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The genomic relationship between cultivated sorghum [*Sorghum bicolor* (L.) Moench] and Johnsongrass [*S. halepense* (L.) Pers.]: a re-evaluation*

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Summary. The genomic relationship between cultivated sorghum [*Sorghum bicolar* (L.) Moench, race bicolor, De Wet, $2n=20$] and Johnsongrass [*S. halepense* (L.) Pers., $2n=40$] has been a subject of extensive studies. Nevertheless, there is no general consensus concerning the ploidy level and the number of genomes present in the two species. This research tested the validity of four major genomic models that have been proposed previously for the two species by studying chromosome behaviors in the parental species, 30-chromosome hybrids [sorghum, ($2n=20$) X Johnsongrass, ($2n=40$)], 40-chromosome hybrids [sorghum, ($2n=40$) X Johnsongrass, ($2n=40$)] and 60-chromosome amphiploids. Chromosome pairings of amphiploids are reported for the first time. Chromosomes of cultivated sorghums paired exclusively as 10 bivalents, whereas Johnsongrass had a maximum configuration of 5 ring quadrivalents with occasional hexavalents and octovalents. In contrast, 40-chromosome cultivated sorghum had up to 9 ring quadrivalents and 1 hexavalent. Pairing in the 30-chromosome hybrids showed a maximum of 10 trivalents, and that in the 40-chromosome hybrids exhibited 8 quadrivalents, 5 of which were rings, together with a few hexavalents. Amphiploid plants showed up to 3 ring hexavalents, 1 chain hexavalent and a chain of 12 chromosomes. The data suggest that cultivated sorghum is a tetraploid species with the genomic formula AAB1B1, and Johnsongrass is a segmental auto-allo-octoploid, AAAA B1B1B2B2. The model is further substantiated by chromosome pairing in amphiploid plants whose proposed genomic formula is AAAAAA B1B1B1B1 B2B2.

Key words: Breeding – Cytogenetic – Genomic analysis – Interspecific cross

Introduction

The genus *Sorghum* is divided into five sections: *Sorghum, Parasorghum, Heterosorghum, Stiposorghum* and *Chaetosorghum*, and includes species with $2n=10$, 20, 30 and 40 chromosomes (Celarier 1958; De Wet 1978; Garber 1954). Both cultivated sorghum [*Sorghum bicolor* (L.) Moench] ($2n=20$) and Johnsongrass [*S. halepense* (L.) Pers.] ($2n=40$) belong to the section *Sorghum*. Recently cultivated sorghum was classified as *S. bicolor* subspecies *bicolor* race bicolor, whereas the wild species with $2n=20$ were considered as races in subspecies *arundinaceum* and *drummondii* (De Wet 1978). Names of races are not underlined or italicized as proposed by De Wet (1978) and Harlan and De Wet (1971). Two other recognized species in the section were *S. halepense* and *S. propinguum* (Kunth) Hitchcock, $2n=20$. For the sake of brevity in this report, the term cultivated sorghum (or sorghum) refers to *S. bicolor* subspecies *bicolor* race bicolor, and race virgatum refers to *S. bicolor* subspecies *arundinaceum* race virgatum, as recognized by De Wet (1978). The terms Johnsongrass and *S. halepense* are synonymous. It should be noted that Johnsongrass has been speculated to be a derivative of the introgression of sorghum into the original *S. halepense* (Celarier 1958).

The genomic relationship between *S. bicolor* and *S. halepense* has been investigated extensively, since the first report on the cytological studies of a hybrid between the two species by Karper and Chisholm (1936). Nevertheless, there is no general consensus concerning the ploidy level and the number of genomes present in the

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two species. *Sorghum bicolor* was considered to be a diploid species (De Wet 1978; Duara and Stebbins 1952; Sangduen and Hanna 1984) or a tetraploid species (Celavier 1958; Doggett 1976; Endrizzi and Morgan 1955; Garber 1950; Magoon and Ramana 1961). It was also speculated that *S. bicolor* is a secondary polyploid with a basic number of $x=7$ or 8 (Huskins and Smith 1932; Pritchard 1965). Correspondingly, *S. halepense* was considered to be an autotetraploid (Casady and Anderson 1952; Duara and Stebbins 1952), an autooctoploid (Bennett and Merwine 1966) or an auto-allo-octoploid (Hadley 1953). Evidences of tetraploid behavior in *S. halepense* consist of the occurrence of a number of quadrivalents at meiosis (De Wet 1978) and the observation of ten bivalents in natural polyhaploids (Duara and Stebbins 1952; Raman and Khrishnaswamy 1955). Arguments presented to support the contention that *S. bicolor* is a tetraploid were based on chromosome pairings in hybrids of the cross between the two species (Bennett and Merwine 1966; Hadley 1953), quadrivalent formation during meiosis in *S. bicolor* (Bennett and Merwine 1966; Hadley 1953), bivalents in natural haploids (Brown 1943; Endrizzi and Morgan 1955; Kidd 1952), the occurrence of secondary association at meiosis (Sharma and Bhattacharjee 1957) and the existence in the genus of other species whose gametic chromosome number is $n=5$ (Celarier 1958; Garber 1944). The problem in accepting these arguments is that no genome donor is known for *S. bicolor*. Attempts to cross 10- and 20-chromosome species have failed, including a recent attempt in our laboratory (Endrizzi 1957; Garber 1950; Karper and Chisholm 1936). Finally, karyotypes of most 10- and 20-chromosome species are so different that existing 10-chromosome species are unlikely to be progenitor(s) of *S. bicolor* (Garber 1944; Gu et al. 1984; Karper and Chisholm 1936).

Four major genomic models previously proposed to describe the relationship between sorghum and Johnsongrass (Bennett and Merwine 1966; Casady and Anderson 1952; Duara and Stebbins 1952; Hadley 1953) are tested by studying chromosome behaviors at meiosis in the 20- and 40-chromosome sorghum, Johnsongrass, synthetic and natural 30-chromosome hybrids, 40-chromosome hybrids and 60-chromosome amphiploids. The genomic formulas for Bennett and Merwine's model are our interpretations based on their conclusions; otherwise, all genomic designations are from the original reports.

Materials and methods

Five genotypes of sorghum were used: Combine Kafir (CK) 60, ATX651, KS34A, KS37A and KS39A. All but CK 60 were A lines (cytoplasmic male sterile). Race virgatumn was an introduction accession (PI302233). One breeding line of 40-chromosome sorghum, designated as 6750, was used. Three sources of Johnsongrass were used, two of which were collected from the midwestern and the southeastern United States. They are designated as Sal and Tift, respectively. The third source was PI266965, a plant introduction to the United States. All genotypes of sorghum were used as females in all crosses for the ease of hand emasculation and pollination. All crosses were conducted in a greenhouse.

Immature embryos at 18–21 days after pollination were cultured onto either B5 (Gamborg et al. 1968) or MS (Murashige and Skoog 1962) medium. The average success rate was 5%–10%. Most seedlings were removed from Petri dishes after having been on culture media for 2–3 weeks, then they were transplanted to 5 cm pots in a growth chamber maintained at 25 ± 1 °C with a diurnal cycle of 16 h light/8 h dark. They were kept in the growth chamber for 7–10 days and then transferred to the greenhouse. Hybrid seedlings intended for chromosome doubling were grown in the growth chamber for 2–4 weeks and then treated with colchicine.

Amphiploid plants were produced by immersing 30-chromosome hybrids in 0.5% colchicine (w/v) + 2% DMSO (dimethyl sulfoxide) (v/v) solution for 5 h with air-bubbling. Treated plants were then kept in a dark, humid growth chamber for 2 days before being returned to the light regime described earlier. In the first trial, 9 of the 20 plants at 3–4 weeks old (after transplanting) survived the treatment; the chromosome number in 2 of them was effectively doubled. In the second trial, 28 plants approximately 2 weeks old were treated and only 1 of 14 surviving plants doubled its chromosome number.

Young flowers were fixed in Carnoy's solution (6 ethanol: 3 chloroform: 1 glacial acetic acid). Pollen mother cells (PMCs) were squashed in 1% aceto-carmine. About 50 PMCs at diakinesis and metaphase I (MI) were analyzed for chromosome pairings in each plant. Chromosome configurations at diakinesis are sometimes difficult to interpret because of chromosome stickiness or the presence of fibrillike materials of unknown nature connecting chromosomes. These phenomona are widespread in sorghum and Johnsongrass (Bennett and Merwine 1966; Celarier 1958; Kidd 1952).

Results

Cytology of parental species and interracial hybrids

Results of cytological analyses of the parental species, hybrids and amphiploids are summarized in Table 1. Two genotypes, CK60 and TX403, were used to represent sorghum. Chromosomes paired exclusively as bivalents. Secondary association was observed in both genotypes (Fig. 1 A). Chromosome pairing in race virgatum as well as in reciprocal crosses with sorghum was complete, with 10 ring bivalents at diakinesis (Fig. 1 B), indicating a complete homology of genomes present in these two races.

Meiotic analysis indicates that Johnsongrass (Sal and PI 266965) had a lower number and a lower mean value of quadrivalents than the 40-chromosome sorghum, but it had a higher mean value of bivalents (Table 2). Figure 1 C is a photograph of a meiocyte that contained 4 ring- and 1 chain-quadrivalents and 10 bivalents. Four of the bivalents were secondarily associated in 2 groups. Sixteen

Table 1. Summary of chromosome pairings in parental species, hybrids and amphiploids of crosses between cultivated sorghum and Johnsongrass

Populations	No. of plants		Chromosome pairing								No. of cells analyzed
			I	II	III	IV	V	VI	VIII	XII	
Sorghum, $2n=20$	10	Mean		10							500
Race virgatum, $2n=20$	5	Mean		10							250
Sorghum × virgatum, $2n=20$	5	Mean		10							250
Sorghum, $2n=40$	9	Mean	0.21	12.19	0.09	3.79		0.002			496
		Range	(0–12)	(2–20)	(0–4)	(0–9)		(0–1)			
Johnsongrass, $2n=40$	10	Mean	0.12	16.28	0.06	1.75		0.02	0.003		676
		Range	(0–5)	(7–20)	(0–2)	(0–5)		(0–1)	(0–1)		
30-chromosome hybrids	10	Mean	3.30	3.80	6.37						585
		Range	(0–10)	(0–10)	(0–10)						
40-chromosome hybrids	5	Mean	0.31	16.02	0.04	1.87		0.006			348
		Range	(0–4)	(4–20)	(0–1)	(0–8)		(0–1)			
60-chromosome amphiploids	3	Mean	2.58	22.72	0.49	2.15	0.004	0.30	0.02	0.004	259
		Range	(0–10)	(13–30)	(0–5)	(0–5)	(0–1)	(0–4)	(0–1)	(0–1)	

Table 2. Summary of proposed genomic formulas and expected maximum pairings (EMP); derivation of EMP for four previous models is based on the assumption that only homologous chromosomes pair with each other (see "Discussion"); r=ring

	S. bicolor	*S. halepense*	30-chromosome hybrids	40-chromosome hybrids	60-chromosome amphiploids
Casaday and Anderson's					
Formula	A_VA_V	$A_hA_hA_hA_h$	$A_VA_hA_h$	$A_VA_VA_hA_h$	$A_VA_VA_hA_hA_hA_h$
EMP:		10 rIV	10 III	10 rIV	10 rVI
Duara and Stebbins's					
Formula	V_1V_1	$V_{12}V_{12}V_{12}V_{12}$	$V_1V_{12}V_{12}$	$V_1V_1V_{12}V_{12}$	$V_1V_1V_{12}V_{12}V_{12}V_{12}$
EMP:		10 rIV	10 I+10 rII	20 rII	10 rII+10 rIV
Hadley's					
Formula	AABB	AAAABBCC	AAABBC	AAAABBBC	AAAAAABBBBCC
EMP:		5 rIV+10 rII	5 III+5 rII+5 I	5 rIV+5 III+5 I	5 rVI+5 rIV+5 rII
Bennett and Merwine's					
Formula	AAA_1A_1	$AAAAA_1A_1A_1A_1$	$AAAA_1A_1A_1$	$AAAAA_1A_1A_1A_1$	$AAAAAAA_1A_1A_1A_1A_1A_1$
EMP:		10 rIV	10 III	10 rIV	10 rVI
Presently proposed model					
Formula	AAB_1B_1	$AAAAB_1B_1B_2B_2$	$AAAB_1B_1B_2$	$AAAAB_1B_1B_1B_2$	$AAAAAAB_1B_1B_1B_2B_2$
EMP:		5 rIV+10 rII occasional octovalent	5 III+5 III occasional hexavalent	5 rIV+5 IV* occasional octovalent	5 rVI+5 rIV+5 rII occasional 12-valent
Observed maximum configuration:					
		5 rIV occasional haxavalent and octovalent	10 III	5 rIV+3 IV* occasional hexavalent	3 rVI+1 cVI, 5 rIV occasional octovalent and 12-valent

* may not be ring configurations (see "Discussion")

of 676 (2%) cells had a maximum of 5 ring quadrivalents (Fig. 1 D), indicating 5 sets of 4 completely homologous chromosomes. Occasional hexavalents and octovalents were observed in less than 2% of the cells (Fig. 1 E). Laggards appeared in about 20% of AI cells, ranging from 1–5; less than 10% of the quartets had 1–4 micronuclei.

Although line 6750 was the only genotype used to produce 40-chromosome hybrids, another 40-chromosome sorghum, line 3197B (Lo 1983), was included in

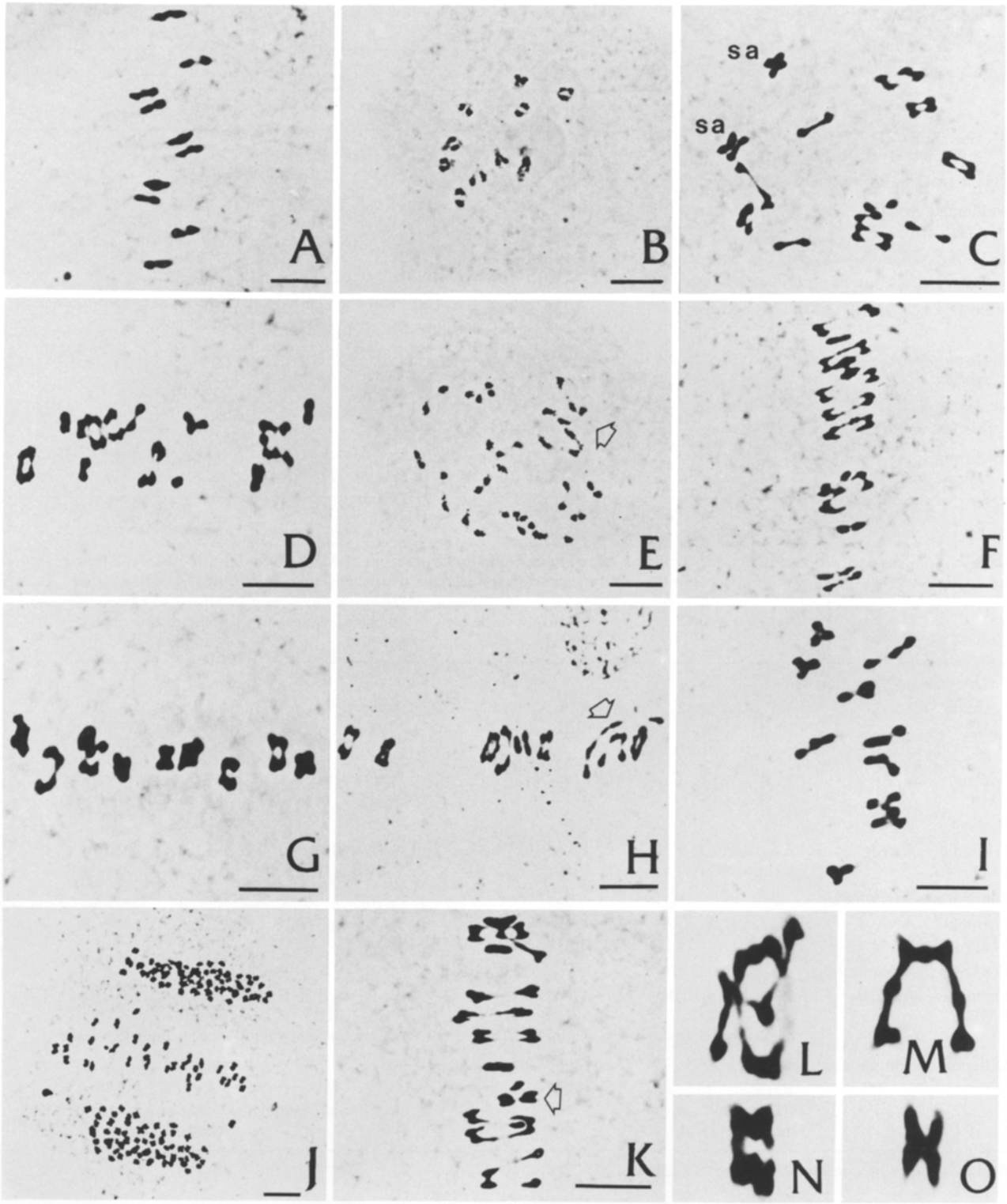

Fig. 1 A–O. Meiosis of sorghum, sorghum × virgatum hybrid, Johnsongrass and sorghum × Johnsongrass hybrids. **A** 10 bivalents in sorghum; **B** 10 ring bivalents in race bicolor × race virgatum hybrids; **C–E** meiosis in Johnsongrass; **C** 4 ring quadrivalents, 1 chain quadrivalent and 10 bivalent, *sa* secondary association of bivalents; **D** 5 ring quadrivalents, 9 bivalents, 2 univalents; **E** 1 octovalent (*arrow*), 16 bivalents; **F–G** meiosis in 40-chromosome sorgum; **F** 7 quadrivalents, 6 bivalents. Six ring quadrivalents are clearly visible; the other one is "H" type. **G** Pairings and/or associations of 10 quadrivalents; **H** a hexavalent (*arrow*), 7 quadrivalents, 2 bivalents. A bivalent is missing from this cell; **I–J** meiosis in 30-chromosome hybrids; **I** 10 trivalents; **J** a highly polyploid cell; **K** meiosis in 40-chromosome hybrids, 8 quadrivalents, 4 bivalents. Five of 8 quadrivalents are rings, 2 are chains; a rare quadrivalent configuration is overlapping with a ring structure. Two of 4 bivalents exhibit secondary association (*arrow*). **L–O** some commonly observed quadrivalent configurations; **L** a ring and "Z" chain; **M** a chain; **N** Figure 8. **O** "H" type. *Bars* represent 10 μm

cytological analysis. Chromosome pairing in these two lines was similar and, therefore, results were combined (Table 1). Four of 496 cells contained 9 ring quadrivalents (Figure 1 F), which was never observed in Johnsongrass or 40-chromosome hybrids. One cell had associations and/or pairings of 10 quadrivalents (Fig. 1 G). However, 10 cells were found to have 20 bivalents. The only difference in chromosome behavior of these two genotypes was the occurrence of a single hexavalent in line 3197B (Fig. 1 H). Laggards ranging from 1–8 were found in about 8% of the anaphase I (AI) cells. The number of micronuclei at the quartet stage ranged from 1–6 in about 18% of the quartets.

Cytology of 30-chromosome hybrids

Five spontaneous hybrids collected from the field and five synthetic hybrids made in the greenhouse were analyzed. The spontaneous hybrids were identified by their resemblance in morphology to Johnsongrass and by the presence of rhizomes. Since their pairing patterns were quite similar, data were combined (Table 1). Ten trivalents were observed in 42 of 585 cells (Fig. 1 I). The frequency of these configurations, however, varied from plant to plant. In 1 natural hybrid, the frequency was 20% and 10% when spikes were collected in September and February, respectively. In 2 synthetic hybrids, the average frequency was 23%. Chromosome behavior was very irregular from AI to later stages, as expected. Laggards appeared in about 95% of AI cells and about 90% of the quartets had micronuclei. Some hybrids also contained a large number of highly polyploid cells. Exact counts were not attempted, but these cells could have had 200 or more chromosomes. An example of highly polyploid cells is shown in Fig. 1 J. This phenomenon was also observed by others (Hadley 1958; Merwine and Bennett 1966). Endoreplication, cell fusion, cytokinesis failure or a combination of these processes may be involved.

Cytology of 40-chromosome hybrids

Cytological studies were conducted in five 40-chromosome hybrids, four of which were hybrids of the cross 6750 X Sal. The other hybrids had ATX651 X PI266569 in its parentage. These hybrids could be easily identified by morphology. Since ATX651 was an A line with $2n=20$, the hybrid apparently resulted from the union of an unreduced gamete from ATX651 with a normal, reduced gamete from PI266965. Hybrids of this nature have been encountered often (Bennett and Merwine 1966; Endrizzi 1957; Hadley 1953). Four hybrids of 6750 X Sal contained 1–5 quadrivalents in 73% meiocytes. Three of 260 cells had 5 ring quadrivalents (Fig. 1 K), indicating that the 2 parental species had in common 5 chromosome sets of complete homology. The hybrid ATX651 X PI266569 had 1–8 quadrivalents in 86 of 88 cells. A cell with 5 ring quadrivalents and 5 groups of secondarily associated bivalents was observed. A total of 7 meiocytes were observed to contain more than 5 quadrivalents. Six cells had 5 ring quadrivalents plus a chain quadrivalent. One single cell had 5 rings and 2 chain quadrivalents, plus another type of quadrivalent configuration in which a bivalent was seen to attach to one side of its partner (Fig. 1 K). The latter configuration is rarely seen in sorghum and Johnsongrass (Celarier 1958; Endrizzi 1958). A secondary association of 2 bivalents is indicated by an arrow in Fig. 1 K. The difference between true quadrivalents and secondary association is obvious. The size of bivalents in a secondary association is similar to that of individual bivalents, whereas quadrivalents are larger and/or longer than bivalents. Some common types of quadrivalents we recognized are shown in Fig. 1 L–O. Two of the 348 cells studied contained a single hexavalent. Chromosome behavior was slightly irregular during AI and later stages. Up to 8 laggards at AI and 7 micronuclei could be seen at the quartet stage, but they appeared in only 5% of AI cells and 12% of quartets.

Cytology of amphiploids

Meiotic chromosome behaviors of three 60-chromosome amphiploids (KS34A X PI266965, KS37A X Tift, KS39A X Sal) at metaphase were quite similar (Fig. 2). There was a strong preponderance of bivalent formation in all 3 plants (Table 1). Seven of 259 cells (3%) contained 30 bivalents. Three ring hexavalents plus 1 chain hexavalent was recorded in 1 cell. Hexavalents (Fig. 2 D–E) appeared in 16% of the meiotic cells. A single octovalent was recognized in 4 cells and a 12-valent (Fig. 2 C) in another cell. Other chromosome configurations were also recorded (Table 1).

These amphiploids had irregular chromosome behaviors at AI and quartet stage. Two amphiploids had 1–9 laggards in 72% of AI cells and 1–10 micronuclei in 96% of the quartets. One amphioid, KS34A X PI266965, appeared to be more regular having only 1–5 laggards in 42% of AI cells and 1–4 micronuclei in 28% of the quartets.

Discussion

Four major genomic models attempting to explain the relationship between sorghum and Johnsongrass are summarized (Table 2). Based on genomic formulas, expected maximum pairings are derived on the assumption that only homologous chromosomes pair with each other. The Av and Ah genomes are identical in Casady and

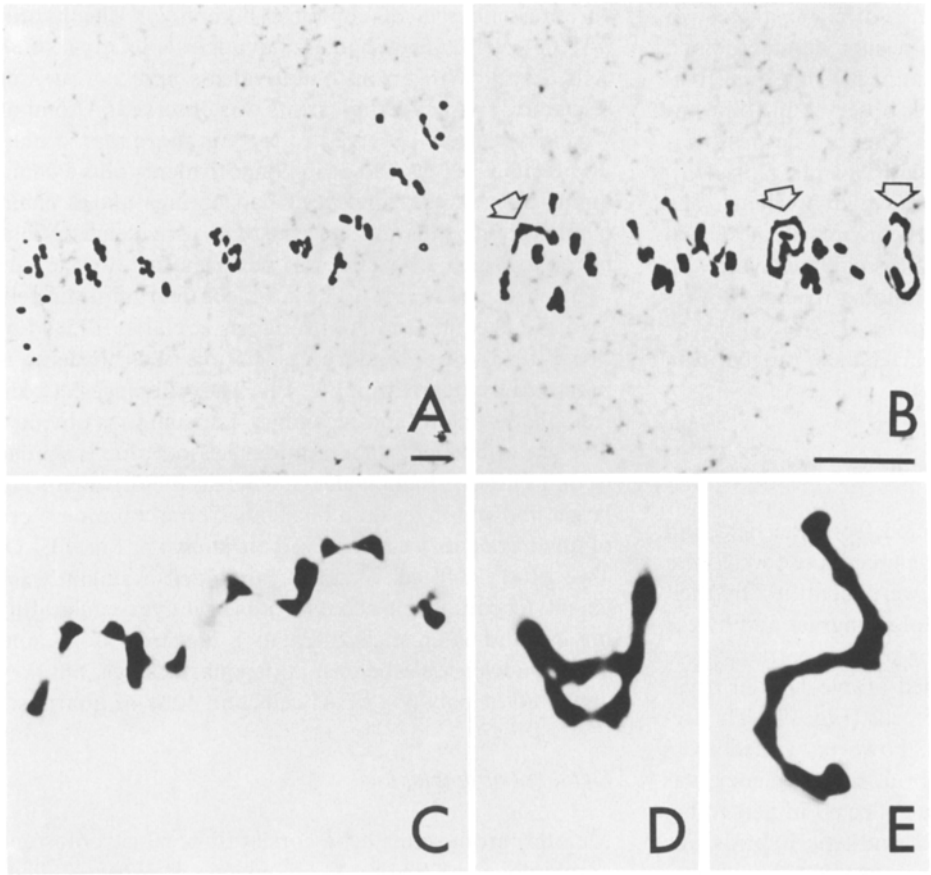

Fig. 2 A – E. Meiosis in amphiploids. **A** 1 quadrivalents, 3 trivalents, 20 bivalents, 7 univalent; **B** 2 ring hexavalents and 1 chain quadrivalent, indicated by *arrows*; **C** a chain of 12-valent, partially overlapped by 2 bivalents; **D** a ring hexavalent; **E** a chain hexavalent. *Bars* represent 10 μm

Anderson's (CA's) model, so that 10 IIIs and 10 IVs are expected in the 30- and the 40-chromosome hybrids, respectively (Casady and Anderson 1952). Duara and Stebbins (1952) hypothesized that the V12 genome in modern Johnsongrass contains predominantly genetic materials from the V1 genome present in sorghum, with a little genetic material from an unknown V2 genome. Therefore, trivalents and quadrivalents may be expected to occur in the 30- and 40-chromosome hybrids, in addition to the expected maximum pairing in Table 1. The B and C genomes in Hadley's model (H's model) are related and, therefore, can pair intergenomically to result in more than 5 IIIs and 5 IVs in the 30- and the 40-chromosome hybrids, respectively (Hadley 1953).

Our data do not fit any of these models. The maximum pairing of 5 ring quadrivalents observed in Johnsongrass agrees most closely with H's model and eliminates all other models. However, H's model fails to explain the occurrence of 10 trivalents in about 10%–26% of the cells in some of the 30-chromosome hybrids. Such a high frequency can be best explained by CA's and Bennett and Merwine's (1966) (BM's) models. Meiotic behaviors of 40-chromosome hybrids seem to fit better with H's model than the others, since a maximum of 5 ring quadrivalents was observed in 4 hybrids from the cross 6750 X Sal. In contrast, the hybrid ATX651 X PI266965 had a total of 8 quadrivalents, which comes closer to CA's and BM's predictions. The detection of 3 ring hexavalents plus 1 chain hexavalent in the amphiploid plants, again, supports H's model, which predicts a maximum of 5 hexavalents. The number of hexavalents observed was far below the predicted number of 10 VIs by CA's and BM's models, but was too high to fit the Duara and Stebbins (1952) (DS's) model, which predicts at most only occasional hexavalents.

The argument that sorghum is a tetraploid species based on the occurrence of occasional quadrivalents is not substantiated by our studies. Not a single quadrivalent was observed during the course of this research or in thousands of other sorghum plants from various genotypes studied in our laboratory for various purposes (unpublished data). Observation of quadrivalents in other reports could be due to translocations (Schertz 1970). Also, there may be differences in interpreting some chro-

mosome associations at meiosis. For example, the phenomenon shown in Fig. 1 A was interpreted as 3 groups of secondarily associated bivalents, whereas it has been recorded as 3 quadrivalents by other authors (Bennett and Merwine 1966).

Johnsongrass is unlikely to be an autopolyploid that arose through chromosome doubling of *S. bicolor*. If it were, its chromosome behaviors at meiosis would be similar to those of the 40-chromosome sorghum, a colchicine induced-polyploid from 20-chromosome sorghum. Johnsongrass had a maximum of only 5 ring quadrivalents, whereas the 40-chromosome sorghum had up to 9–10 ring quadrivalents (Fig. 1 G). It is possible that secondary association of bivalents may have been confused with quadrivalents by some workers.

One may argue that after the origin of Johnsongrass as an autopolyploid of sorghum, it may have become diploidized to some extent during the course of evolution. Differences in chromosome behaviors of colchicine induced-autoploids and natural ones can be identified (Charpentier et al. 1986). However, Johnsongrass is a perennial rhizomatous species whereas taxa in the species *S. bicolor* do not have any rhizomes. Doubling the chromosome number of taxa in the *S. bicolor* would not automatically give rise to rhizomes (Endrizzi 1957). The chromosome complement of Johnsongrass obviously did not contain a duplicate set of that of sorghum as shown by the karyotype analyses (Gu et al. 1984). Furthermore, chromosome pairings in the hybrids of *S. bicolor* and *S. halepense* also do not support the autopolyploidy of Johnsongrass.

The observation of 5 ring quadrivalents in 4 hybrids of 6750 X Sal suggests that the basic chromosome number is 5 in both species. In the hybrid ATX651 X PI266965, more than 5 quadrivalents were observed (Fig. 1 K), but additional ones were always of configurations other than rings. These observations prompt us to hypothesize that the genomic structure of the 40-chromosome hybrids is AAAA B1B1B2B2 instead of AAAA BBCC, as proposed by Hadley (1953). Our model predicts that chromosome pairing among the A-genome chromosomes results in 5 ring quadrivalents. In certain genotypes, homoeologous pairing between B1 and B2 may occur, but such pairing probably results in configurations other than the ring-quadrivalent structures. Chromosomes in the B1 and B2 genomes appear to be closely related, since they usually form either bivalents or quadrivalents and seldom form trivalents and univalents in 40-chromosome hybrids.

Our proposed genomic formulas for the two species are further substantiated by meiotic chromosome behavior in the amphiploid plants. The occurrence of 3 ring plus 1 chain hexavalents is more compatible with our model than with other models. The occurrence of an octovalent in 4 cells of the amphiploid plants and a single 12-valent (Fig. 2 C) constitute additional evidence in favor of our model. Two of three amphiploid plants were found to be chimeric. Chromosome pairing in panicles with 30 chromosomes was essentially the same as that in 30-chromosome hybrids (data not shown); i.e., no configurations higher than trivalents were detected. There is no reason, therefore, to think that octovalents and a 12-valent occurring in the same plants were the consequences of translocation. These high multivalents can be explained by homoeologous pairings among three genomes, A, B1 and B2, assuming that the A genome has residual homology with the other two. The presence of hexavalents and octovalents in Johnsongrass and 40-chromosome hybrids also may be explained on this basis. Low frequency of multivalents in polyploid plants is an indication of homoeologous pairings (Burnham 1974, Dvorak and Appels 1982). In our materials, hexa- and octovalents occurred in about 2% of the cells in Johnsongrass and 0.5% of the cells in 40-chromosome hybrids. These frequencies, together with high pollen stainability, suggest that the multivalents were the manifestation of homoeologous pairing among the three genomes, A, B1 and B2.

Hadley (1953) suggested that Johnsongrass could have arisen from a cross between a species with the same genome as sorghum and an unknown species. If so, the latest female parent in the evolution of Johnsongrass may have come from a taxon within *S. bicolor*, since the mitochondrial DNA restriction patterns of Johnsongrass were similar to several patterns of different races within *S. bicolor* (Lee 1986). It was suggested that race arundinaceum (Doggett 1976), race virgatum (Bhatti et al. 1960), or *S. propinquum* (Celarier 1958) could have been one of the progenitors of Johnsongrass. Race virgatum can be eliminated from this list because our results indicate that race bicolor and race virgatum have completely homologous genomes (Fig. 1 B).

For breeding purposes, use of Johnsongrass with chromosome behaviors in hybrids similar to those of PI266965 is advantageous because greater recombination is expected at both 30- and 40-chromosome levels. If it is desirable to transfer genes from Johnsongrass to sorghum at the 20-chromosome level, backcrossing of sorghum to 30-chromosome hybrids or to progeny of the hybrids would be suggested. Although highly sterile, the 30-chromosome hybrids did set a few seeds that gave rise to plants with chromosome numbers ranging from 20–22, as seen in our laboratory. Selection of backcross progeny at the 20-chromosome level would be easier and more effective than at the 40-chromosome level with subsequent reduction to the 20-chromosome level. With the use of embryo rescue techniques, a large number of 30-chromosome hybrids can easily be obtained for any backcross breeding strategy. Thus, selection at the 40-chromosome level is no longer necessary.

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