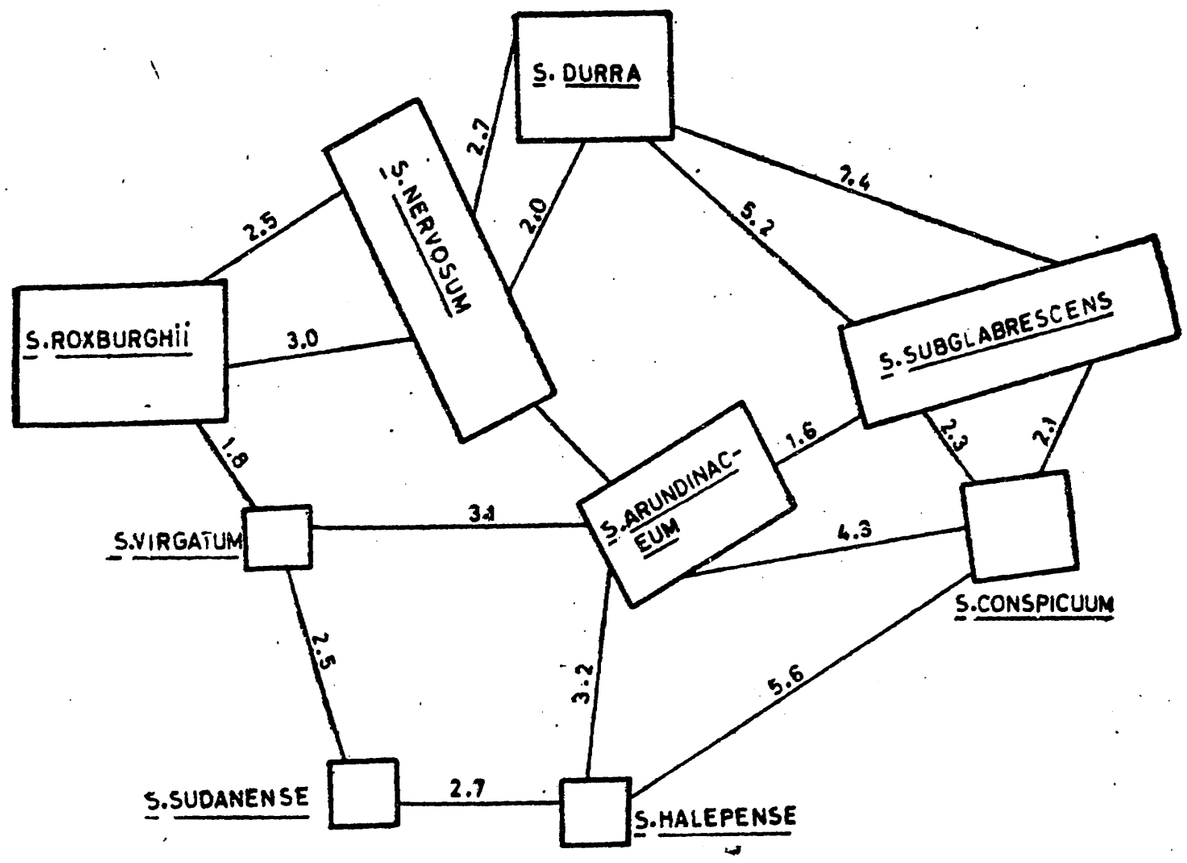

FIG. 4. Interrelationships between the different gene complexes in *Eu-Sorghum*.

On the above basis it is possible to divide *Eu-Sorghums* into the following major categories, each with a specific rank.

Proposed categories		Species of Snowden and commercial types
1	*S. virgatum*	*S. virgatum*
2	*S. sudanense*	*S. sudanense* and *S. splendidum*
3	*S. arundinaceum*	(*a*) *Arundinaceum* sub-group *S. arundinaceum*, *S. drummondii* and grassy types of *S. roxburghii*
		†(*b*) *Dochna* sub-group *S. dochna* and *S. bicolor*
4	*S. halepense*	*S. halepense*
*5	*S. roxburghii*	All types included in this complex
6	*S. nervosum*	*S. nervosum*, *S. basutorum*, *S. caffrorum*, Milo, *S. nigricans*, *Feterita*, *Hegari*, *S. milliforme* and *S. caudatum*
*7	*S. durra*	All types included in this complex
*8	*S. subglabrescens*	*S. subglabrescens*, *S. cernuum* and *S. membranaceum*
9	*S. conspicuum*	*S. conspicuum* and *S. guineense*

* Indicate complexes with wide range of forms.
† Can be considered for a separate specific rank.

S. splendidum would appear to be related to *S. sudanense* and is separated from the sub-series *nervosa*. *S. dochna* and *S. bicolor* were included under *S. arundinaceum* but could be formed into a sub-group within this category. This sub-group could be considered for a separate specific rank. The intermediate forms between these categories were obviously the products of introgressive hybridization between them. It would appear unnecessary to give a specific rank to most of the species, particularly when their distinctive features are no longer maintained and a plethora of intermediate forms are found in nature as well as under cultivation.

To give specific rank to each of these categories may be questioned by some. However, the following evidence was taken into consideration in suggesting specific rank. *S. roxburghii* had been spatially isolated from other grain types as evident from its distribution in hilly areas and sub-marginal lands. However, its hybrid derivatives with *S. durra, S. caffrorum, S. subglabrescens* and *S. cernuum* were used in evolving useful strains for grains. Temporal isolation was found between the grass species and grain types. Inheritance of blocks of characters in crosses between *durra* group with *S. subglabrescens* and *S. nervosum* categories was an adequate indication of the role of modifier complexes in divergence between them. Therefore they could be given specific ranks.

The inheritance between members within each category was simple. It is likely that, in course of time, with controlled gene exchange they might evolve into new species. At present there is no need to give them a specific rank.

Based on this study, a comprehensive project for the classification of nearly 5,000 lines representing all the species in the genus *Sorghum* is now under way. utilizing multivariate analysis for regrouping the material. It is expected that a wider grouping into categories and types under each of these categories would be done effectively after the above project is completed.

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