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Cytogenetic Studies in the Sub-Section *Halepensia* of the Genus *Sorghum**

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Summary. Salient morphological characters of seven interspecific hybrids were studied and compared with their respective parental species. The dominance relationship of several qualitative characters were also determined.

Based on cytological findings from species and species hybrids, the interrelationships among the parental species involved were discussed. The data obtained suggest a closer relationship between *S. almum* and *S. halepense* and also show that *S. miliaceum* and *S. controversum* do not differ from each other nor from *S. halepense*. It is suggested that these *Halepensia Sorghum* varieties are more or less closely related and they may be geographical races of one and the same species. The nature of ploidy of these 40-chromosomed species was determined and the probable role of some 20-chromosomed species in the origin of the former is discussed.

SNOWDEN (1935) classified the section *Eu-Sorghum* into two subsections viz. *Arundinacea* and *Halepensia*. The former is characterized by annual non-rhizomatous forms having somatic chromosome number 20, while the latter is distinguished by perennial wild grasses having well developed rhizomes. All the species within this sub-section have $2n = 40$ chromosomes except one species, *S. propinquum* which has $2n = 20$ chromosomes. SNOWDEN (1955) described the following species under this group; (i) *S. halepense* (widely spread in Mediterranean region, Indo-china and Burma), (ii) *S. controversum* (coastal South East Asia), (iii) *S. miliaceum* (widely spread in India) and (iv) *S. propinquum* (South East Africa, Indonesia and Phillipine Islands). Subsequently, PARODI (1943) and RANDOLPH (1955) added *S. almum* and *S. randolphianum* to this group respectively.

The present investigation was undertaken with a view to throw some light on the interrelationships amongst the 40-chromosomed species included in the sub-section *Halepensia* and a detailed account of the morphological and cytological behaviour of seven interspecific hybrids not subjected to such an analysis before is presented below.

Material and Methods

The material listed below were used in the present investigation:

1. *S. almum* × *S. halepense*
2. *S. almum* × *S. miliaceum*
3. *S. miliaceum* × *S. almum*
4. *S. controversum* × *S. miliaceum*
5. *S. controversum* × *S. almum*
6. *S. halepense* × *S. miliaceum*
7. *S. halepense* × *S. controversum*.

The seeds of various *Sorghum* species used in the present study were obtained through the courtesy of the Rockefeller Foundation, Division of Botany, I.A.R.I., New Delhi. All cross combinations were effected under controlled conditions. The crossed seeds thus obtained were sown in pots in the green house along with the parental species. Salient morphological features of F_1 hybrids were studied and compared with their respective parental species. For meiotic studies the simple propiono-carmine smear technique (see SWAMINATHAN, MAGOON and MEHRA, 1954) was followed.

Results

External morphology of parents and their F_1 hybrids

Comparative morphological studies of the parents and their F_1 hybrids were made laying emphasis on both quantitative as well as qualitative characters (see Table 1). F_1 hybrids were generally intermediate between the two parental species in respect of the metrical characters such as plant height, leaf number, leaf length and breadth. However, in *S. controversum* × *S. miliaceum* and *S. controversum* × *S. almum* tendency towards heterosis was noted for plant height. Similarly, the hybrids such as *S. controversum* × *S. miliaceum*, *S. controversum* × *S. almum* and *S. almum* × *S. halepense* also exhibited heterosis with respect to leaf breadth. The hybrid *S. almum* × *S. miliaceum* and its reciprocal did not exhibit any morphological differences. The profused tillering

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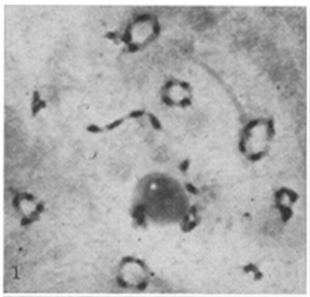
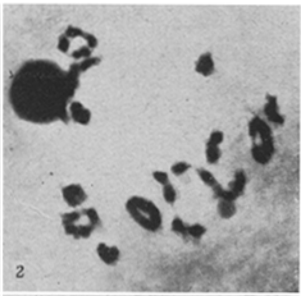
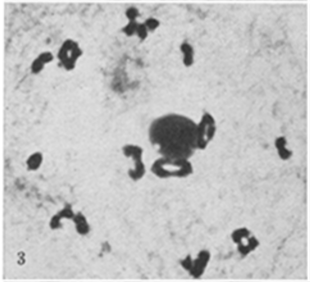
Table 1 *showing morphological characters of the F_1 hybrids and their parents.*

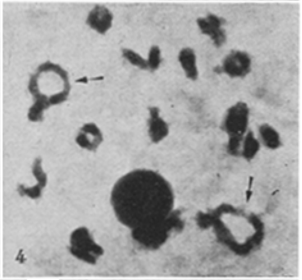
Characters	*S. almum*	*S. almum* × *S. halepense*	*S. halepense*	*S. almum* × *S. miliaceum*	*S. miliaceum*	*S. controversum* × *S. miliaceum*	*S. controversum*	*S. controversum* × *S. almum*	*S. halepense* × *S. miliaceum*	*S. halepense* × *S. controversum*
Plant height (cm)	221.5	215.4	217.4	218.3	223.5	225.6	215.0	227.4	209.7	203.7
Leaf number	16	12.5	14	15.3	17.4	16.3	14	14.3	16.8	13.5
Length of 5th leaf (cms)	64.5	64.8	61.3	61.7	62.5	59.6	65.3	64.2	58.6	57.4
Breadth of 5th leaf (cms)	3.5	3.9	3.3	3.2	3.4	3.5	3.2	3.7	3.2	3.2
Sessile spikelets	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Lanceolate	Ovate-elliptic	Lanceolate	Lanceolate	Lanceolate
Lemma	Awned	Awned	Awned	Awned	Awned	Awned	Awned	Awned	Awned	Awned
Colour of stigma	Yellow	Purple	Purple	Yellow	Yellow	Purple	Purple	Purple	Purple	Purple
Pedicellate spikelets	Staminate	Staminate	Staminate	Staminate	Staminate	Staminate	Staminate	Staminate	Staminate	Staminate
Grain colour	Brown	Brown	Brown	Brown	Brown	Brown	Brown	Brown	Brown	Brown
Grain condition	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed	Enclosed
Average % pollen stainability	80	60	75	72	82	73	85	71	76	77
Seed setting	Good	Moderate	Good	Moderate	Good	Moderate	Good	Moderate	Good	Good

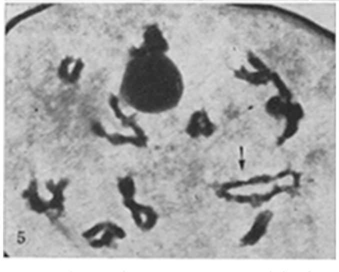
habit present in *S. halepense* and *S. almum* and purple stigma colour of *S. halepense* showed dominance in the F_1 hybrids. Generally, in *S. almum* the colour of the glume turns black at the time of maturity and this character was found to be dominant in the hybrids where *S. almum* is involved as one of the parents. The pollen stainability in parents ranged from 75 to 85% and the seed setting was good in all the species. The hybrids exhibited about 60 to 77% of pollen stainability followed by moderate to good seed setting.











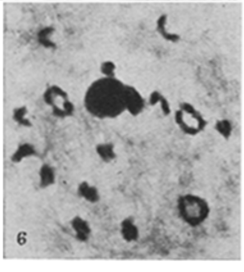


Fig. 1. Diakinesis stage in the F_1 of *S. almum* × *S. halepense* showing more than 5 IV's (× 1000).

Fig. 2. Diakinesis stage in the F_1 of *S. almum* × *S. miliaceum* showing more than 4 IV's (× 1500).

Fig. 3. Diakinesis stage in the F_1 of *S. miliaceum* × *S. almum* showing 4 IV's (× 1250).

Fig. 4. Diakinesis stage in the F_1 of *S. controversum* × *S. miliaceum* showing 2 VI's (↑) (× 1750).

Fig. 5. Diakinesis stage in the F_1 of *S. controversum* × *S. miliaceum* showing a clear hexavalent (↑) (× 1440).

Fig. 6. Diakinesis stage in the F_1 of *S. halepense* × *S. controversum* showing 4 IV's + 12 II's (× 1250).

Cytology of the F_1 hybrids

The spreading of chromosomes at mid-pachytene stage was comparatively poor. However, observations in some analysable cells revealed the presence of certain unpaired, both terminal and interstitial, regions in only a few bivalents.

Diakinesis: The observations obtained on the range and mean frequencies of each of the different chromosome configurations at diakinesis (Figs. 1 to 6) are summarized in Table 2. Generally, quadrivalents ranging from 0—7 were present in *S. almum* × *S. halepense* (Fig. 1). However, in the case of *S. almum* × *S. miliaceum* and its reciprocal; *S. controversum* × *S. almum* and *S. halepense* × *S. miliaceum*, the range of quadrivalents was found to be 1—6 per cell (Figs. 2 and 3). Again, in *S. halepense* × *S. controversum* and *S. controversum* × *S. miliaceum*, the number of quadrivalents per cell ranged from 0—5 and 1—5 respectively (Fig. 6). In addition to quadrivalents, trivalents ranging from 0—1 were noted in *S. almum* × *S. miliaceum* and its reciprocal as well as in *S. halepense* × *S. controversum*. Further, a maximum range of 0—3 trivalents per cell was also observed in *S. controversum* × *S. miliaceum*. However, in the case of *S. almum* × *S. halepense*; *S. controversum* × *S. almum* and *S. halepense* × *S. miliaceum*, trivalents were not usually observed at this stage. Varied number of univalents were also present in all the hybrids except in the case of *S. halepense* × *S. miliaceum* where univalents were not found at diakinesis. Generally, univalents ranging from 0—4 occurred in *S. almum* × *S. miliaceum* and its reciprocal, *S. controversum* × *S. miliaceum* and *S. controversum* × *S. almum*. However, the range of univalents in *S. almum* × *S. halepense* and *S. halepense* × *S. controversum* was found to be 0—2 and 0—3 respectively. It may be pointed out that the maximum chromosome association noted in the present study was only hexavalent as may be seen in the hybrids, *S. controversum* × *S. miliaceum*;

S. halepense × *S. controversum*; *S. controversum* × *S. almum* and *S. halepense* × *S. miliaceum*. The range of hexavalents, however, varied in the different hybrids. Usually 0—1 hexavalent occurred in *S. controversum* × *S. almum* and *S. halepense* × *S. controversum*. Further, hexavalents as high as 0—2 were also noted in the hybrids, *S. controversum* × *S. miliaceum* and *S. halepense* × *S. miliaceum* (Figs. 4 and 5). The data on the average chiasma frequency per cell of these hybrids are given in Table 2.

Metaphase I: The data on the range and the mean frequencies of various types of chromosome configurations noted at this stage (Figs. 7 to 11) are presented in Table 2. Usually, 0—4 and 1—4 IV's per cell were noted in *S. halepense* × *S. controversum* and *S. controversum* × *S. miliaceum* respectively. However, in the case of *S. controversum* × *S. almum* and *S. halepense* × *S. miliaceum*, the range of IV's was 1—5 per cell (Fig. 11). Further, the hybrids, *S. almum* × *S. halepense* and *S. almum* × *S. miliaceum* and its reciprocal had 0—5 IV's per cell (Figs. 7 and 8). Trivalents ranging from 0—1 were noted in *S. almum* × *S. halepense*; *S. almum* × *S. miliaceum* and its reciprocal and *S. halepense* × *S. miliaceum*. However, the range of trivalents was 0—2 in *S. controversum* × *S. miliaceum* and *S. halepense* × *S. controversum* (Fig. 10). Again, the hybrid *S. controversum* × *S. almum* did not show any trivalent at this stage. In addition to these configurations, univalents also occurred with varied frequencies. Usually 0—4 univalents per cell were noted in the hybrids *S. almum* × *S. halepense* and *S. almum* × *S. miliaceum* and its reciprocal and 0—6 per cell were, however, found in *S. controversum* × *S. miliaceum*; *S. controversum* × *S. almum* and *S. halepense* × *S. controversum*. Further, the hybrid, *S. halepense* × *S. miliaceum* had univalents ranging from 0—5. Hexavalents ranging from 0—1 were also observed in all the hybrids under study with the exception of *S. almum* × *S. halepense* and *S. almum* × *S. miliaceum* and its reciprocal (Fig. 9). The mean chiasma frequency per cell was also determined at this stage in the hybrids and the data are given in Table 2.

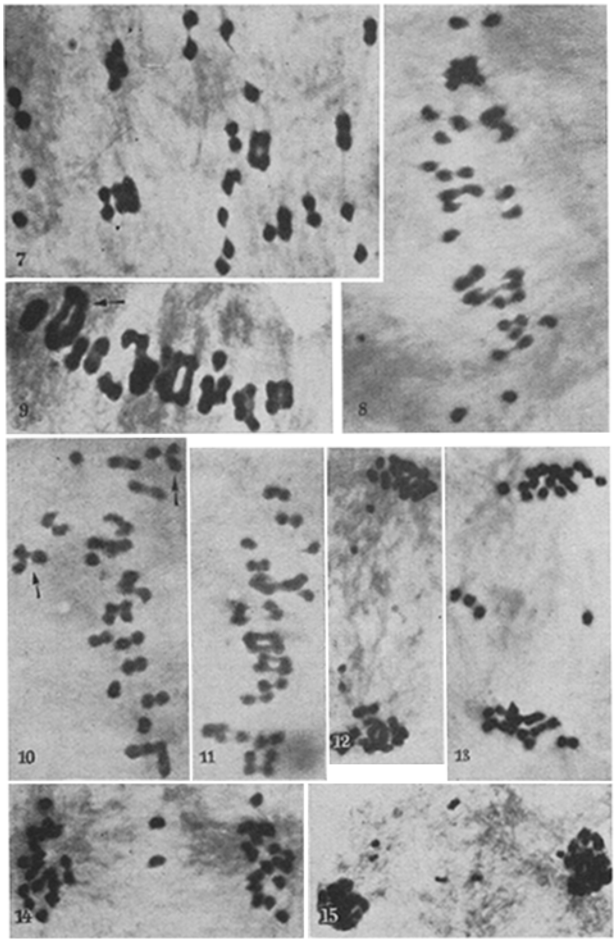


Fig. 7. Metaphase I in the F_1 of *S. almum* × *S. halepense* showing 2 IV's (× 1550).

Fig. 8. Metaphase I in the F_1 of *S. almum* × *S. miliaceum* showing 1 IV (× 1550).

Fig. 9. Metaphase I in the F_1 of *S. controversum* × *S. miliaceum* showing 1 VI (↑) + 4 IV's + 9 II's (× 1500).

Fig. 10. Metaphase I in the F_1 of *S. halepense* × *S. controversum* showing 2 III's (↑) + 3 I's (× 1750).

Fig. 11. Metaphase I in the F_1 of *S. halepense* × *S. miliaceum* showing a maximum of 5 IV's (× 1500).

Figs. 12 and 13. Anaphase I in the F_1 of *S. almum* × *S. halepense* showing division of 2 I's chromosome and laggards respectively (× 1250 and 1300).

Figs. 14 and 15. Anaphase I and telophase I in the F_1 of *S. almum* × *S. miliaceum* showing lagging chromosomes respectively (× 1250 and 1100).

Anaphase I and later stages: Usually normal distribution of 20/20 chromosomes was observed at AI. However, abnormalities such as lagging of 2—4 chromosomes, division of 1—2 univalent chromosomes, delayed separation of 1—2 bivalents etc. were also observed at this stage in about 10 to 12% of the microsporocytes analysed (Figs. 12, 13, 14 and 15). Likewise, a few lagging chromosomes were also observed at AII in about 10—15% of the cells studied in these hybrids. Rarely, micronuclei ranging from 1—4 also occurred at the tetrad stage. The hybrids exhibited about 60 to 77% of pollen stainability. The seed setting was moderate to good.

Table 2 *showing chromosome associations and mean chiasma frequencies per cell in interspecific hybrids.*

Material	2 n	Stage	No. of cells analysed	Range per cell					Mean per cell					Mean chiasma frequency per cell
				I	II	III	IV	VI	I	II	III	IV	VI	
S. almum × *S. halepense*	40	Dia	34	0—2	6—20	—	0—7	—	0.76	13.85	—	2.88	—	36.44 ± 0.336
		MI	30	0—4	10—20	0—1	0—5	—	1.07	15.70	0.07	1.83	—	32.17 ± 0.438
S. almum × *S. miliaceum*	40	Dia	30	0—4	8—18	0—1	1—6	—	0.67	14.37	0.07	2.60	—	37.20 ± 0.246
		MI	37	0—4	10—20	0—1	0—5	—	0.97	15.73	0.11	1.81	—	32.88 ± 0.433
S. controversum × *S. miliaceum*	40	Dia	25	0—4	10—16	0—3	1—5	0—2	0.92	12.10	0.40	2.80	0.40	36.76 ± 0.458
		MI	25	0—6	12—18	0—2	1—4	0—1	0.64	15.74	0.36	2.40	0.20	32.28 ± 0.866
S. controversum × *S. almum*	40	Dia	25	0—4	8—16	—	1—6	0—1	0.92	15.96	—	1.67	0.08	36.48 ± 0.481
		MI	25	0—6	8—18	—	1—5	0—1	1.08	16.13	—	1.60	0.04	30.26 ± 0.560
S. halepense × *S. miliaceum*	40	Dia	40	—	10—16	—	1—6	0—2	—	13.95	—	2.65	0.25	36.65 ± 0.310
		MI	40	0—5	10—18	0—1	1—5	0—1	1.05	15.40	0.05	1.70	0.20	32.75 ± 0.464
S. halepense × *S. controversum*	40	Dia	40	0—3	10—20	0—1	0—5	0—1	0.15	15.10	0.05	2.15	0.15	36.40 ± 0.286
		MI	40	0—6	12—20	0—2	0—4	0—1	0.36	16.20	0.10	1.60	0.15	32.27 ± 0.130

Discussion

Different views have been proposed regarding the origin and nature of ploidy of the species of the subsection *Halepensia* (see for review MAGOON and SHAMBULINGAPPA, 1962a). Microsporogenesis has been studied in the four *Halepensia* species involved in the hybrids used in the present investigation by MAGOON and SHAMBULINGAPPA (1962a). They found that except for the species *S. halepense*, hexavalent formation was almost lacking in other species. In *S. halepense* also the hexavalent formation was very infrequent. In almost all the species, the maximum limit of quadrivalents recorded never exceeded 5 with the exception of *S. almum* where rarely upto 6 IV's were noted at diakinesis. In fact, 3 to 4 IV's were most frequent. Occasionally, as high as 20 II's have also been recorded. These findings support the earlier conclusion of $x = 5$ for this genus drawn on the basis of karyomorphological studies of *Eu-Sorghums* (MAGOON and SHAMBULINGAPPA, 1961, MAGOON *et al.*, 1961 a and 1964). In view of the above, it is probable that one of the two genomes of the parental species involved is common since the maximum number of five quadrivalents have been realized. The occasional hexavalent formation in *S. halepense* may be explained by assuming that the other genome of the species is similar to but not completely identical with this genome and hence may cause occasional segmental allosyndesis between them. The hypothesis of allopolyploidic origin of *S. halepense* (MAGOON *et al.*, 1961 b, MAGOON and SHAMBULINGAPPA, 1962 a and b and 1964) finds support also by the observations of several earlier workers (see for review ENDRIZZI, 1957). The latter author proposed that *S. propinquum* ($2n = 20$) is derived from *S. halepense* ($2n = 40$) and held that *S. halepense* is no doubt allopolyploid since by doubling the chromosome number of non-rhizomatous forms (belonging to the subsection *Arundinacea*) the perennial habit is not incorporated. On the other hand, CASADY and ANDERSON (1952) studied in detail the cytological and genetical behaviour of the hybrid between induced tetraploid sudangrass (*S. sudanense*) and *S. halepense*, where the maximum quadrivalent frequency was found to be 5, of which 4 IV's were most frequent. The genetical segregation of some of the characters was found to be between the ratios expected on the basis of random chromosome and random chromatid segregation. Consequently, they suggested that *S. halepense* is an auto-polyploid. It must, however, be pointed out that such an observation is not sufficient enough to explain the occurrence of rhizome formation in these species. The tetrasomic inheritance can also be possible in the light of the earlier hypothesis of allopolyploid origin where one genome between the two parent species is common. Hence, the genetic factors situated on these genomes are expected to show tetrasomic segregation. However, to draw any definite conclusion on the basis of genetical factors, extensive studies on the mode of inheritance of the various other characters are indeed essential. Even, if the allopolyploid origin of *S. halepense* is taken into consideration, still the origin of rhizome in these forms remains a paradoxical problem and nothing can be said with certainty concerning the rhizome donor parental species at this stage. If one of the genomes of *S. halepense* is considered identical to that of *S. vulgare* (as expressed by HADLEY, 1953), then the other parent must have the rhizome since the non-rhizomatous forms on crossing together followed by doubling the chromosome number can give only the annual habit. MAGOON and SHAMBULINGAPPA (1961) based on karyomorphological data expressed the possibility of *S. propinquum* as being the rhizome donor species in the origin of *S. halepense*. Similar possibility has also been suggested based on geographical data by CELARIER (1958). However, ENDRIZZI (1957) considered *S. propinquum* to have originated as a polyhaploid from *S. halepense*. Such an occurrence, however, is quite inconclusive to throw much light on the progenitor and progeny since there is always a rare probability of getting the complete segregation of the genomes of *S. propinquum* from the *S. halepense* constitution. Even, in the light of the earlier hypothesis of *S. propinquum* being the donor parent there is always a possibility of getting *S. propinquum* like plants as the polyhaploid.

A different view regarding the origin of *S. halepense* has also been proposed by BHATTI *et al.* (1960) wherein the possibility of *S. virgatum* being the rhizome donor, has been expressed. They recorded the occurrence of two plants resembling *S. halepense* in the population of 400 plants obtained in the S_1 generation of the induced tetraploid hybrid between *S. vulgare* × *S. virgatum*. The cytological behaviour of these plants was also found to be the same as is recorded in the normal *S. halepense* species. The origin of rhizome in these segregates have been explained on the basis of the STEBBINS' (1950) suggestion, who on reviewing the literature in the genus *Sorghum* has postulated that doubling of chromosomes number in the annuals with perennial tendency often results in strong perennials. Since *S. virgatum* has got a slight tendency to form rhizome, bears deciduous spikelets and is grassy in habit, it was held as the rhizome donor species in the origin of this group of *Sorghums*.

However, nothing definite would be said about the origin of *S. halepense* at this stage, since BHATTI *et al.* (l. c.) could record only 2 out of 400 segregates in the segregating generation of the tetraploid hybrid. Even, if STEBBINS' (1950) view is considered, then the appearance of rhizome bearing forms in the segregates should have been frequent rather than a rarity. Secondly, the rhizomatous tendency should have been exhibited in the tetraploid parent rather than obtained in the segregating generation. The fact that such a condition was not found in induced tetraploid parent, indicates the possibility of such an occurrence due to mutation rather than polyploid effect. Hence, it is necessary to substantiate such findings by further data.

Regarding the interrelationships amongst the various species in the sub-section *Halepensia*, it may be pointed out that on the basis of cytological data and on the basis of resemblance in morphological features like rhizome formation, spikelet characters, narrow leaves and panicle shape, a close relationship between *S. almum* and *S. halepense* has been suggested (see MAGOON and SHAMBULINGAPPA, 1962 a). From the cross M. S. Kafir × *S. halepense*, ENDRIZZI (1957) reported the occurrence of both 30-chromosomed and 40-chromosomed plants. On raising the F_3 generation of 40-chromosomed hybrid plants, he noticed three plants closely resembling *S. almum*, on the basis of which he considered that *S. almum* might have originated as a result of the fertilization of the unreduced egg of the 20-chromosomed grain *Sorghum* species with the normal gamete of *S. halepense*. From the cytomorphological data presented by MAGOON and SHAMBULINGAPPA (1962 a and b), it seems apparent that the chromosome complement of *S. almum* is composed of genetic material of grain *Sorghum* and *S. halepense*. Besides, both *S. almum* and *S. halepense* appear well distributed in Argentina and it is, therefore, likely that *S. almum* might have arisen as a result of a natural hybridization in that region between *S. halepense* and a 20-chromosomed species of the sub-section *Arundinacea*, probably by the fertilization of an unreduced egg of the latter as stated earlier. In the present investigation, cytomorphological studies of the seven interspecific hybrids were carried out with a view to throw more light on the phylogenetic relationships amongst the different species of this sub-section. Usually heterosis was not exhibited by the hybrid plants. However, pollen stainability and seed setting were slightly reduced. The data obtained on the range and average of the different chromosome associations in the hybrids show, in general, the increase in higher associations like III's, IV's and VI's. Such associations can best be explained by assuming segmental homology between the genomes of the parental species involved in the present study. The data obtained also clearly suggest that out of the four sets of 5 chromosomes each, two sets between the species are identical while the other two are segmentally similar to these sets and hence the frequent occurrence of 5 IV's and occasional hexavalents are found in the hybrids.

The cytological observations on the species (MAGOON and SHAMBULINGAPPA, 1962 a and b, 1964) also show that they do not differ much from each other. However, they carry segmental homology in different genomes in their constitution. It may probably be the reason why the higher associations especially hexavalent formation is sometimes recorded in *S. halepense*. In this species such a segmental homology between the genomes is probably more extensive than in other species and therefore due to the occasional intergenomic pairing between the chromosomes, a tendency towards hexavalent formation is markedly seen in the hybrids where *S. halepense* has been involved as one of the parental species. The data obtained also favour segmental allopolyploid origin of these 40-chromosomed *Halepensia Sorghums*.

In general, the hybrids exhibited comparable values in mean chiasma frequency to those of the parents (unpub. data) both at diakinesis and MI stages. The slight reduction in pollen fertility and seed setting which is generally observed in the hybrids may be attributed to the 'cryptic' structural differences between the hybrid complements, which is likely to occur in the geographically distant species. The preliminary observation on the pachytene analysis of chromosome pairing in these hybrids supports such a suggestion. The cytological behaviour of the interspecific hybrids recorded in the present investigation suggest a closer interrelationship between *S. halepense* and *S. almum* and also shows that the other two species (*S. miliaceum* and *S. controversum*) do not differ much from each other and from *S. halepense* as well. It is likely that they may be geographical races of one and the same species. Thus it must be evident from the data presented above that the *Halepensia Sorghums* are more or less closely related forms.

Zusammenfassung

An 7 interspezifischen Hybriden der Subsection *Halepensia* der Gattung *Sorgum* wurden hervorstechende morphologische Merkmale untersucht und mit denen der betreffenden Elternarten verglichen. Für einige qualitative Merkmale wurden außerdem die Dominanz-Beziehungen festgestellt.

Auf der Grundlage der cytologischen Untersuchung von Arten und Arthybriden wurden die Beziehungen zwischen den jeweiligen Elternarten diskutiert. Die erhaltenen Ergebnisse deuten auf eine engere Verwandtschaft zwischen *S. almum* und *S. halepense* und zeigen weiterhin, daß *S. miliaceum* und *S. controversum* sich nicht voneinander und auch nicht von *S. halepense* unterscheiden. Es wird angenommen, daß diese *Halepensia-Sorgum*-Arten mehr oder weniger eng verwandt und wohl geographische Rassen ein und derselben Art sind.

Die Art der Polyploidie dieser 40chromosomigen Arten wurde bestimmt; die mögliche Rolle einiger 20chromosomiger Arten bei ihrer Entstehung wird besprochen.

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