Sorghum macrospermum* and its Relationship to the Cultivated Species *S. bicolor

Ta-pen Wu

Department of Botany, National Taiwan University,
Taipei, Taiwan, Republic of China

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Sorghums show highly morphological variability and adaptability to different habitats and have differentiated into numerous taxa. The variability and diversity make it to be a heterogeneous genus. Mainly on morphological basis, the general subdivisions of the genus into the following five subgenera are recognized: *Eu-sorghum*, *Chaetosorghum*, *Heterosorghum*, *Para-sorghum* and *Stiposorghum* (Celarier 1959). Of these five subgenera, the former three subgenera form one circle of affinity and the latter two constitute a second circle of affinity (Garber 1950).

Pachytene analyses in species and species hybrids have proved to be very useful in elucidating the probable relationships, origin and nature of ploidy of many species of plants. However, the knowledge of the pachytene karyotype in the genus *Sorghum* is still very limited due partially to the difficulty in getting good preparations for critical analysis of the entire complement. Moreover, such cytological studies have, in the main, been restricted to the agronomically important subgenus *Eu-sorghum*. Very little is known about the karyomorphologies in the other four subgenera which have comparatively little or no economic value.

In recent years, the author serially completed the thorough analyses on pachytene karyotypes of some *Eu-sorghum*, *Para-sorghum* and *Stiposorghum* species (Wu 1979, 1982, 1984, 1987), and made the comparisons among them. The present work deals with the pachytene karyomorphologies and the taxonomic characteristics of *Sorghum macrospermum* and *S. bicolor*, two species included under the subgenera *Chaetosorghum* and *Eu-sorghum* respectively, with a view to ascertain the relationship between the two subgenera. This report on the pachytene chromosome morphology of *S. macrospermum* is believed to be the first such description for this species.

Materials and methods

The materials used in this study are *Sorghum macrospermum* ($2n=40$) and *S. bicolor* ($2n=20$); *S. macrospermum*, an endemic Australian species, is a single species accommodated in the subgenus *Chaetosorghum* and *S. bicolor* belonging to subgenus *Eu-sorghum* is a cultivated sorghum. All plants of the two species were grown at the campus of National Taiwan University, Taipei.

Some major morphological characteristics of the two species were examined and compared. For meiotic study and pachytene analysis, young spikes of these materials were fixed in 3:1 ethanol acetic acid for 24 hours and then transferred to 70 percent ethanol for storage. Pollen mother cell smears were stained with propiono-carmin. Considerable patience and practice are essential for obtaining good preparations of the pachytene chromosomes. Phase contrast optics were used for observations and photomicrography. Measurements of chromosome and heterochromatic lengths for the individual pachytene chromosomes of the two species were obtained mainly from those cells in which all pachytene chromosome pairs could be

traced along all their lengths and the positions of all centromeres were readily detectable. These have totalled up to five cells in *S. macrospermum* and eight in *S. bicolor*. However, some chromosome landmarks were identified not only from pachytene chromosomes of these cells but also from those of other cells, because individual chromosome landmarks were not clearly visible in every cell. According to the morphology of the chromosomes, the karyotypes of the two species were constructed and compared. Frequencies of chromosome associations at diakinesis and metaphase I were scored for the two species.

Sorghum bicolor used as the female parent in this experiment was emasculated and then crossed with *S. macrospermum*, but no seed was obtained from this intersubgeneric hybridization.

Table 1. Morphological characteristics and their measurements in *Sorghum macrospermum* and *S. bicolor*

Characteristic	<i>S. macrospermum</i>	<i>S. bicolor</i>
Callus shape	Obtuse	Obtuse
Callus length (mm)	1.0–1.3	0.5–0.9
Seed shape	Obovoid	Obovoid
Pedicel scar of sessile spikelet	Transverse	Transverse
Sessile spikelet (mm)	9.5–10.5	4.5–5.2
Pedicelled spikelet (mm)	9.0–12.0	5.0–6.0
Sex of pedicelled spikelet	Stamens, lemmas and palea absent, glumes only present.	Staminate or neuter, never lacking lemmas
No. of nerves of lower glume in sessile spikelet	13–17	12–17
No. of nerves of upper glume in sessile spikelet	7–10	7–10
No. of nerves of lower glume in pedicelled spikelet	10–14	9–14
No. of nerves of upper glume in pedicelled spikelet	5–8	10–12
Lodicule	Glabrous, cup shaped, thick	More or less pubescent, membranous
Awn length (mm)	37–49	Awnless
Glume color (sessile spikelet)	Reddish purple	Pale white
Growth habit	Annual	Annual

Results

The external morphological characteristics of the two species were examined and are described as follows:

Sorghum macrospermum

Annual; nodes of the culm glabrous; primary branches of the panicle not whorled, simple; pulvinus prominent; sessile spikelets 9.5–10.5 mm long, reddish purple; callus of the sessile spikelets obtuse, 1.0–1.3 mm long; pedicel scar of the sessile spikelet transverse; awns of the sessile spikelets 37–49 mm long; lodicules glabrous, cup-shaped, thick; pediceled spikelets lacking stamens, lemmas and palea, glumes only present, 9.0–12.0 mm long; mature caryopsis obovoid.

The specimens were grown in the campus of National Taiwan University, Taipei, from seeds supplied by the Division of Plant Industry, CSIRO, Australia.

Figs. 1a, b. Photomicrograph and interpretative drawing of the pachytene chromosome complement of *Sorghum macrosperrum*.

Sorghum bicolor

Annual; nodes of the culm glabrous; primary branches of the panicle whorled, divided; pulvinus prominent; sessile spikelets 4.5–5.2 mm long, pale white; callus of the sessile spikelets obtuse, 0.5–0.9 mm long; pedicel scar of the sessile spikelet transverse; awnless; lodicules

Figs. 2a, b. Photomicrograph and interpretative drawing of the pachytene chromosome complement of *S. bicolor*.

more or less pubescent, membranous; pediceled spikelets staminate or neuter, never lacking lemmas, 5.0–6.0 mm long; mature caryopsis obovoid.

The materials were furnished by the Department of Agronomy, NTU, Taipei.

The morphological characteristics and their measurements of the two species described above are listed in Table 1.

Cytological studies of these two species were made below: The pachytene chromosomes of *S. macrospermum* and *S. bicolor* exhibited a considerable degree of entanglement so that it was difficult to analyze the pachytene chromosomes. However, the well spread pachytene configurations were occasionally observed in the pollen mother cells which were selected for this pachytene analysis. These pachytene chromosomes selected for analysis are characterized by the proximal darkly staining heterochromatic regions and light staining distal euchromatic

Table 2. Mean values (μ) for pachytene chromosome lengths in *Sorghum macrospermum* and *S. bicolor*

Chromosome pair No.	Total	Long arm	Short arm	Heterochromatic region on long arm	Heterochromatic region on short arm	Arm ratio
<i>S. macrospermum</i>						
1*	72.16 $\pm$ 1.83**	39.44 $\pm$ 1.04	32.72 $\pm$ 1.02	3.25	2.90	1.21
2	69.40 $\pm$ 1.87	38.36 $\pm$ 1.19	31.04 $\pm$ 1.00	3.59	3.76	1.24
3	61.65 $\pm$ 1.66	37.64 $\pm$ 1.19	24.01 $\pm$ 0.65	3.55	3.10	1.57
4	58.70 $\pm$ 1.55	36.16 $\pm$ 0.90	22.54 $\pm$ 0.79	3.90	3.40	1.60
5	57.83 $\pm$ 1.76	37.71 $\pm$ 1.15	20.12 $\pm$ 0.72	4.20	4.25	1.87
6	56.16 $\pm$ 1.69	36.74 $\pm$ 0.87	19.37 $\pm$ 0.86	3.85	3.60	1.90
7	52.47 $\pm$ 1.61	33.77 $\pm$ 1.15	18.70 $\pm$ 0.61	3.75	3.75	1.81
8	50.84 $\pm$ 1.64	32.20 $\pm$ 1.27	18.62 $\pm$ 0.47	3.35	3.75	1.73
9	39.83 $\pm$ 1.81	22.16 $\pm$ 1.28	17.67 $\pm$ 0.57	3.12	3.55	1.25
10	37.72 $\pm$ 1.77	21.32 $\pm$ 0.86	16.40 $\pm$ 0.97	3.10	3.23	1.30
11	35.77 $\pm$ 1.41	29.70 $\pm$ 1.35	6.07 $\pm$ 0.24	2.80	2.51	4.89
12	34.95 $\pm$ 1.23	29.12 $\pm$ 1.11	5.79 $\pm$ 0.32	3.12	2.35	5.03
13	33.54 $\pm$ 1.51	21.01 $\pm$ 1.07	12.53 $\pm$ 0.55	3.51	3.75	1.68
14	32.03 $\pm$ 1.45	20.38 $\pm$ 1.07	11.65 $\pm$ 0.45	3.85	4.02	1.75
15	28.53 $\pm$ 1.30	15.48 $\pm$ 0.84	13.05 $\pm$ 0.62	4.45	3.42	1.19
16	26.61 $\pm$ 1.47	14.48 $\pm$ 0.97	12.14 $\pm$ 0.57	4.22	3.51	1.19
17	24.74 $\pm$ 1.18	13.60 $\pm$ 0.83	11.14 $\pm$ 0.43	5.40	2.89	1.22
18	23.49 $\pm$ 1.31	13.04 $\pm$ 0.81	10.45 $\pm$ 0.57	4.51	2.70	1.25
19	21.65 $\pm$ 1.28	12.07 $\pm$ 0.81	9.58 $\pm$ 0.54	4.05	3.25	1.26
20	20.38 $\pm$ 1.21	11.00 $\pm$ 0.43	9.38 $\pm$ 0.80	3.75	3.25	1.17
<i>S. bicolor</i>						
1*	59.60 $\pm$ 1.48**	31.82 $\pm$ 1.05	27.78 $\pm$ 0.82	2.98	2.65	1.15
2	48.62 $\pm$ 1.54	30.17 $\pm$ 1.04	18.46 $\pm$ 0.67	3.47	3.45	1.63
3	46.18 $\pm$ 1.46	30.26 $\pm$ 1.12	15.92 $\pm$ 0.41	3.12	3.42	1.90
4	43.17 $\pm$ 1.37	27.23 $\pm$ 0.96	15.94 $\pm$ 0.51	4.15	2.87	1.71
5	31.09 $\pm$ 1.52	16.96 $\pm$ 0.98	14.13 $\pm$ 0.63	3.26	3.34	1.20
6	29.18 $\pm$ 1.38	24.15 $\pm$ 1.41	5.03 $\pm$ 0.10	4.06	2.56	4.80
7	26.06 $\pm$ 1.33	16.56 $\pm$ 0.98	9.50 $\pm$ 0.39	3.95	4.06	1.74
8	24.29 $\pm$ 1.19	12.37 $\pm$ 0.59	11.92 $\pm$ 0.62	4.25	4.37	1.04
9	22.84 $\pm$ 1.06	12.05 $\pm$ 0.76	10.80 $\pm$ 0.31	3.66	4.54	1.12
10	21.50 $\pm$ 1.20	12.02 $\pm$ 0.74	9.48 $\pm$ 0.52	4.54	3.79	1.27

* Nucleolus chromosome.

** Standard error of the mean.

regions on each pachytene chromosome pair. Nonstained centromeres are discernible. Observations on the pairing behaviour of homologous chromosomes in the two species revealed the presence of normal and complete pairing at pachytene stage. The conspicuous landmarks such as the presence of deeply knobs did not appear in these pachytene chromosome pairs and the distribution of the chromomeres could not be accurately ascertained. Consequently, the identification of the individual chromosome in the two species was mainly based on the

chromosome length, the arm ratio, heterochromatic pattern and the nucleolus organizer; no other morphological features of chromosomes were useful in analyzing these pachytene chromosomes. The pachytene chromosomes of *S. macrospermum* (Figs. 1a, b) could be divided into three groups on the basis of total length. The eight long pairs range from 51–72 μ , the six medium-sized pairs, two with a sub-terminal centromere, from 32–40 μ , and six small pairs, all with a median region centromere, from 20–28 μ . Of these twenty pachytene chromosome pairs, one nucleolar and two asymmetric pairs were easily identified by their conspicuous features. This nucleolar pair is the longest and has a nucleolus organizing region in the

Fig. 3. The idiograms of the pachytene chromosomes of *S. macrospermum* (a) and *S. bicolor* (b). The spaces in the lines represent centromeres. The thickened portions of lines represent heterochromatic regions, the thin lines represent euchromatic regions and the circles indicate the nucleoli.

short arm lying close to the centromere (Figs. 1a, b). Two similar asymmetric pairs are number eleven and twelve respectively in terms of length with the other pairs in the complement (Figs. 1a, b). The same features were also observed in *S. bicolor*; its nucleolus is organized on the short arm of the longest chromosome and near the centromere (Figs. 2, 4), one asymmetric pair is present and this is regularly number six (Figs. 2a, b). The remaining eight chromosome pairs of *S. bicolor* have no distinct feature except the chromosome length, the heterochromatic pattern and the arm ratio to aid in their identification. The measurements of total length, heterochromatic lengths and arm ratio for the individual pachytene chromosome

Fig. 4. Chromosome 1 of *S. bicolor* associated with the nucleolus at an intercalary position on short arm.

Figs. 5, 6. Diakinesis in *S. macrospermum* and *S. bicolor* respectively.

Figs. 7, 8. Metaphase I in *S. macrospermum* and *S. bicolor* respectively.

Fig. 9. Anaphase I in *S. macrospermum* with 20:20 distribution of the chromosomes.

Fig. 10. Anaphase I in *S. bicolor* with 10:10 distribution of the chromosomes.

Fig. 11. Somatic chromosome complement of *S. macrospermum*. Arrows point to two observable nucleolus organizing regions.

of the two species were obtained and are given in Table 2. The idiograms of pachytene chromosome complements of them were constructed (Fig. 3), utilizing the data given in Table 2, and incorporating the distinctive features of each chromosome.

Chromosome associations at diakinesis and metaphase I were determined for these two species. In *S. macrospermum*, two types of the chromosome associations viz., twenty bivalents and eighteen bivalents plus one quadrivalent, present at both diakinesis and metaphase I (Figs. 5, 7). The configuration of twenty bivalents in one pollen mother cell occurred in 32 of 66 pollen mother cells at diakinesis and in 28 of 39 cells at metaphase I. The other configuration of eighteen bivalents plus one quadrivalent per pollen mother cell at both these stages appeared in the remaining pollen mother cells examined. Neither univalent nor trivalent could be definitely observed, and cells with more than one quadrivalent were absent. The data are summarized in Table 3. The chromosome association of *S. bicolor* appeared to be normal in that only bivalents were observed at both diakinesis (Fig. 6) and metaphase I (Fig. 8). No multivalent could be definitely established in this species. Anaphase I (Figs. 9, 10) and later meiotic stages for the two species were also examined and found to be regular resulting in high percentage of pollen fertility and good seed setting.

Table 3. A summary of chromosome association at diakinesis and metaphase I in *S. macrospermum*

No. of pollen mother cells	Chromosome association							
	Univalents	Bivalents			Trivalents	Quadrivalents		
		Absolute	Mean	Percent		Absolute	Mean	Percent
Diakinesis								
66	0	1252	18.97	97.36	0	34	0.52	2.64
Metaphase I								
39	0	756	19.38	98.44	0	11	0.31	1.56

Root tip cells of *S. macrospermum* show 40 chromosomes (Fig. 11). The somatic chromosomes are very small ranging from 1.24 to 4.82 μ at metaphase. They have dark staining regions on both sides of the centromere. Distally, the chromosomes are very light staining and are not sharply differentiated from the cytoplasm. Two longest chromosomes of the complement are the nucleolus chromosomes, each nucleolus chromosome has an intercalary nucleolus organizing region near the centromere (Fig. 11). These observations paralleled the results obtained from the study of pachytene chromosomes. Excepting the nucleolus chromosomes, studies of the other somatic chromosomes are handicapped by the very small size of the chromosomes and the lack of the conspicuous landmarks for revealing the details of chromosome morphology. Therefore no analysis of the mitotic complement has yet been satisfactory.

Discussion

Taxonomic studies by Garber (1950) and Celarier (1959) show that the subgenera *Chaetosorghum* and *Eu-sorghum* are more closely related to each other, morphologically, than either is to any of the other three subgenera of *Sorghum*. From the data presented in Table 1, the author found that *S. macrospermum* may be distinguished morphologically from *S. bicolor* by its type of panicle branching, morphology of the lodicule, development of the pedicel spikelet and length of the awn; the former is the wild *Chaetosorghum* species with non-whorled simple panicle branches, glabrous lodicules, lemma-absent pedicel spikelets and

well-developed awns, while the latter is a cultivated *Eu-sorghum* species with whorled divided panicle branches, ciliated lodicules, lemma-persistent pediceled spikelets and awnless. The principal tendencies in the evolution of the three important morphological characteristics above mentioned, according to the Garber's view (1950), are as follows: (1) From the divided branching to the simple branching of a panicle. (2) The gradual reduction of the pediceled spikelet from a staminate to a lemma present and finally to a lemma absent condition. (3) From a poor developed to a well developed awn. The *Chaetosorghum* is a clearly marked subgenus with these advanced characteristics as shown by its simple branching panicle, lemma-absent pediceled spikelet and well-developed awn. While the *Eu-sorghum* possesses these relatively primitive characteristics, such as its divided branching panicle, staminate pediceled spikelet and poor developed awn. Therefore, *Chaetosorghum* may be considered to be a more advanced subgenus than *Eu-sorghum* in the line of evolutionary development. Garber (1950) pointed out that differences in the morphology of the lodicules do not seem to have any phylogenetic meaning, but they certainly have taxonomic significance in distinguishing the *Chaetosorghum* from the other subgenera of *Sorghum*.

Considering all the available observations on the morphology of pachytene chromosomes in many plants, pachytene chromosomes may be broadly classified as (1) the differentiated type, such as those reported in *Zea mays*, *Lycopersicum*, *Plantago* and *Solanum*, and (2) the undifferentiated type like those found in *Secale*, *Agapanthus* and *Hordeum* (Magoon *et al.* 1967). The pachytene chromosomes of *Chaetosorghum* like those of the *Eu-sorghum* species are of the differentiated types with centromeres flanked by proximal dark staining heterochromatin and distal light staining euchromatin (Wu 1979). Their pachytene chromosomes are well differentiated into the euchromatic and heterochromatic regions without difficulty. It may, however, be noted that this behavior is not a characteristic feature of the entire genus *Sorghum* since undifferentiated types of chromosomes where the pachytene chromosomes take uniform stain throughout their length have also been reported in *Heterosorghum*, *Para-sorghum* and *Stiposorghum* of this genus (Wu 1982, 1984, 1987).

The pachytene karyotype of *S. bicolor* presented here is essentially similar to those of the other 20-chromosome *Eu-sorghum* species based on comparisons with published descriptions of sorghum chromosomes (Sharma and Bhattacharjee 1957, Magoon and Shambulingappa 1961, Magoon *et al.* 1964, Magoon *et al.* 1967, Wu 1979). Detailed analysis of pachytene chromosomes of *S. macrospermum* indicates that every two sequential bivalents of its chromosome complement are similar to each other in appearance viz., bivalents 1 and 2, 3 and 4, 5 and 6 and so on show resemblance with respect to length, heterochromatic pattern and arm ratio. Therefore the twenty bivalents (bivalent 1 to 20) of *S. macrospermum* may constitute ten different sets of chromosome bivalents (Fig. 3a). The two chromosome bivalents of each set are similar in morphology but cannot synapse in meiosis (Figs. 1a, b). The comparative study of pachytene chromosomes between *S. macrospermum* and *S. bicolor* revealed no gross structural difference other than difference in chromosome number; the former species has twenty chromosome pairs which is twice chromosome number of the latter.

The ten sets of pachytene chromosomes of *S. macrospermum* are morphologically like the ten corresponding chromosome bivalents of *S. bicolor* respectively (Fig. 3): e. g. (1) The longest chromosome pair of *S. macrospermum* is a nucleolar pair. The nucleolus is formed on the short arm very close to the centromere. And this chromosome pair has a more or less medium point centromere (Figs. 1, 3). All these features have also been observed on longest chromosome pair of *S. bicolor* (Figs. 2, 3 and 4). Both of them closely resemble each other. (2) The eleventh and the twelfth chromosome bivalents of *S. macrospermum* grouped into the sixth chromosome set are striking similar to the sixth chromosome bivalent of *S. bicolor* in appearance (Figs. 1, 2 and 3). The three corresponding chromosome bivalents are all the

most asymmetrical ones of their chromosome complements. Their arm ratios exceed 4. (3) The remaining chromosome bivalents of *S. macrospermum* also seem to be like the corresponding chromosome bivalents of *S. bicolor* with respect to relative length, heterochromatic pattern and arm ratio (Fig. 3).

As previously mentioned, the chromosome complement of *Chaetosorghum* is morphologically like those of the 20-chromosome *Eu-sorghum* species, but the former has twenty chromosome pairs which is twice chromosome number of the latter. On the contrary, the chromosome complement of *Chaetosorghum* differs much from those of *Para-sorghum* and *Stiposorghum* (Wu 1982, 1984, 1987). These results accompanied with the facts that the meiotic behavior of *Chaetosorghum* is fairly regular with only a few quadrivalents and followed by normal fertility indicate that the *Chaetosorghum* has a closer evolutionary relationship to *Eu-sorghum* than to other subgenera of the sorghum and support the hypothesis that the *Chaetosorghum* is probably a segmental allopolyploid which arose as a result of the doubling of chromosomes of a natural hybrid between two putative 20-chromosome *Eu-sorghum* species whose chromosome complements are closely related but not identical. Nevertheless, the present type of *Chaetosorghum* might have been established from this first segmental allopolyploid through further mutations, cryptic structural changes in chromosomes and natural selections. The above hypothesis concerning the probable origin of *Chaetosorghum* is based almost entirely on morphological and cytological data. Unfortunately, the *S. macrospermum* and *S. bicolor* did not yield any intersubgeneric hybrids, hence this hypothesis suggested in this report is difficult to be checked by genetic experiments as was demonstrated for *S. halepense* by Hadley (1953), Celarier (1958) and Bhatti *et al.* (1960).

The subgenus *Chaetosorghum* is now represented by only one species *S. macrospermum*. Since this species appears to be confined to the Port Darwin-Katherine area of the northern Australia (Garber 1950), this area may therefore be considered the probable center of origin of *Chaetosorghum*. However, no *Eu-sorghums* proposed as the ancestor of *Chaetosorghum* by this report are indigenous to Australia. As a matter of speculation, the ancestral *Eu-sorghums* may have migrated to the northern Australia from their original habitats and then given rise to this new subgenus *Chaetosorghum*. At present, the progenitors of *Chaetosorghum* may be either lost or undiscovered in Australia. But no evidence is available for this hypothesis.

Summary

Comparing the important morphological characteristics between *Sorghum macrospermum* a single species accommodated in *Chaetosorghum* and *S. bicolor* a 20-chromosome *Eu-sorghum* species, the former was found to be more advanced than the latter. Detailed analysis of the karyotype of *S. macrospermum* at pachytene stage shows that the karyotype of this species is essentially similar to that of *S. bicolor*, but the former species has forty somatic chromosomes which is twice chromosome number of the latter species. The meiotic behavior of *S. macrospermum* is fairly regular with only a few quadrivalents and followed by normal fertility. Based on these morphological and cytological data, the author speculates that the *Chaetosorghum* is probably a segmental allopolyploid which arose as a result of the doubling of chromosomes of a natural hybrid between two putative 20-chromosome *Eu-sorghum* species whose chromosome complements are closely related but not identical.

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