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Plasmon Diversity in *Eu-Sorghum* - A Barrier to Free Interbreeding *

by

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Introduction: Since the discovery of Cytoplasmic-genic male-sterile system in Milo-Kafir Crosses (Stephens and Holland 1954) many reports of spontaneous occurrence of male steriles in *Sorghum* have been made. (Mital, *et al* 1958; Sreeramulu, 1961; Ganga Prasad Rao, 1962; Cialzeta, 1963 and Hussaini and Venkata Rao, 1964). A comparative study of the plasmon types of diverse origin, was taken up in the present investigation and the results are presented in this paper.

Materials and Methods: Male-sterile Combine Kafir-60 (m. s. C. K. 60) with its maintainer, Combine Kafir–60 (CK. 60) formed the cytoplasmic-genic male-sterile system of American origin. These types come under the species *Sorghum caffrorum* (Beauv) Snowden, (1935, 1936). *Sorghum* type "G. 2-s male sterile" (*S. durra* stapf) with its maintainer G. 1 *(S. durra)* formed the cytoplasmic-genic male-sterile system of Guntur origin. *S. roxburghii* (Stapf) (type A. S. 3880) one of the promising lax panicled type popularly known as 'Shallu', *S. subglabrescens* (Schweinf et Aschers) (Strains Co. 18 and K. 2) two popular *Sorghum* strains with compact panicles, type A. S. 5037, another compact panicled *S. subglabrescens* and *S. dochna* (Forsk) (Strain K. 3), a medium loose panicled strain for the southern region, were utilised for testing their comparative fertility restoration in m. s. C. K. 60 and in G. 2-s.

By effecting suitable crosses and studying the expression of male fertility when the same type of genic combination was brought under the influence of the two kinds of cytoplasm and when different types of genic combinations were brought under the influence of the same kind of cytoplasm, the identity or dissimilarity of the two kinds of cytoplasm was sought to be inferred. The pollen fertility was assessed by stainability in 1:1 glycerine-aceto-carmine and also by the seed set in panicles covered with paper bags before flowering. Micro-sporogenesis was also studied in the male sterile lines by the aceto-carmine smear technique (Smith 1947).

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Results: The anthers of male-sterile Combine Kaffir-60 are shrivelled, seldom contain pollen and do not dehisce to shed pollen. The disintegrated pollen grains which have no contents become agglutinated with the other issues of the anthers and do not stain with 1:1 glycerine-aceto-carmine. The anthers of Combine Kafir-60 are normal which dehisce and bring out numerous well filled pollen grains that stain deep purple with 1:1 glycerine-aceto-carmine. The anthers of G. 2-S look well developed, but do not dehisce and shed pollen. They are however packed with pollen grains all of which are completely devoid of contents and do not get stained with 1:1 glycerine-aceto-carmine. The anthers of isogenic, G. 1 are normal, and similar to those of C. K. 60. Meiosis in m. s. C. K. 60 as observed by Singh and Hadley (1961) as also in the present study proved to be quite normal. Meiosis in male-sterile G. 2-S studied at present also revealed no irregularities. But the contents of the microspores receded away from the walls and finally got lost. The pollen grains retained their round shape and the two walls were distinct.

(a) *Tests for plasmon diversity:* In the hybrid combinations G. 2-S x C. K. 60 *(S. caffrorum)* and m. s. C. K. 60 x G. 1 *(S. durra)* the genotypes are identical while the cytoplasm differed in origin. Initial tests of pollen fertility in these hybrids revealed that all the plants in the former hybrid were pollen sterile of the type G. 2-S with nil seed set in selfed panicles while all the plants in the latter hybrid were fully pollen fertile with full seed set when selfed (Appadurai 1964) (Table. 1). The clue thus obtained was sought to be comfirmed by studying the expression of male-fertility in the following sets of hybrid combinations.

Set (i): Combination G. 2-S x C. K. 60 (male-sterile) was dusted with pollen from C. K. 60. Combination m. s. C. K. 60 x G. 1 was hand emasculated and crossed with C. K. 60. Any difference in the segregation pattern for male-fertility between these two new hybrid generations might be caused only by the difference in the cytoplasm they possessed. All the plants in the hybrid (G. 2-S x C. K. 60) x C. K. 60 were completely pollen sterile, of the G. 2-S type, giving no seed set when selfed. There was segregation for male-fertility in the hybrid (m. s. C. K. 60 x G. 1) x C. K. 60. Thirteen out of thirty one plants were completely pollen fertile, thirteen partially fertile and five were male-sterile, of the m. s. C. K. 60 type. Nineteen plants gave good seed set when selfed, seven plants had partial seed set and five plants had no seed set (Table 1).

Set (ii): G. 2-S was crossed with pollen from the cross m. s. C. K. 60 x G. 1. The cross G. 2-S x C. K. 60 (male sterile) was dusted with pollen from G. 1. As expected, being identical in genotypic

segregation and in cytoplasm, both the crosses behaved similarly and all the plants in both the combinations were pollen sterile of the type G. 2-S giving no seed set when selfed (Table 1).

SET (iii): The combination G. 2-S x C. K. 60 (male sterile) was crossed with pollen from the combination, m. s. C. K. 60 x G. 1. The combination m. s. C. K. 60 x G. 1 was also selfed. Both the hybrid and selfed generations so produced are similar for the nuclear genes, but differ in their cytoplasm. All the plants in the intercross (G. 2-S x C. K. 60) x (m. s. C. K. 60 x G. 1) were male-sterile. Segregation was observed for male-fertility in the selfed generation of the hybrid m. s. C. K. 60 x G. 1 (Table 1a). Ninety seven out of 136 were completely pollen fertile, 35 were partially fertile while four plants were completely male-sterile of the type m. s. C. K. 60. Eighty three plants had full seed set, eight plants had partial seed set, while one plant had no seed set when selfed.

Pollen from hybrid m. s. C. K. 60 x G. 1 was test crossed with m. s. C. K. 60. Fifty two plants in the test cross were completely pollen fertile, 32 were partially fertile while sixteen plants were completely male-sterile of the type m. s. C. K. 60. Thirty two plants had full seed set when selfed, eleven plants had partial seed set and eleven plants had no seed set.

(b) *The inheritance of genes causing fertility restoration by G. 1 (S. durra) in m. s. C. K. 60:* The F1, m. s. C. K. 60 x G. 1 was completely male-fertile indicating the presence of dominant gene for fertility restoration in G. 1. The expected ratio for the F2 was formulated based on the assumption that one dominant major gene restoring complete male-fertility and two partial restorers were segregating for the expression of male-fertility. The observed ratio was accordingly tested for a good fit, with a 48 fully fertile : 15 partially fertile : 1 male sterile ratio, a modified version of the trigenic 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1 ratio. All the phenotypic classes possessing (the dominant major gene for complete fertility restoration) would be fully pollen fertile irrespective of the presence or absence of the partial restorers, making the two double dominant classes (9/64 - 9 64) and one single dominant class (3/64) indistinguishable from the triple dominant class (27/64) forming one single composite fully pollen fertile class forming 48/64 $\frac{(27 - 9 - 9 - 3)}{(\quad 64 \quad)}$ of the total. The rest of the single and double dominant classes forming 15/64 $\frac{(9 - 3 - 3)}{(\quad 64 \quad)}$ of the total would be partially fertile due to the presence of the partial restorers. The genotype which possessed no dominant genes forming 1/64 of the F2 population would be male-sterile. A good fit was obtained, between the observed and expected segregation (Table 2).

TABLE 1. *Comparative study of Cytoplasm from male sterile S. caffrorum–(m. s. C. K. 60) and male sterile S. durra (G. 2-S)*

Nature of population studied		Pollen stainability				Selfed seed set			
		No. of plants				No. of plants			
		F	PF	S	Total	Full	Part	Nil	Total
(a) Tests of plasmon diversity :									
PARENTS :									
m. s. C. K. 60 *(S. caffrorum)*	...	—	—	22	22	—	—	22	22
C. K. 60 *(S. caffrorum)*	...	44	—	—	44	44	—	—	44
G. 2-S *(S. durra)*	...	—	—	120	120	—	—	120	120
G. 1 *(S. durra)*	...	95	—	—	95	95	—	—	95
HYBRIDS : INITIAL TEST :									
male-sterile *S. durra* (G. 2-S) x *S. caffrorum* (C. K. 60)	...	—	—	90	90	—	—	90	90
male-sterile *S. caffrorum* (m. s. C. K. 60) x *S. durra* (G. 1)	...	88	—	—	88	88	—	—	88
SET (i) :									
(male-sterile *S. durra*—G. 2-S x *S. caffrorum*—C. K. 60) x *S. caffrorum*—C. K. 60	...	—	—	11	11	—	—	11	11
(male-sterile *S. caffrorum*—m. s. C. K. 60 x *S. durra*-G. 1) x *S. caffrorum*—C. K. 60	...	13	13	5	31	19	7	5	31
SET (ii) :									
male-sterile *S. durra*—G. 2-S x (male-sterile *S. caffrorum*—m. s. C. K. 60 x *S. durra*-G1)	...	—	—	83	83	—	—	83	83
(male-sterile *S. durra*—G. 2-S x *S. caffrorum*—C. K. 60) x *S. durra*-G. 1	...	—	—	66	66	—	—	66	66
SET (iii) :									
(male-sterile *S. durra*—G. 2-S x *S. caffrorum*—G. K. 60) x (male-sterile *S. caffrorum*—m. s. C. K. 60 x *S. durra*-G. 1	...	—	—	52	52	—	—	52	52
male-sterile *S. caffrorum*—m. s. C. K. 60 x *S. durra*-G1	...	97	35	4	136	83	8	1	92

TABLE 1 *(Contd.)*

Nature of population studied	Pollen stainability				Selfed seed set			
	No. of plants				No. of plants			
	F	PF	S	Total	Full	Part	Nil	Total
(b) Comparative fertility restoration in m. s. C. K. 60 *vs* G. 2-S :								
1. (i) male-sterile *S. caffrorum* (m. s. C. K. 60) × *S. roxburghii* (A. S. 3880) ...	23	1	—	24	24	—	—	24
(ii) male-sterile *S. durra* (G. 2-S) × *S. roxburghii* (A. S. 3880) ...	—	—	48	48	—	—	48	48
2. (i) male-sterile *S. caffrorum* (m. s. C. K. 60) × *S. subglabrescens* (Co. 18) ...	—	32	—	32	32	—	—	32
(ii) male-sterile *S. durra* (G. 2-S) × *S. subglabrescens* (Co. 18)	—	—	21	21	—	—	21	21
3. (i) male-sterile *S. caffrorum* (m. s. C. K. 60) × *S. subglabrescens* (A. S. 5037) ...	—	15	—	15	—	15	—	15
(ii) male-sterile *S. durra* (G. 2-S) × *S. subglabrescens* (A. S. 5037) ...	—	54	—	54	—	54	—	54
4. (i) male-sterile *S. caffrorum* (m. s. C. K. 60) × *S. subglabrescens* (K. 2) ...	—	7	—	7	7	—	—	7
(ii) male-sterile *S. durra* (G. 2-S) × *S. subglabrescens* (K. 3) ...	—	—	29	29	—	—	29	29
5. (i) male-sterile *S. caffrorum* (m. s. C.K. 60) × *S. dochna* (K. 3)...	2	43	—	45	45	—	—	45
(ii) male-sterile *S. durra* (G. 2-S) × *S. dochna* (K. 3) ...	—	16	—	16	—	16	—	16
(c) Study of backcross hybrids with G. 2-S :								
1. (i) [(G. 2-S) × *S. roxburghii* (A. S. 3880)] × *S. roxburghii* (A. S. 3880) (1) B_1 ...	—	—	40	40	—	—	40	40
(ii) [(G. 2-S) × *S. roxburghii* (A. S. 3880)] × *S. roxburghii* (A. S. 3880) (2) B_2 Line 1 ...	—	—	72	72	—	—	72	72
Line 2 ...	—	—	21	21	—	—	21	21
(iii) [(G. 2-S) × *S. roxburghii* (A. S. 3880)] × *S. roxburghii* (A. S. 3880) (3) B_2 ...	—	—	23	23	—	—	23	23

TABLE 1 *(Contd.)*

Nature of population studied	Pollen stainability				Selfed seed set			
	No. of plants				No. of plants			
	F	PF	S	Total	Full	Part	Nil	Total
2. (i) [(G. 2-S) x *S. subglabrescens* (Co. 18)] x *S. subglabrescens* (Co. 18) (1) B_1 ...	—	—	40	40	—	—	40	40
(ii) [(G. 2-S) x *S. subglabrescens* (Co. 18)] x *S. subglabrescens* (Co. 18) (2) B_2 ...	—	—	28	28	—	—	28	28
(iii) [(G. 2-S) x *S. subglabrescens* (Co. 18)] x *S. subglabrescens* (Co. 18) (3) B_3 ...	—	—	26	26	—	—	26	26
3. (i) [(G. 2-S) x *S. subglabrescens* (K. 2)] x *S. subglabrescens* (K. 2) (1) B_1 ...	—	—	21	21	—	—	21	21
4. (i) [(G. 2-S) x *S. caffrorum* (C. K. 60)] x *S. caffrorum* (C. K. 60) (2) B_2 ...	—	—	22	22	—	—	22	22

TABLE 2. *Inheritance of fertility restoration by S. durra (G. 1) in m. s. C. K. 60*

S. No.	The hybrid populations	Pollen stainability				Expected ratio	χ^2	P Between
		No. of plants						
		F	PF.	S.	Total			
1.	m. s. C. K. 60 x *S. durra*—G. 1 (F. 2) ...	97	35	4	136	48 : 15 : 1	2·191	0·30 — 0·50
2.	m. s. C. K. 60 x (m. s. C. K. 60 x *S. durra*—G. 1) test cross ...	52	32	16	100	4 : 3 : 1	1·867	0·30 — 0·50
3.	(m. s. C. K. 60 x *S. durra*—G. 1) x C. K. 60 test cross ...	13	13	5	31	4 : 3 : 1	0·892	0·50 — 0·70

On the above hypothesis the cross of the F1 hybrid (m. s. C. K. 60 x G. 1) with *S. caffrorum* (m. s. C. K. 60 or C. K. 60) should segregate male-sterile plants in 1/8 of its population, 3/8 would be partially fertile, while 4/8 would be completely male-fertile. The observed segregations fitted well, with the expected 4 fertile : 3 partially fertile : 1 sterile ratios. (Table 2)

(c) *Test of fertility restorers of m. s. C. K. 60 in the cytoplasm of G. 2-S male-sterile :* *Sorghum roxburghii* (A. S. 3880) completely restored male-fertility in m. s. C. K. 60, *S. subglabrescens* (Co. 18 and K. 2) and *S. dochna* (K. 3) sufficiently restored fertility to give a full seed set when selfed, while fertility restoration by *S. subglabrescens* (A. S. 5037) was of a very low degree ranging from 4 to 25% of stainable pollen (Appadurai, 1965; 1967). These five types were crossed with G. 2-S and the five different F1s were studied for male-fertility (Table 1. b)

The hybrids G. 2-S x *S. roxburghii* (A S. 3880) and G. 2-S x *S. subglabrescens.* (Co. 18 and K. 2) produced anthers similar to those of G. 2-S male-sterile and none of the pollen grains in them was stainable. There was no seed set in any of the selfed panicles in all the three hybrid combinations. The combinations G. 2-S x *S. subglabrescens* (A. S. 5037) and G. 2-S x *S. dochna* (K. 3) consisted of plants all of which produced a little of stainable pollen. There was partial seed set in the selfed panicles. The seed set ranged from 25 to 85 per cent in G. 2-S x *S. subglabrescens* (A. S. 5037) and from 1 to 10 per cent in G. 2-S x *S. dochna* (K. 3). No plant in any different backcross generations studied under the different crosses proved to be fertile or partially fertile (Table 1. c.).

Discussion : Male sterile *S. caffrorum* (m. s. C. K. 60) originated in the United States of America, while male-sterile *S. durra* (G. 2-S) was of Indian origin. The course of meiosis in m. s. C. K. 60 as well as in G. 2-S was normal, proving that the sterility in both these male-steriles is not due to meiotic break down. However there were differences in the nature of anthers between the two male-sterile types. When identical genic combinations were brought under the influence of the two kinds of cytoplasm (those of m. s. C. K. 60 and G. 2-S) a difference in the expression of male-fertility was observed (Table 1). When similar types of a genic segregations were created in the two types of cytoplasm the expression and segregation for male-fertility differed (Table 1. a). When similar types of genic segregations were made to interact with the same kind of cytoplasm the expression of male-fertility was similar (Table 1. a). It was observed that in all the hybrid combinations where the seed parent was G. 2-S, irrespective of the nature of nuclear genes, all the plants proved to be male-sterile of the G. 2-S type. In combinations where the seed parent was m. s. C. K. 60

there was fertility restoration or segregation for male-fertility depending on the nature of genic segregation. The inheritance of fertility restoration by *S. durra* (G. 1) in m. s. C. K. 60 revealed that while three genes for fertility restoration in m. s. C. K. 60 were present in G. 1 (Table 2) none of them could restore fertility in G. 2-S. A comparative study of fertility restoration in m. s. C. K. 60 and G. 2-S. by five different *Sorghum* types revealed that while all the pollen parents restored male-fertility in m. s. C. K. 60 to a greater or lesser extent giving diverse inheritance patterns for fertility restoration, three of them did not restore fertility in G. 2-S, either in the F1 or in any of the backcross generations and the other two restored only a low level of fertility in G. 2-S (Table 1. b & c).

The above results indicate that the two cytosteriles m. s. C. K. 60 and G. 2-S differ in the type of plasmon they possess. In other words the 'Cytotype' (Yen, 1959) or 'plasmatype' (Jones, 1960) of m. s. C. K. 60 and G. 2-S are not the same. Occurrence of diverse plasmon has been reported in other crops also. Jones (1956), Jones *et al* (1957, 1960) and Briggle (1957) gave evidence that differences in the cytoplasm of maize existed and that the same genomes reached differently in these diverse plasmon. Rhoades (1954) referring to dissimilar effect of specific fertility restorer genes on different sources of sterile cytoplasm in maize suggested that these cytoplasmic mutations might not be identical. Savitsky (1958) observed new sources of cytoplasm in the different races of *Beta vulgaris* which varied in their effects on the degree of male-sterility (Duvick, 1959 and Bhan, 1964). A system of diverse plasmatypes occurs in *Sorghum* also is evident from the results of the present study.

The role of plasmon in genetic differentiation: Stephens and Holland (1954) recognised two types of cytoplasm in *Sorghum*. A third type, that of male-sterile *S. durra* (G. 2-S) was brought to light in the present studies. One plasmatype in *Sorghum* got transformed into another type by the action of mutagen, colchicine (Erichsen and Ross, 1963 a and b). Jones (1951, 1953) suggested that the interaction of the cytoplasm, and geno-type leading to the failure to produce functional gametes in the genera such as *Zea*, *Nicotiana* and *Sorghum* is an early stage in speciation. Sonneborn (1951) observed that "Since changes in either the genes or the cytoplasmic materials of heredity can disturb normal development and since these two components of abnormally interacting combinations are found in nature in other combinations that yield normal development, it follows that in the course of evolution, changes must occur in both the genic and cytoplasmic materials of heredity". Fukasawa (1953, 1955) adduced evidence to show that the male-sterility observed in *Aegilops-Triticum* hybrid was rather due to the disharmonious interaction of the genome from *T. durum* on the

cytoplasm from *Ae-ovata*, than due to chromosomal disturbances. Michaelis (1954) showed that extra-nuclear hereditary elements also, play a role in race differentiation. Stebbins, (1958) suggested that a system of genic and cytoplasmic determiners of sterility could create reproductive isolation and initiate speciation. Laven (1959) and Kitzmiller and Laven (1949) considered that the delimitation of sub-units in *Culex pipens* is based in part upon cytoplasmic factors and offered cytoplasmic mutation as one of the causes of differentiation.

In *Sorghum* the cytoplasm of *S. roxburghii* (A. S. 3880) was found to be similar to that of 'Kafir' *(S. caffrorum)* while that of *S. subglabrescens* (Co. 18), and 'Milo' were found to be sterility inducing, as that of m. s. C. K. 60 (Kafir' genome in 'Milo' cytoplasm; Appadurai 1965). The present study revealed that the genes from *S. durra* (G. 1), *S. roxburghii* (A. S. 3880) and *S. subglabrescens* (Co. 18 and K. 2) interacted normally with the cytoplasm from m. s. C. K. 60. On the other hand, their interaction with the cytoplasm from G. 2-S was defective. Genes that can react normally with G. 2-S were also available in many of the *Sorghum* types studied by Sreeramulu (1961). In the present study *S. subglabrescens* (A. S. 5037) and *S. dochna* (K. 3) possessed genes which were partially defective in their interaction with one cytoplasm from G. 2-S. These evidences agree with the cytoplasm from G. 2-S. These evidences agree with the suggestions proposed by Shambulingappa and Magoon (1963) and Magoon (1964) that cytoplasmic differentiation appeared to have played a significant role in species differentiation in the sub-genus *Eu-Sorghum*.

Summary: Genetic tests comparing the nature of cytoplasm in the two cytosteriles m. s. C. K. 60 and G. 2-S *(S. durra)* revealed that they differed in their plasmatypes. When identical genic combinations were brought under the influence of the two kinds of cytoplasm, as in the crosses, m. s. C. K. 60 x G. 1 *(S. durra)* and G. 2-S x C. K. 60 *(S. caffrorum)*, a difference in the expression of male-sterility was observed.

When similar types of genic segregation were created in the two types of cytoplasm as in the two sets of hybrid populations *viz.*, (1) (G. 2-S x C. K. 60) x C. K. 60 and (m. s. C. K. 60 x G. 1) x C. K. 60 and (2) (G. 2-S x C. K. 60) x (m. s. C. K. 60 x G. 1) and the F_2 of (m. s. C. K. 60 x G. 1) the expression and segregation for male-fertility differed. When similar types of genic segregation were made to interact with the same kind of cytoplasm as in the hybrid populations (G. 2-S x C. K. 60) x G. 1 and G. 2-S x (m. s. C. K. 60 x G. 1), the expression of male-fertility was similar. While three genes for fertility restoration in m. s. C. K. 60 were found to be present in G. 1 *(S. durra)*, the isogenic maintainer of G. 2-S male sterile,

none of them was found to restore fertility in G. 2-S. A comparative study of fertility restoration in the two male steriles by five different *Sorghum* types revealed that while all the pollen parents restored male fertility in m. s. C. K. 60 to a greater or lesser extent, three of them did not restore fertility in G. 2-S and the other two restored only a low level of fertility.

The male sterility brought about by the nucleo-cytoplasmic interaction and the occurrence of diverse plasmon systems as evident from the present studies could be considered as a natural mechanism to prevent free inter-breeding and thereby initiate speciation.

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Dormancy in Seeds and Buds II.*

by

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Dormancy mechanisms: In an attempt to understand the physiological causes underlying dormancy, detailed investigations were carried out during the current century to correlate dormancy with biochemical changes occurring in the dormant organs. In recent years, the emphasis has passed over to a study of the role of endogenous growth regulators in controlling dormancy and a fairly clear picture seems to be emerging now to explain dormancy.

Biochemical changes during dormancy: Low-water-content (as in seeds), accumulation of reserve substances in insoluble form, low rate of respiration, low enzyme activity (particularly oxidative enzymes), less of sugars and soluble organic nitrogen, *etc.*, are found to be generally associated with dormancy. Results obtained by Baijal (1961), working in association with the present author, on physiological changes occurring in potato tubers under cold storage during the rest period, also reveal a similar relationship between dormancy and rate of respiration, activity of catalase and polyphenolase, sugars, *etc.*, however, it was difficult to locate the completion of dormancy from the above studies alone.

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