Genetical Studies in the Genus *Sorghum*[*]

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Summary. The mode of inheritance of one seedling character and nine mature plant characters has been worked out in detail in the different interspecific crosses in the genus *Sorghum*. The majority of the factor pairs exhibited simple inheritance. However, clear evidence for breakdown of dominance in different genetic backgrounds and data for the presence of 'modifier gene complexes' has also been obtained. The implication of these results to the genetic evolution of the various *Sorghums* species, is critically discussed. Further, the bearing of loci found duplicate with respect to various qualitative characters, has also been considered in relation to the polyploid origin of *Arundinacea Sorghums*. The genetics of the two new variants have been studied and the taxonomic importance of such anomalies is brought out.

It is now an accepted fact that species problems are too complex to be solved by simple herbarium work alone since geographical barriers and ecological isolation over a long period of time, lead to a gradual accumulation of evolutionary changes by mutation and selection. HARLAND (1936), working on the different cotton species, postulated that series of genes in allelomorphic relationships exist even in distantly related species. The gene passes from identical to the allelomorphic state due to accumulation of such evolutionary changes over a long period in geographical isolation. Furthermore, such cases of species alleles when put to genetical tests exhibit differences not only in the mode of distribution of alleles functioning as main genes but also in their modifier complexes. It has been further suggested that Darwinian process of evolution by natural selection, involving mere gene substraction, has probably been the mechanism involved in bringing about genetic changes in the genus *Gossypium*. This process may ultimately lead to the internal biological or cytological barriers which prevent hybridization in distantly placed species. Before this condition is reached, the extent of accumulated differences and the degree of speciation can be determined either by immunological and physiological basis or by suitable genetical tests (VAVILOV, 1950).

The genetical studies presented in this report were undertaken with a view to detect, if any, such different genetic architects in the various *Sorghum* species and assess the true interrelationships between them.

Material and methods

The following interspecific hybrids were used in the present investigation.

1. *S. saccharatum* × *S. durra*
   (E.S. 11608) (C.A. 208)
2. *S. saccharatum* × *S. verticilliflorum*
   (I.S. 2868) (P.I. 153850)
3. *S. verticilliflorum* × *S. caudatum*
   (P.I. 153850) (I.S. 3144)
4. *S. sudanense* × *S. caudatum*
   (P.I. 208578) (I.S. 3144)
5. *S. basutorum* × *S. sudanense*
   (I.S. 3134) (P.I. 208578)
6. 'M.S. Kafir' 60 × *S. guineense*
   (I.S. 1601) (I.S. 1160)
7. *S. melaleucum* × Variant I (multiflorus)
   (P.I. 208708)
8. *S. technicum* × Variant I (multiflorus)
   (P.I. 209792)
9. 'M.S. Kafir' 60 × Variant 2 (Hermaphrodite pedicelled spikelets)
   (I.S. 1601)

Seeds of the various parental species were obtained through the courtesy of the Rockefeller Foundation, Division of Botany, I.A.R.I., New Delhi and were sown in the green house as well as under field conditions for four sowing seasons adopting normal cultural practices. All interspecific crosses were effected under controlled conditions. For the study of awned and awnless condition of sessile spikelets, LAUBSCHER's (1945) method was followed and the exact condition was determined by carefully opening the florets. Dominance of multiflorus variant was determined by opening sessile florets and counting the number of pistils in them. Presence of two or more pistils was considered to be multiflorus condition. For certain qualitative characters where complete dominance was lacking in F_1 generation and gradient in expressivity and penetrance was found in F_2 generation, e.g. multiflorus condition, counting was done first by determining the total number of plants and then deducting the plants exhibiting one parental character (single floret) which could easily be differentiated and thereby determining the proportion of each phenotypic class — single floret and multiflorus (which included all the gradients of multiflorus, double floret or combination of both). Identical procedure was also followed for the study of other characters such as seedling pigmentation, telescope leaf sheath, plant pigmentation and leaf axil pigmentation. Colour of stigma was recorded first at the time of opening of the floret and subsequently also confirmed on their drying. The white stigma turned buff colour on drying whereas the dull white or a very light yellow turned red or brown. Leaf sheaths which were completely covering internodes of the plants were included in telescopic type. Plant having panicle bearing even a single staminate pedicelled spikelet was included in 'staminate pedicelled spikelet class' and the absence of it was treated as 'neuter class'. Simple

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segregation of each character and also joint segregation of combination of characters were worked out by the usual statistical procedures.

Observations

The mode of inheritance of one seedling character and nine matured plant characters has been studied. Several interesting genetic patterns which emerged out as a result of this study are briefly described below.

A. State of dominance and mode of segregation of different characters

(1) Seedling pigmentation: The status of dominance of seedling colour was studied in the four interspecific hybrids and the results are given below in Table 1.

Table 1. *State of dominance of seedling colour in the various hybrids.*

Interspecific hybrids	Parental phenotypes	Phenotype of F_1 hybrids
1. *S. saccharatum* × *S. durra*	Non-pigmented × pigmented	Intermediate
2. 'M. S. Kafir' × *S. guineense*	Non-pigmented × pigmented	Intermediate
3. *S. saccharatum* (I.S. 2868) × *S. verticilliflorum*	Non-pigmented × pigmented	Intermediate
4. *S. basutorum* × *S. sudanense*	Non-pigmented × pigmented	Intermediate

The intermediate intensity of pigmentation in F_1 was found to be a common feature in all the four hybrids. However, in the F_2 generation of individual hybrid, all the plants showing even the slightest pigmentation were grouped under the major phenotypically pigmented class and the plants which were totally white or pale green were considered in non-pigmented category. The data on the frequency of two classes were put to statistical test of goodness of fit of normal Mendelian ratio and the results obtained in the segregating F_2 generation are presented in Table 2.

Table 2. *Mode of segregation of seedling colour in the F_2 generation of various hybrids.*

Hybrids	Segregating ratio	Phenotypic classes		Total	χ^2 value	P
		Pigmented	Non-pigmented			
1. *S. saccharatum* × *S. durra*	3:1	O 363 E 372.00	133 124.00	496 670	0.8709	0.30—0.50
2. 'M. S. Kafir' × × *S. guineense*	15:1	O 621 E 628.13	49 41.87	670	1.2931	0.20—0.30
3. *S. saccharatum* × × *S. verticilliflorum*	15:1	O 619 E 620.63	43 41.37	662	0.0681	0.70—0.80
4. *S. basutorum* × × *S. sudanense*	15:1	O 562 E 569.06	45 37.94	607	1.402	0.20—0.30

O = Observed; E = Expected

(2) Leaf sheath character: Two interspecific crosses between parents possessing contrasting characters have been studied and the data obtained is as given below in Table 3.

Table 3. *State of dominance in F_2 hybrids.*

Hybrids	Parental phenotypes	Phenotype of F_1 hybrid
1. *S. basutorum* × *S. sudanense*	Telescopic × normal	Telescopic
2. 'M. S. Kafir' × *S. guineense*	Telescopic × normal	Telescopic

Mode of segregation of the various phenotypic classes was critically analyzed in F_2 generation of each cross, recording the observations at the heading stage of the crop and the data obtained is presented in Table 4.

Table 4. *Mode of segregation of telescopic and normal leaf-sheath in F_2 generation.*

Hybrid	Segregating ratio	Phenotypes		Total	χ^2 value	P
		Telescopic	Normal			
1. *S. basutorum* × *S. sudanense*	9:7 9:7	O 262 E 264.38	208 205.62	470	0.0488	0.70—0.80
2. 'M. S. Kafir' × *S. guineense*	3:1	O 343 E 351.00	125 117	468	0.7293	0.30—0.50

O = Observed; E = Expected

(3) Leaf axil pigmentation: Sorghum durra possesses light red or purple pigmentation at the axil of leaves. However, such pigments are lacking in *S. saccharatum*. In the cross *S. saccharatum* × *S. durra*, the pigmented condition was found to be intermediate in the F_1 generation and a simple monogenic segregation, having 360 pigmented, 122 non-pigmented giving the χ^2 value 0.0249; with '*P*' between 0.80 and 0.90 was observed in F_2.

(4) Photoperiod sensitivity: In order to determine the mode of inheritance of this character, *S. guineense* (photo-sensitive; this species enters the reproductive phase only during the short-days of winter under Delhi conditions) was crossed with 'M.S. Kafir' (non-sensitive). The F_1 hybrid was found to be short-day sensitive and the typical monogenic segregation for sensitive (339 plants) and non-sensitive (129 plants) was noticed in the F_2 generation (which showed goodness of fit in 3:1 ratio giving the χ^2 value $= 1.6410$ with the '*P*' lying between 0.20 to 0.30).

(5) Stigma colour: The following five crosses between species showing contrasting characters of stigma colour were effected and the nature of dominance observed in the F_1 plants is as given below in Table 5.

An interesting case of dominance was observed in the different cultures of *S. saccharatum*. The accession

Table 5. *State of dominance of stigma colour in* F_1 *generation.*

Hybrids	Parental phenotypes	Phenotype of F_1 hybrid
1. *S. basutorum* × *S. sudanense*	White × yellow	Yellow
2. *S. sudanense* × *S. caudatum*	Yellow × white	Yellow
3. 'M. S. Kafir' × *S. guineense*	White × yellow	Yellow
4. *S. saccharatum* × (E.S. 11608) *S. durra*	Yellow × white	Yellow
5. *S. saccharatum* × *S. verticilliflorum* (I.S. 2868)	White × yellow	White

Table 6. *Mode of segregation of stigma colour in* F_2 *generation.*

Hybrid	Segregating ratio	Phenotype		Total	χ^2 value	P
		Yellow	White			
1. *S. basutorum* × *S. sudanense*	3:1	O 363 E 353.5	107 117.5	470	1.2511	0.20–0.30
2. *S. sudanense* × *S. caudatum*	3:1	O 354 E 346.5	108 115.5	462	0.6494	0.30–0.50
3. 'M. S. Kafir' × *S. guineense*	9:7	O 258 E 263.3	210 204.7	468	0.2393	0.50–0.70
4. *S. saccharatum* × (EC 11608) *S. durra*	9:7	O 271 E 271.1	211 210.9	482	0.0001	above 0.99
5. *S. saccharatum* × (I. S. 2868) *S. verticilliflorum*	3:13	O 79 E 79.1	343 342.9	422	0.0002	0.98–0.99

O = Observed; E = Expected.

Table 7. *Nature of lemma tip in the* F_1 *hybrids.*

Hybrids	Phenotype of the parents	Phenotype of the F_1 hybrid
1. *S. basutorum* × *S. sudanense*	Awnless × Awned	Awned
2. *S. saccharatum* × *S. verticilliflorum*	Awned × Awned	Awned
3. 'M. S. Kafir' × *S. guineense*	Awnless × Awned	Awned
4. *S. sudanense* × *S. caudatum*	Awned × Awnless	Awned

Table 8. *Mode of segregation of the nature of lemma tip in* F_2 *generation.*

Hybrids	Segregating ratio	Phenotypes		Total	χ^2 value	P
		Awned	Awnless			
1. *S. basutorum* × *S. sudanense*	3:1	O 348 E 352.5	122 117.5	470	0.2298	0.50–0.70
2. *S. saccharatum* × *S. verticilliflorum*	15:1	O 392 E 395.6	30 26.4	422	0.5314	0.30–0.50
3. 'M. S. Kafir' × *S. guineense*	15:1	O 430 E 438.8	38 29.2	468	2.792	0.50–0.10
4. *S. sudanense* × *S. caudatum*	?	O 220 E ?	242 ?	462	—	—

O = Observed; E = Expected

number E.C. 11608 showed dominance of its yellow stigma colour over white of *S. durra*. While the accession No. I.S. 2868 exhibited dominance of its white stigma over yellow of *S. verticilliflorum*.

The mode of segregation observed in F_2 generation of these crosses is presented in Table 6.

(6) Awned lemma: Mode of inheritance of this character was studied in the four interspecific crosses and the data is given in Table 7.

The data obtained in F_2 generation is given in Table 8.

(7) Condition of pedicelled spikelets: Generally, the florets in *Eu-Sorghums* are either staminate or neuter. In the former condition, normally the apical florets of terminal whorls of panicle branches only show the staminate nature, while the rest of them are neuter. Besides, a hermaphrodite pedicelled spikelet variant selected from the variety Ramkel, was also used in the present study.

Any pedicelled spikelet on the whole panicle, showing anther development was considered in the staminate class. Taking the above criterion as working guide, the status of dominance and mode of inheritance of these characters observed in the various interspecific combinations are presented in Table 9.

Table 9. *State of dominance of pedicellate spikelet condition in inter-specific hybrids.*

Hybrids	Phenotype of the parents	Phenotype of F_1 hybrid
1. *S. sudanense* × *S. caudatum*	Staminate × neuter	Staminate
2. *S. saccharatum* × *S. durra*	Staminate × Neuter	Staminate
3. *S. basutorum* × *S. sudanense*	Neuter × Staminate	Staminate
4. *S. saccharatum* × *S. verticilliflorum*	Staminate × Staminate	Staminate
5. 'M. S. Kafir' × Variant (hermaphrodite)	Neuter × hermaphrodite	Neuter

In the F_2 generation, the segregating ratios obtained for various phenotypic classes are given in Table 10.

(8) Multiflorus condition: A multiflorus variant located in the variety Sheosagar (a twin seeded variety), belonging to the species *S. durra* was crossed onto the single floret species, *S. melaleucum* and *S. technicum*. In the hybrids, the double floret condition was observed in both the crosses and the frequency

Table 10. *Mode of segregation of pedicellate spikelet condition in the F_2 generation.*

Hybrids	Segregating ratio	Phenotypic classes			Total	χ^2 value	P
		Neuter	Staminate	Hermaphrodite			
1. *S. sudanense* × *S. caudatum*	1:3	O 103 E 115.5	359 346.5	— —	462	1.8038	0.10—0.20
2. *S. saccharatum* × *S. durra*	1:3	O 131 E 120.5	351 361.5	— —	482	1.2199	0.20—0.30
3. *S. basutorum* × *S. sudanense*	1:15	O 37 E 29.3	433 440.7	— —	470	2.1112	0.10—0.20
4. *S. saccharatum* × *S. verticilliflorum*	1:15	O 32 E 26.3	390 395.7	— —	422	1.2796	0.20—0.30
5. 'M. S. Kafir' × Variant (hermaphrodite)	49:12:3	O 153 E 151.6	33 37.1	12 9.4	198	1.2696	0.50—0.70

O = Observed; E = Expected

of the various phenotypes in the F_2 generation was found to be as given in Table 11.

Table 11. *Segregation of multiflorus and single floret condition in the F_2 generation.*

Hybrids	Multiflorus (including twin florets)	Single floret	Total	χ^2 value (3:1)	P
1. *S. melaleucum* × variant (multiflorus)	89	34	123	0.4580	0.30—0.50
2. *S. technicum* × variant (multiflorus)	77	23	100	0.2133	0.50—0.70

Pooled $\chi^2 = 0.0373$
$\chi^2 h = 0.6713 - 0.0373 = 0.6340$
P between $= 0.30 - 0.50$
Hence the fit is good.

(9) Glume shape: In the crosses, *S. basutorum* × *S. sudanense* and 'M. S. Kafir' × *S. guineense*, lanceolate shape of glumes of the pollen parent was found to be dominant over the ovate shape of glumes of the pistillate parent. Similarly in a cross, *S. saccharatum* × *S. durra* the obovate condition of the latter was found to be completely dominant over the ovate of the former. The segregation of these crosses is given in Table 12.

Table 12. *Mode of segregation of glume shape in the interspecific hybrid.*

Characters and hybrids	Segregating ratio	Phenotypes		Total	χ^2 value	P
		A	a			
Lanceolate: ovate						
1. *S. basutorum* × *S. sudanense*	3:1	O 344 E 352.5	126 117.5	470	0.8199	0.30—0.50
2. 'M. S. Kafir' × *S. guineense*	3:1	O 348 E 351.0	120 117.0	468	0.1026	0.70—0.80
Obovate: ovate						
3. *S. saccharatum* × *S. durra*	3:1	O 359 E 361.5	123 120.5	348	0.0692	0.70—0.80

O = Observed; E = Expected

B. Studies on independent assortment of the various factors in the different hybrids

1. S. basutorum × S. sudanense

Out of the six qualitative characters studied, five of them were found to be independent and linkage could not be detected between them, as is evident from 2/2 joint segregation given in Table 13.

2. S. saccharatum × S verticilliflorum

(I. S. 2868)

Four qualitative characters have been studied in this hybrid. Of these, the data recorded for the three characters were put to the test of independent assortment as given in Table 14 which revealed the independent assortment of these factors from each other.

3. M.S. Kafir × S. guineense

The segregation of six qualitative characters was studied in F_2. The test of independence performed by working out joint segregation of character combination and then statistically analysing them (Table 15) revealed independent assortment of these factors.

4. S. saccharatum × S. durra

(E.C. 11608)

The mode of inheritance of five characters was studied. The test of independent assortment of four characters was worked out by putting the joint segregation of characters in 2/2 combination to statistical test of goodness of fit (Table 16) which revealed an independent assortment of these factors.

5. S. sudanense × S. caudatum

The inheritance of only three pairs of contrasting characters was studied in this hybrid. Of which the staminate and yellow stigma condition showed dominance over their respective alleles neuter and white stigma and each showed monogenic segregation. However, the segregation in the awned and awnless was found to be difficult to explain on simple Mendelian basis (Table 8). The first two characters showed independent assortment as is evident from the data given in Table 17 below.

Discussion

The genus *Sorghum* offers a wide scope for an extensive analysis of its genetic architecture, as it

Table 13. *Joint segregation of the characters.*

Character combination and joint segregating ratios	Phenotype				Total	χ^2 value	P
	AB	Ab	aB	ab			
Telescopic: normal & staminate: neuter 135:9:105:7	O 241 E 247.8	20 16.5	191 192.8	18 12.8	470	2.9931	0.30—0.50
Telescopic: normal & Yellow: white 27:9:21:7	O 197 E 198.3	65 66.1	166 154.2	42 51.4	470	2.6640	0.30—0.50
Telescopic: normal & awned: awnless 27:9:21:7	O 193 E. 198.3	69 66.1	155 154.2	53 51.4	470	0.3218	0.95—0.98
Telescopic: normal & Lanceolate: ovate 27:9:21:7	O 193 E 198.3	69 66.1	151 154.2	57 51.4	470	0.9444	0.80—0.90
Staminate: neuter & Yellow: white 45:15:3:1	O 335 E 330.5	98 110.2	28 22.0	9 7.3	470	3.3942	0.30—0.50
Staminate: neuter & awned: awnless 45:15:3:1	O 325 E 330.5	108 110.2	23 22.0	14 7.3	470	6.2085	0.10—0.20
Staminate: neuter & lanceolate: ovate 45:15:3:1	O 319 E 330.5	114 110.2	25 22.0	12 7.3	470	3.8845	0.20—0.30
Yellow: white & awned: awnless 9:3:3:1	O 271 E 264.4	92 88.1	77 88.1	30 29.4	470	1.7541	0.50—0.70
Yellow: white & Lanceolate: ovate 9:3:3:1	O 272 E 264.4	91 88.1	72 88.1	35 29.4	470	4.3413	0.20—0.30
Awned: awnless & Lanceolate: ovate 9:3:3:1	O 263 E 264.4	85 88.1	81 88.1	41 29.4	470	5.2946	0.10—0.20

O = Observed; E = Expected

possesses diversified characters, growth habits, relatively low number of chromosomes, high level of compatibility and fertility of interspecific hybrids; abundant pollen and seed production on the hybrid plants. However, despite these advantages unlike maize, genetical studies in this group of plants are indeed very fragmentary (see for review MAGOON, 1964).

Table 14. *Joint segregation ratio of characters.*

Character combinations and joint segregating ratios	Phenotype				Total	χ^2 value	P
	AB	Ab	aB	ab			
Staminate: neuter & white: yellow 195:45:13:3	O 318 E 321.5	72 74.2	25 21.4	7 4.9	422	1.5495	0.50—0.70
Staminate: neuter & awned: awnless 225:15:15:1	O 363 E 370.9	27 24.7	29 24.7	3 1.7	422	2.2238	0.50—0.70
White: yellow & awned: awnless 195:13:45:3	O 318 E 321.4	25 21.4	74 71.2	5 5.0	422	0.6327	0.80—0.90

O = Observed; E = Expected.

1. Seedling pigmentation: Both monogenic and duplicate (polymeric) pattern of inheritance for this character have earlier been reported (see for review, SADASIVAIAH and MAGOON, 1965). In the present study, a simple mono-factorial segregation of purple vs non-pigmented was obtained in the cross *S. saccharatum* × *S. guineense* while the other three crosses (Table 2) showed duplicate factor inheritance giving a segregating ratio 15 pigmented: 1 non-pigmented. As a result of the genetical data, two considerations emerge out. (a) The parents involved in these four crosses, even though they are distantly related according to SNOWDEN's (1936) classification, still show a simple Mendelian inheritance in respect of this character and the genetic disturbance which is a characteristic feature of interspecific hybrids is lacking here. (b) The existence of duplicate factor governing pigmentation in these species also points towards the allo-polyploid origin of these *Eu-Sorghums*. Further 'modifier complexes' for the factor under consideration do not appear to be existing in these species. The results obtained thus point towards the existence of a non-allelic independent duplicate factor (Rs 2) series for colour production parallel with RS 1 factor. In the light of the above findings, the species *S. durra* is homozygous dominant in respect of only one factor and homozygous recessive for others. On the other hand, the species *S. guineense*, *S. verticilliflorum* and *S. sudanense* carry both the dominant factors in their genetic constitution, while *S. saccharatum*, 'M.S. Kafir' and *S. basutorum* are homozygous recessive for both the factors.

2. Nature of leaf sheath: Two interspecific crosses between the species bearing contrasting characters

Table 15. *Joint segregation of characters.*

Character combinations and joint segregating ratio	Phenotypes				Total	χ^2 value	P
	AB	Ab	aB	ab			
Sensitivity: non-sensitivity & lanceolate: ovate 9:3:3:1	O 245	94	103	26	468	4.7218	0.10—0.20
	E 263.2	87.8	87.8	29.2			
Sensitivity: non-sensitivity & awned: awnless 45:3:15:1	O 311	28	119	10	468	4.4452	0.20—0.30
	E 329.1	21.9	109.7	7.3			
Telescopic-normal & lanceolate: ovate 9:3:3:1	O 247	96	101	24	468	4.7217	0.10—0.20
	E 263.2	87.8	87.8	29.2			
Telescopic: normal & awned: awnless 45:3:15:1	O 313	30	117	8	468	4.2993	0.20—0.30
	E 329.1	21.9	109.7	7.3			
Telescopic: normal & yellow: white 27:21:9:7	O 193	150	65	60	468	1.7096	0.50—0.70
	E 197.4	153.6	65.8	51.2			
Lanceolate: ovate & awned: awnless 45:3:15:1	O 323	25	107	13	468	5.0287	0.10—0.20
	E 329.1	21.9	109.7	7.3			
Lanceolate: ovate & yellow: white 27:21:9:7	O 199	149	59	61	468	2.7342	0.30—0.50
	E 197.4	153.6	65.8	51.2			
Awned: awnless & yellow: white 135:105:9:7	O 238	192	20	18	468	3.1938	0.30—0.50
	E 246.8	191.9	16.5	12.8			

O = Observed; E = Expected

Table 16. *Joint segregating ratio of characters in F_2 generation.*

Character combinations and joint segregating ratios	Phenotypes				Total	χ^2 value	P
	AB	Ab	aB	ab			
Pigmented: non-pigmented and staminate: neuter pedicelled spikelets 9:3:3:1	O 272	79	88	43	482	7.0000	0.05—0.10
	E 271.1	90.4	90.4	30.1			
Pigmented: non-pigmented leaf axil and yellow: white stigma 27:21:9:7	O 211	149	60	62	482	3.3457	0.30—0.50
	E 203.3	158.2	67.8	52.7			
Pigmented: non-pigmented leaf axil & obovate: ovate-elliptic glumes 9:3:3:1	O 263	96	97	26	482	1.6441	0.50—0.70
	E 271.1	90.4	90.4	30.1			
Staminate: neuter ped. spikelets & yellow: white stigma 27:21:9:7	O 203	148	68	63	482	2.6585	0.30—0.50
	E 203.3	158.2	67.8	52.7			
Staminate: neuter ped. spikelets and obovate: ovate-elliptic glume 9:3:3:1	E 260	99	91	32	482	1.4006	0.70—0.80
	O 271.1	90.4	90.4	31.1			
Yellow: white stigma & obovate: ovate-elliptic glume 27:9:21:7	O 203	68	156	55	482	0.1294	0.98—0.99
	E 203 .3	67.8	158.2	52.7			

O = Observed; E = Expected

Table 17. *Joint segregation of the characters.*

Character combination and joint segregating ratio	Phenotypes				Total	χ^2 value	P
	AB	Ab	aB	ab			
Staminate: neuter pedicellate spikelets & yellow: white stigma 9:3:3:1	O 277	82	77	26	462	2.7311	0.30—0.50
	E 259.88	86.62	86.62	28.88			

O = Observed; E = Expected.

have been studied viz. (i) *S. basutorum* (telescopic) × *S. sudanense* (normal), (ii) 'M.S. Kafir' (telescopic) × *S. guineense* (normal). The telescopic condition being dominant, a digenic complementary segregation (9 telescopic:7 normal) in the former and a simple monofactorial segregation (3 telescopic:1 normal) in the latter were observed under the uniform condition of planting in the present study.

On the basis of least assumption, such an inheritance may be explained by assuming two complementary dominant factors, both are necessary for bringing telescopic condition but the absence of any one of them will result in normal types. With this assumption the genetic constitution of 'M.S. Kafir' and *S. basutorum* appear to have both the homozygous dominant factors, while *S. guineense* possesses only one dominant factor. However, *S. sudanense* seems to have the double recessive condition.

3. *Leaf axil pigmentation:* A single cross, *S. saccharatum* (non-pigmented) × *S. durra* (pigmented) was studied. In F_1 generation, the pigmented condition was found to be dominant and in the F_2 generation, a single monogenic Mendelian segregation was observed. However, the colour intensity of all the F_2 segregates were showing gradient from plant to plant which suggests that the two species may have a certain modifying gene complex in them, which on differential segregation results in continuous variation.

4. *Photoperiodic response:* The species belonging to the sub-series *Guineensia* are very sensitive to day length and enter the reproductive stage only during the extreme short days of winter and as described by QUINBY and MARTIN (1954) are ultralate. To assess and determine the exact mode of inheritance of this character, a cross combination of *S. guineense* (ultralate) and 'M.S. Kafir' (early) was thoroughly studied. In F_1, the photoperiod sensitivity was completely dominant over non-sensitive condition and a simple monogenic segregation was recorded in F_2 generation.

Recently, a mechanism for commercial utilization of heterosis in *Sorghums* has been discussed on the lines of maize by STEPHENS and HOLLAND (1954) and QUINBY and MARTIN (1954) by exploiting and inducing the cytoplasmic male sterility which involves interaction of 'Kafir' genes upon 'milo' cytoplasm. Hybrid of this variety with the suitable fertility restorer showed about 25% increase in grain and 50% increase in fodder yield in U.S.A. in 1956. However, in India, one of the main *Sorghum* growing countries, such a venture is handicapped by the mere fact that the principle *Sorghum* growing area is limited to the late maturity zone and it has been the experience of *Sorghum* breeders that the hybrids involving 'M.S. Kafir' (early) and good agronomic variety of late tract, resulted in the hybrid of intermediate maturity, which could not outyield the standard cultivars of the late zone. Hence, the factor responsible for photoperiod sensitivity, if suitably incorporated in the pollen donor of the late maturity, holds some promise in such a hybrid seed production programme; and since it simply mendlizes in its inheritance and also is dominant in nature, the work of plant breeders will be made still more easier, in the expansion of hybrid *Sorghum* growing area in India.

5. *Stigma colour:* The stigma colours in *Sorghums* are purple, yellow and white. SIEGLINGER (1933) studied inheritance of stigma colour and due to its association with red grain, explained this as the pleiotropic effect of *R* factor responsible for red grain and yellow stigma colour. LAUBSCHER (1945) noticed that in a cross between Shallu (*S. Roxburghii*) and Blackhull (*S. caffrorum*) yellow stigma colour of the former was dominant and segregated normally in 3:1 ratio in F_2. On the contrary, in a cross between Shallu and Katengu (*S. caudatum*) white stigma colour of the latter was dominant and segregated into 3:1 ratio. He also provided data against pleiotropic effect of *R* gene or yellow stigma colour but he was unable to get data to explain the existence of two types of dominant and recessive yellow in the grain *Sorghums*.

Out of the parents involved in the five cross combinations studied in the present investigation (see Tables 5 and 6), *S. sudanense*, *S. guineense* and *S. saccharatum* (EC 11608) had yellow stigma while the rest of the parents possessed white stigma. In the first four crosses, dominance of yellow over white was observed in F_1 and the characters showed monogenic segregation (3 yellow to 1 white) only in the first two combinations. While digenic complementary ratio (9 yellow to 7 white) was recorded in the subsequent two crosses. However, in the cross between *S. saccharatum* (I.S. 2868) and *S. verticilliflorum* the dominance of white stigma of the former parent was noticed over yellow of *S. verticilliflorum* and in F_2 generation inhibitory factor interaction resulting in 13 white to 3 yellow segregation was realized. The suitable explanation for getting such ratios could be provided on the basis of the following assumptions:

I = Independent dominant factors imparting inhibition in colour development. It is epistatic to all other non-allelic dominant factors concerned in colour production.

Yc and Yp = Two independent non-allelic dominant factors. Together are complementary for producing yellow pigment in the absence of I.

Thus the genotypes and phenotypes of parents, hybrid and F_2 progeny would be as given below:

S. saccharatum × *S. verticilliflorum*
(White — IIycycYpYp) (Yellow — iiYcYcYpYp)

F_1 hybrid
(white IiYcycYpYp)

13 white (I—YpYp)
3 yellow (iiYc—YpYp)

Similarly in the absence of I factor, the 9:7 complementary ratio obtained in the hybrids 'M.S. Kafir' × *S. guineense* and *S. saccharatum* (E.C. 11608) × *S. durra* could be easily explained. Such assumption also appears to be sufficient to explain even the inheritance data reported by LAUBSCHER (1945).

However, all the white segregates in the cross *S. saccharatum* × *S. verticilliflorum* did not show the same brightness but differed in degree. Hence, it is suspected that probably the inhibitory factor (I) is not absolute in its effect of colour suppression and the fact that intensity gradation in brightness of white colour is observed, though to a very little extent, points towards the presence of an 'inhibitory complex' system of modifier genes, rather than a discrete inhibitory unit. However, to further support such an assumption extensive studies involving new material are necessary.

6. Condition of lemma: Awn development and its inheritance have always been contradictory in *Sorghum* literature (see for review SADASIVAIAH and MAGOON, 1965). Of the parental species involved in the four crosses studied, *S. basutorum*, 'M.S. Kafir' and *S. caudatum* were truly awnless while the remaining parents were all having the prominent awn (Table 7). Invariably in all the above crosses awned condition was found to be dominant over awnless with a single factor difference in *S. basutorum* × *S. sudanense* and duplicate factor interaction in the crosses, *S. saccharatum* × *S. verticilliflorum* and 'M.S. Kafir' × *S. guineense.* But the data obtained in the fourth cross, *S. sudanense* × *S. caudatum,* did not lend itself for a satisfactory explanation on the simple Mendelian ratios alone (Table 8). The F_2 data regarding awned condition, however, suggests that (1) the character showed duplicate factor inheritance which points towards the allopolyploid origin of this genus and (2) the segregation exhibited by the hybrid *S. sudanense* × *S. caudatum* is not amenable for easy genetic analysis, which is the characteristic feature of a inter-specific hybrid between the wider species. Such a condition is parallel with the mode of inheritance of 'species alleles' which have acquired different genetic architectures on long separation and accumulation of micromutations in different species.

7. Condition of pedicelled spikelets: This is one of the important characters of classificatory value used in the genus *Sorghum.* Normally staminate or neuter condition is prevalent, however, mutants bearing hermaphrodite conditions are also occasionally found. In the present study, such a variant was recorded in the variety, Ramkel (*S. cernum* var. *orbiculatum* Snowden). Structurally, the pedicelled spikelets are composed of two glumes, covering one lower abortive and upper staminate floret. Many times they are neuter and are represented by glumes enclosing lemma of upper floret only. But when they are staminate they are represented by glumes, lemma, palea, stamens and generally, glumes of lower floret. Occasionally, pistil is also present. In the variant selected in this study, the pistil was functional and consequently seed formation was found, generally in the uppermost florets in the panicle branch.

The inheritance of sex development in pedicelled spikelets has been studied in the five interspecific hybrids (see Tables 9 and 10). Out of the parental species involved, *S. sudanense, S. saccharatum, S. basutorum* and *S. verticilliflorum* possess the staminate pedicelled spikelets while *S. caudatum. S. basutorum* and 'M.S. Kafir' are neuter. Hermaphrodite condition is present in the variant. It could be seen from the data given in table 9 that in the first four interspecific crosses, staminate condition was dominant. In the F_2 generation of the first two crosses single gene difference between staminate and neuter condition was found with the segregating ratio 3 staminate to 1 neuter. But in the subsequent two interspecific crosses duplicate gene interaction with the segregation ratio 15 staminate to 1 neuter was recorded (Table 10).

In the last cross involving neuter and hermaphrodite condition of pedicelled spikelets, neuter condition was dominant in F_1 hybrid which on selfing gave segregating ratio of 49 neuter:12 staminate:3 hermaphrodite in F_2 generation. The plausible genetic explanation has been advanced by assuming the interaction among the factors

I = An inhibitory, independent dominant factor, epistatic to the other two non-allelic dominant factors which are responsible for staminate and hermaphrodite condition.
S = Factor responsible for staminate condition and is epistatic over H (the dominant, non-allelic factor governing hermaphrodite condition).

If the genotypic constitution of the parents is proposed as given in the following scheme, the ratio 49:2:3 could be worked out as follows:

'M.S. Kafir' × Variant (hermaphrodite)
(Neuter)
IISShh iissHH
F_1 (neuter)
IiSsHh
F_2 segregation on selfing.

27 ISH	48 neuter
9 ISh	
9 IsH	
3 Ish	
9 iSH	12 staminate
3 IsH	
3 isH	3 hermaphrodite
1 ish	1 neuter

The above proposition explains the situation well and incidentally shows the independent existence of the factor responsible for hermaphrodite condition, which is dominant in nature over its allele. The occurrence of such a condition can be explained on the basis of the dominant mutation at H locus in the plant of the genetic constitution iisshh (neuter) which probably is the genetic make-up of the variety Ramkel with respect to this character.

Occurrence of spontaneous dominant mutants is very infrequently found in the natural population and are also very rare in the mutants produced by irradiation. LINDSTROM (1941) reported a case of spontaneous dominant mutation 'Teopod' in maize. BRINK and SEN (1931) recorded a case of spontaneous dominant mutation — the ragged leaf character in the same crop. It may, however, be mentioned that the hermaphrodite condition of pedicelled spikelet is very common and is a characteristic feature in some of the allied tribes. Occurrence of this character in the genus *Sorghum* points towards the phylogenetic relationships between these groups. It is likely that in course of evolution and diversification, this factor got suppressed and mutated to recessive condition in the genus *Sorghum,* while it is fully expressed in other tribes. The law of homologous series in the inherited variations proposed by VAVILOV (1950) that the variability within species showed the striking parallelism to the inherited variations of the closely related genera, appears to be clear by yet another instance. During the course of this investigation it was also observed that the expression of sex factors in the staminate and hermaphrodite plants was not complete but a graded expressivity was recorded. It points towards the presence of weak or graded 'inhibitory system' in the plants rather than a single discrete inhibitory unit.

8. Multiflorus condition: Normally in single grained *Sorghums*, the sessile spikelet has one functional and one abortive florets. Often both may develop as is very common in double grained varieties. However, the abnormality reported here is different in its structure in that at the earlier stages of development or at anthesis of flower, 3 to 4 pistils along with lemma of different florets could be detected on dissection of florets. Presence of more than two florets was also evident from the even number of awns in the sessile spikelets. However, at the time of maturity of seed generally twin seeds were found in the basal florets but the apical ones invariably had triplets.

KEMPTON (1913) and STRATTON (1923) described in detail the morphology of twin kernel and connate seeds in *Zea mays* but failed to record triplet seeds, though two functional and one abortive florets were noticed. KARPER (1931) recorded frequent occurrence of twins and occasional formation of triplets in maize and subsequently in yellow and white milo-standard dwarf and extra dwarf varieties of *Sorghums*. Twin seeded (TsTs) condition is of common occurrence in Indian *Sorghums* and is found to be dominant over single seededness and monogenic segregation has been reported (see AYYANGAR, 1938). The law of homologous series expounded by VAVILOV (l.c.) appears to be operating in both the *Sorghums* and *Zea mays* and this condition provides still another example of parallel heritable variation between them.

In the present investigation, the multiflorous condition was found to be incompletely dominant over single floret of *S. melaleucum* and *S. technicum*. However, in F_2 generation of the hybrid the phenotypic class multiflorous were predominantly composed of plants with twin florets. The number of multiflorous plants were exceptionally low. While on the panicles of these plants only a few apical florets exhibited multiflorous condition, all the basal portion had the twin florets only. Hence, it is probable that this condition may be another expression of the twin floret (TsTs) factor only since the full expression of this condition was not recorded in any one of the F_2 generation segregates. It is also likely that the fertilization and development of two early blooming florets may be the cause of suppression of development in other florets of the same spikelet. However, further studies are necessary to arrive at a definite conclusion.

9. Glume shape: Shape, texture, size and surface of the glume have a great classificatory value in the genus *Sorghum* since they appear to be least affected and modified due to the external or internal factors. In the present study, the inheritance of lanceolate and ovate glume shape was studied in the two interspecific crosses viz. *S. basutorum* (ovate) × *S. sudanense* (lanceolate) and 'M.S. Kafir' (ovate) and *S. guineense* (lanceolate). In the F_1 generation complete dominance of lanceolate was noticed. In the F_2 generation a simple monogenic Mendelian segregation 3 lanceolate to 1 ovate was recorded. In another cross involving the species *S. saccharatum* (ovate) and *S. durra* (obovate) the complete dominance of the latter condition was recorded with the monogenic segregation 3 obovate to 1 ovate. Since the cross between obovate and lanceolate was not available, allelic relationships between these factors could not be established.

The disturbed segregation of awned and awnless phenotypes in the cross *S. sudanense* × *S. caudatum* and the breakdown of dominance of yellow stigma in different genetic background as found in the hybrid *S. saccharatum* × *S. verticilliflorum* points towards the different genetical architectures of the alleles and the distant relationships between the species.

The occurrence of duplicate or polymeric factors, as defined by BATESON and thoroughly discussed in several crop plants by TJEBBES (1931), may with certain reservations be taken as an indication of polyploidy. MAGOON and his collaborators have presented evidences based on extensive cytomorphological data, concerning the allopolyploid nature of the 20-chromosome *Sorghums* with a basic chromosome number of n = 5 (MAGOON and SHAMBULINGAPPA, 1962a and b, 1963; MAGOON et al., 1964; MAGOON, 1964 and SADASIVAIAH and MAGOON, 1965). ENDRIZZI and MORGAN (1955) based on their studies of meiosis in the haploid plant of *S. vulgare* and its derivatives, also concluded that there is a duplication of genetic material in this species which would reflect on its allopolyploid nature. However, genetic evidence for the allopolyploid nature of *S. vulgare* appears to be fragmentary. It may be seen that in the present study duplicate factor inheritance was found in three of the ten characters studied. Two cases of complementary gene action, a transition between duplicate and independent status of gene, have also been noticed. Hence, both cytological data as well as the presence of duplicate factors in the genome of *S. vulgare* and other genetical evidence strongly reflect on the allopolyploid nature of 20-chromosome *Sorghums*. It may be expected that more and more duplicate factors may be added on to the list by the future workers which will additionally confirm the present views regarding the nature of ploidy in 20-chromosome *Sorghums*.

Zusammenfassung

Die Vererbungsweise von Merkmalen innerhalb der Gattung *Sorghum* wurde an verschiedenen interspezifischen Kreuzungen eingehend untersucht (1 Samenmerkmal, 9 Merkmale der reifen Pflanze). Die Mehrzahl der Faktorenpaare zeigte einfachen Erbgang. Es ergaben sich jedoch auch klare Beweise für Dominanzverschiebungen in verschiedenem genetischem Milieu und Hinweise auf das Vorliegen von Modifikationsgenen. Die Folgerungen aus diesen Ergebnissen für die genetische Evolution der verschiedenen *Sorghum*-Arten wurden kritisch diskutiert und die Bedeutung der für verschiedene qualitative Merkmale gefundenen polymeren Gene in Beziehung zum polyploiden Ursprung der *Arundinacea*-Sippe von *Sorghum* behandelt. Die Genetik zweier neuer Varianten ist untersucht und die taxonomische Bedeutung derartiger Anomalien dargelegt worden.

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Beiträge zur Vererbung der Mehltauresistenz bei *Malus*

III. Beobachtungen zum Frühselektionsproblem

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Contributions to the heredity of mildew resistance in *Malus*

III. Observations on problems of premature selection

Summary. 1. Over a period of several years mildew infections were observed on apple seedlings in the juvenile and generative phase in order to test the possibility of premature selection against the incidence of such infections.

2. For an evaluation of the young seedlings two methods were employed:

a. Seedlings were evaluated once during the second year of development under favorable greenhouse conditions.

b. Seedlings growing in an outdoor nursery were evaluated over a period of three years.

The results were compared with 5–9 years of observations on mature seedlings grown in the field.

3. Correlation-statistical analyses show that results obtained from observations on seedlings grown in greenhouses are unsuitable, those from nursery-grown seedlings to a certain degree useful for premature selection. After three years of observation in a nursery the number of seedlings can be reduced by 35% without loss of valuable material. However, 50% of the seedlings remaining will have to be destroyed later because of inadequate mildew resistance.

4. For premature selection among field-grown seedlings a climate favorable to mildew infections is necessary during the observational period.

1. Einleitung

Die Reduzierung des Züchtungsmaterials schon im Jugendstadium, also eine frühzeitige Selektion, ist für die arbeits- und zeitaufwendige Obstzüchtung besonders dringend erforderlich. Beziehungen zwischen Sämlingsmerkmalen und wertvollen Frucht- oder Ertragsmerkmalen wurden schon mehrfach gefunden (Loewel, Schander und Hildebrandt 1957, Nybom 1959, Kramer 1962, Stolle 1962, 1964). Noch ungenügend ist jedoch geprüft worden, wieweit sich daraus Methoden für die praktische Frühselektion in der Züchtung ergeben. Eine Frühselektion auf der Basis von Resistenzmerkmalen scheint nicht so problematisch zu sein, da es sich dabei vor allem um Merkmale der vegetativen Organe handelt, das spät eintretende Ertragsstadium also nicht unbedingt zum Vergleich herangezogen werden muß, um einen Sämling als resistent beurteilen zu können. So wurden wiederholt Resistenzmerkmale, wie Frost-, Schorf- und Mehltauresistenz, bei verschiedenen Obstarten auf ihre Eignung zur Frühselektion untersucht (Husfeld 1933, Scherz 1938, Shay, Dayton and Hough 1953, Schander 1958, Mittelstädt 1965 u. a.). Es ist jedoch auch für diese Merkmale nicht leicht, den Anfälligkeitsgrad eines Sämlings schon in der Jugend sicher zu erkennen. Die hohe Variabilität der Befallsstärke, die vor allem durch Witterungseinflüsse oder auch durch das Auftreten neuer Rassen der pilzlichen Schaderreger bedingt ist, erschwert die Methoden der Frühselektion.

Das Naumburger Apfel-Sämlingsmaterial bot Gelegenheit, der Frage nach der Berechtigung zur Frühselektion auf Mehltauresistenz nachzugehen, da für viele Sämlinge Mehltaubewertungen sowohl für das Jugend- als auch für das Ertragsstadium vorhanden sind und diese Werte miteinander verglichen werden konnten. In der Literatur wurde schon mehrfach darauf hingewiesen, daß die Mehltauresistenz junger Apfelsämlinge mit der Resistenz der Elternsorten übereinstimmt (Gollmick 1950, Schander 1958, Brown 1959, Vondráček 1960, Mišić 1964 u. a.), und Schander schließt daraus auf die Berechtigung zur Frühselektion. Aber nicht in allen Fällen sind die Ergebnisse eindeutig. Weiterhin