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Cytological studies of triploids and their progeny from male-sterile (*ms1*) soybean *

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Summary. Triploids (2n = 3X = 60) were obtained from genetic male-sterile (*ms1 ms1*) soybean [*Glycine max* (L.) Merr.] plants. Meiosis, pollen fertility, and chromosome number of their progeny were studied. Studies of meiosis in fertile and sterile triploids revealed no distinguishable differences in chromosome associations. Male-sterile plants formed coenocytic microspores characteristic of the *ms1* mutant. Restitution of some dyad and tetrad nuclei were observed in male-sterile plants. Chromosomes of the triploids tended to occur in trivalents during diakinesis and metaphase I (MI), but multivalents, bivalents, and univalents also were observed. Average types and frequencies of chromosome associations per cell in diakinesis and MI from 542 pollen mother cells were 0.004 IX + 0.06 VI + 0.002 V + 0.005 IV + 16.99 III + 1.79 II + 5.03 I. Some secondary associations, nonhomologous pairing, and aberrant nucleolar distributions occasionally were observed. Such behavior support the hypothesis of duplicated genomes and the polyploid origin of soybean. Pollen fertility in male-fertile triploid plants (*Ms1 ms1 ms1*) varied from 57% to 82%, with an average of about 71%. Chromosome numbers of progenies obtained from these fertile triploids varied from 2n = 40 to 2n = 71, and exhibited a near-random distribution, with the majority (about 60%) being between 56 and 65. Progenies of the fertile triploids gave segregation ratios for the *ms1* allele, which confirmed the *Ms1 ms1 ms1* genotype.

Key words: *Glycine max* (L.) Merr. – Meiosis – Chromosome pairing – Aneuploid

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Introduction

Triploids are one of the primary sources of aneuploids in most plant species (Khush 1973). In soybean [*Glycine max* (L.) Merr.], previous attempts to produce triploids (2n = 3X = 60) through artificial cross-pollination and natural cross-pollination between autotetraploids and diploids were unsuccessful (Porter and Weiss 1948; Sadanaga and Grindeland 1981). Sadanaga and Grindeland (1981) noted that the failure to obtain triploids from crosses between diploids and induced tetraploids could be explained either by the hypothesis that endosperm development depends on a 2 : 1 ratio of female to male genomes (Nishiyama and Inomata 1966), or by the endosperm balance number (EBN) hypothesis (Johnston et al. 1980). Under either hypothesis, crosses between diploid and induced autotetraploid soybean fail to produce triploids because the maternal : paternal genome or EBN ratio is 4 : 1 when the autotetraploid is the female parent and 1 : 1 when the diploid is the female parent.

Haploids and polyploids (including triploids) can be obtained spontaneously by screening progeny of homozygous recessive male-sterile (*ms1 ms1*) soybean (Kenworthy et al. 1973; Cutter and Bingham 1977; Beversdorf and Bingham 1977; Chen et al. 1985).

Homozygous recessive *ms1 ms1* soybean plants are characterized by formation of coenocytic microspores, which result from failure of cytokinesis after telophase II of meiosis (Albertsen and Palmer 1979). Observations of abnormal embryosac development and multiple nuclei in megagametophytes (Cutter and Bingham 1977; Kennell 1984) provided some clue to the origin of these polyploids. Kennell (1984), in a study of megasporogenesis and megagametogenesis of the *ms1* lines with light and electron microscopy, indicated that partial or complete failure of cytokinesis at meiosis resulted in four-nucleate functional megaspores. These four nuclei may lead to mature megagametophytes with four times the normal number of nuclei. Kennell (1984) pointed out that degeneration

and/or nuclear fusion of developing nuclei result in mature gametophytes varying in nuclear number from 8 to 32. Thus, spontaneous triploids occurring among progeny of *ms1 ms1* plants could be the fusion product of a 2n egg fertilized by an n sperm.

Our objectives were to study the meiotic chromosome associations in triploid soybeans occurring among progeny of male-sterile *ms1 ms1* plants and to determine chromosome numbers of progenies of these triploids.

Materials and methods

Triploid soybeans obtained from a previous study (Chen et al. 1985) were used. Chromosome numbers were determined from root tips of polyembryonic and abnormal seedlings in progeny of homozygous recessive male-sterile (*ms1 ms1*) plants (Palmer and Heer 1973). Triploid plants of these polyembryonic and abnormal seedlings were grown in the greenhouse.

Coenocytic microspores from male-sterile plants generally are large and darkly stained by I_2KI. Pollen grains from fertile plants stain a dark golden brown with I_2KI. At the time of flowering, fresh open flower buds were collected from each triploid plant, fixed in 70% ethanol, and classified as male sterile or male fertile on the basis of pollen stainability. At least two flower buds were collected per plant, and at least 400 coenocytic microspores or pollen grains were classified per sample. Pollen diameters were measured on 100 grains per sample for 10 male-fertile triploid plants, 10 male-sterile triploid plants, two male-fertile diploid plants, and two male-sterile diploid plants.

For meiotic studies, young flower buds from 12 male-fertile triploid plants and eight male-sterile triploid plants were fixed in 6:3:2 ethanol:chloroform:propionic acid, and placed under a vacuum to enhance penetration of the fixative. Samples were fixed for 48 h and then stored in 70% ethanol at 4 °C. For slide preparation, flower buds were dissected, smeared with a drop of 45% acetic acid or propionic acid, and stained with a drop of either aceto-carmine or propio-carmine.

Seeds obtained from fertile triploids were germinated and chromosome numbers were determined from root tips following the method of Palmer and Heer (1973). These seedlings also were transplanted and maintained in the greenhouse and classified as male fertile or male sterile on the basis of stainability and morphology of pollen grains and coenocytic microspores.

Results

Of the 68 triploids obtained, 32 were classified as male fertile and 36 were male sterile, which fit the expected 1:1 segregation ratio ($\chi^2 = 0.24$; $P = 0.75$–0.50), because fertile plants are maintained as heterozygotes (*Ms1 ms1*) and seed are harvested only from the male-sterile plants. Diploid progeny of sterile *ms1 ms1* plants should be either *Ms1 ms1* or *ms1 ms1*. Seed obtained from these sterile plants probably are the result of fertilization of an *ms1* ovule by an *Ms1* or *ms1* gamete, from the *Ms1 ms1* fertile sib plants. Thus, the genotype of male-fertile triploids is *Ms1 ms1 ms1*, and that of male-sterile triploids is *ms1 ms1 ms1*. These plants are the result of fertilization by an *Ms1* or *ms1* male gamete with an *ms1 ms1* ovule.

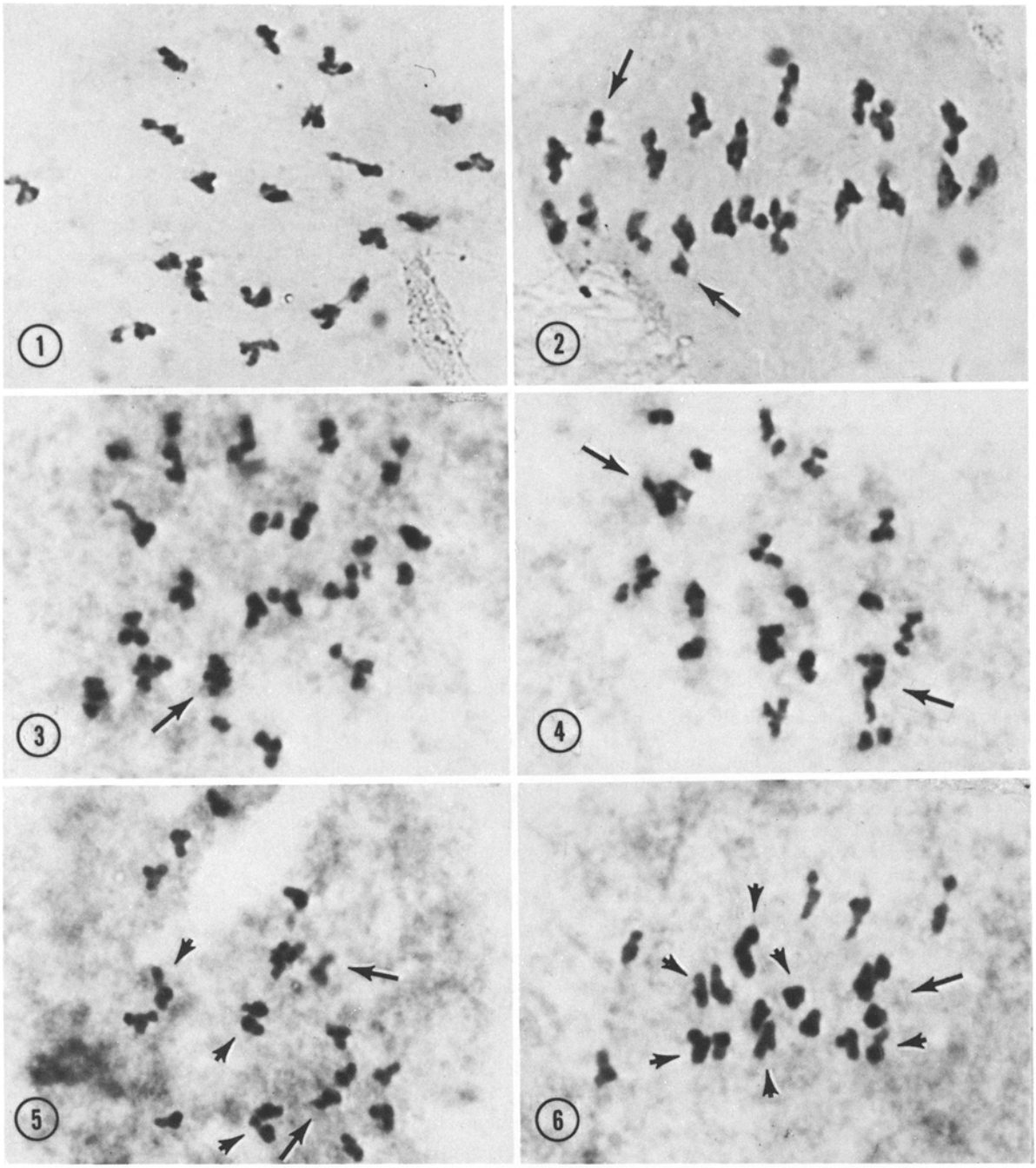
Meiotic studies

In general, meiotic observation of pollen mother cells (PMC) among male-fertile and male-sterile triploids revealed no distinguishable differences, except for the formation of coenocytic microspores after telophase II of meiosis, which characterized the *ms1 ms1 ms1* genotype, and restitution of some dyads and tetrads in the male-sterile plants.

Study of the pachytene stage is difficult because of the large number of chromosomes involved and the overlapping of most chromosomes throughout their entire length. However, in the limited number of cells observed, some chromosomes were loosely paired and association of homologues was not always complete. Frequently segments of chromosome strands were unpaired, or interpaired with a third chromosome. This allowed for formation of trivalents.

Diakinesis through metaphase I (MI) provided cells with more clear figures for interpretation of chromosome associations (Figs. 1–6). Chromosomes of the triploids tended to occur as trivalents from diakinesis to MI. From a total of 542 cells observed, 28% exhibited 20 trivalents and 20% had 19 trivalents (Table 1; Figs. 1 and 2). About 4% of the cells showed no chromosome pairing. Multivalents other than trivalents were observed; they might be the result of nonhomologous pairing or of close secondary association (Figs. 3 and 4). As indicated by an asterisk (*) in Table 1, 10% of the cells observed in male-fertile triploids involved nonhomologous pairing or secondary association, compared with 5% in male-sterile plants. The difference may be due to the number of cells observed. The average types and frequencies of chromosome associations per cell in diakinesis or MI were 0.004 IX + 0.06 VI + 0.002 V + 0.005 IV + 16.99 III + 1.79 II + 5.03 I.

Anaphase I chromosome distribution showed that gametic chromosome numbers between 35 and 26 were most frequent. Chromosome laggards were found in both male-fertile and male-sterile plants. About 65% of the anaphase I cells manifested laggards, the number varying from 1 to 6. However, only one to two laggards were observed most frequently. In prophase II of male-sterile plants, some dyads seemingly tended toward fusion or restitution. This phenomenon was not found in male-fertile plants. About 66% of the cells observed in prophase II, metaphase II, and anaphase II exhibited lagging chromosomes. Laggards were observed infrequently after telophase II, possibly because they formed micronuclei. Coenocytic microspores formed in the male-sterile plants, and a tendency toward restitution of



Figs. 1–6. Meiotic diakinesis or metaphase I cells from triploid soybean plants. **1** 20 trivalents (III) ×1930; **2** 19 III+II (*arrow*)+I (*arrow*) ×2130; **3** 17 III+II+3 I and 1 possible IV or close secondary association (*arrow*) ×2480; **4** 13 III (including 2 III overlapped) +1 VI (*arrow*) +1 V (*arrow*) +3 II+4 I ×2310; **5** 2 associations of 3 III (*long arrows*) and three associations of 2 III (*short arrows*) ×1920; **6** one association of 3 III (*long arrow*) and six associations of 2 III (*short arrows*) ×2390

the four daughter nuclei was observed in some cells. In tetrads, occurrence of more than two nucleoli in microspores and two nucleoli in more than two microspores of a quartet were observed frequently in both male-sterile and male-fertile triploid plants. This is not unexpected because diploid meiocytes with more than one nucleolus in member of a quartet were observed occasionally in our study.

Secondary associations

Groups of trivalents, which are similar in size and in configuration and tend to lie in close approximation in

Table 1. Frequencies and types of chromosome associations in pollen mother cells of triploid soybean at diakinesis or metaphase I of meiosis

Types of chromosome associations	No. of cells observed		Total		%
	Male-fertile plants	Male-sterile plants			
20 III	120	34	154		28.4
19 III + II + I	60	45	105	110	20.3
19 III + 3 I	5	0	5		
18 III + VI*	5	2	7		
18 III + 3 II*	5	3	8	95	17.5
18 III + 2 II + 2 I	38	36	74		
18 III + II + 4 I	3	3	6		
17 III + VI + II + I*	4	0	4		
17 III + IV + II + 3 I*	1	0	1		
17 III + 3 II + 3 I	25	15	40	47	8.7
17 III + 2 II + 5 I	1	0	1		
17 III + II + 7 I	1	0	1		
16 III + 2 VI*	2	0	2		
16 III + VI + 2 II + 2 I*	6	0	6		
16 III + 2 IV + 2 II*	1	0	1		
16 III + 6 II*	1	0	1	39	7.2
16 III + 4 II + 4 I	18	7	25		
16 III + 3 II + 6 I	3	0	3		
16 III + 2 II + 8 I	1	0	1		
15 III + VI + 3 II + 3 I*	1	0	1		
15 III + 6 II + 3 I*	3	0	3		
15 III + 5 II + 5 I	15	5	20	25	4.6
15 III + 2 II + 11 I	1	0	1		
14 III + 3 VI*	1	0	1		
14 III + VI + 2 IV + 2 II*	0	1	1		
14 III + VI + 6 II*	0	1	1		
14 III + 7 II + 4 I*	1	1	2	22	4.1
14 III + 6 II + 6 I	10	4	14		
14 III + 5 II + 8 I	1	1	2		
14 III + 4 II + 10 I	0	1	1		
13 III + VI + V + 3 II + 4 I*	1	0	1		
13 III + VI + 6 II + 3 I*	1	0	1		
13 III + 9 II + 3 I*	1	0	1	6	1.1
13 III + 7 II + 7 I	1	2	3		
12 III + 10 II + 4 I*	1	0	1		
12 III + 9 II + 6 I*	1	0	1		
12 III + 8 II + 8 I	2	1	3	7	1.3
12 III + 6 II + 12 I	1	0	1		
12 III + 3 II + 18 I	0	1	1		
11 III + 2 IX + VI + 3 I*	1	0	1	2	0.4
11 III + 10 II + 7 I*	0	1	1		
10 III to 3 III[a]	4	2	6		1.1
8 II to 1 II[b]	7	0	7		1.3
60 I	19	3	22		4.0
Total no. of cells observed	373	169	542		
Average no. of III's	16.7	17.6	17.0		
No. of cells with non-homologous pairing or secondary association	37	9	46		
%	9.9	5.3	8.5		

* Association involved either nonhomologous pairing or secondary association

[a] Combined data from 10 III to 3 III plus some II's and I's

[b] Combined data from no III but 8 II to 1 II plus some I's

MI, are considered as secondary associations (Figs. 5 and 6). Studies on secondary chromosome associations in soybean are difficult because of the lack of any chromosome morphology marker, the similarity of the small chromosomes, and the obstruction by other chromosome pairs and univalents. Therefore, records were made only from 40 clear MI figures (Table 2).

Types of secondary chromosome associations include association of three trivalents and two trivalents (Figs. 5 and 6). The number of associations of three varied from 0 to 2 per cell, while the number of associations of two varied from 0 to 6 per cell. Most of the cells observed exhibited no association of three, but had some degree of associations of two trivalents. Furthermore, the apparent nonhomologous associations found in some cells might actually have been close secondary associations.

Pollen fertility

Pollen and coenocytic microspores can be distinguished easily by I_2KI stainability as well as diameters from both diploids and triploids (Figs. 7–10). Average pollen

Table 2. Frequency of possible secondary chromosome associations in metaphase I of meiosis in triploid soybean plants

Types of associations	No. of cells observed	%
2 (3) + 5 (2) + 4 (1)[a]	1	
2 (3) + 4 (2) + 6 (1)	2	
2 (3) + 3 (2) + 8 (1)	1	
2 (3) + 2 (2) + 10 (1)	2	
2 (3) + 1 (2) + 12 (1)	2	
Total	8	20.0
1 (3) + 6 (2) + 5 (1)	1	
1 (3) + 5 (2) + 7 (1)	2	
1 (3) + 4 (2) + 9 (1)	2	
1 (3) + 3 (2) + 11 (1)	2	
1 (3) + 2 (2) + 13 (1)	1	
1 (3) + 1 (2) + 15 (1)	1	
Total	9	22.5
0 (3) + 6 (2) + 8 (1)	2	
0 (3) + 5 (2) + 10 (1)	5	
0 (3) + 4 (2) + 12 (1)	5	
0 (3) + 3 (2) + 14 (1)	5	
0 (3) + 2 (2) + 16 (1)	2	
0 (3) + 1 (2) + 18 (1)	1	
Total	20	50.0
0 (3) + 0 (2) + 20 (1)	3	7.5
Grand total	40	

[a] No. in parentheses indicates number of chromosome trivalents associated; e.g., 2 (3) + 5(2) + 4 (1) indicates two groups of associations of three trivalents (18 chromosomes) plus five groups of associations of two trivalent (30 chromosomes) plus four individual trivalents (12 chromosomes)

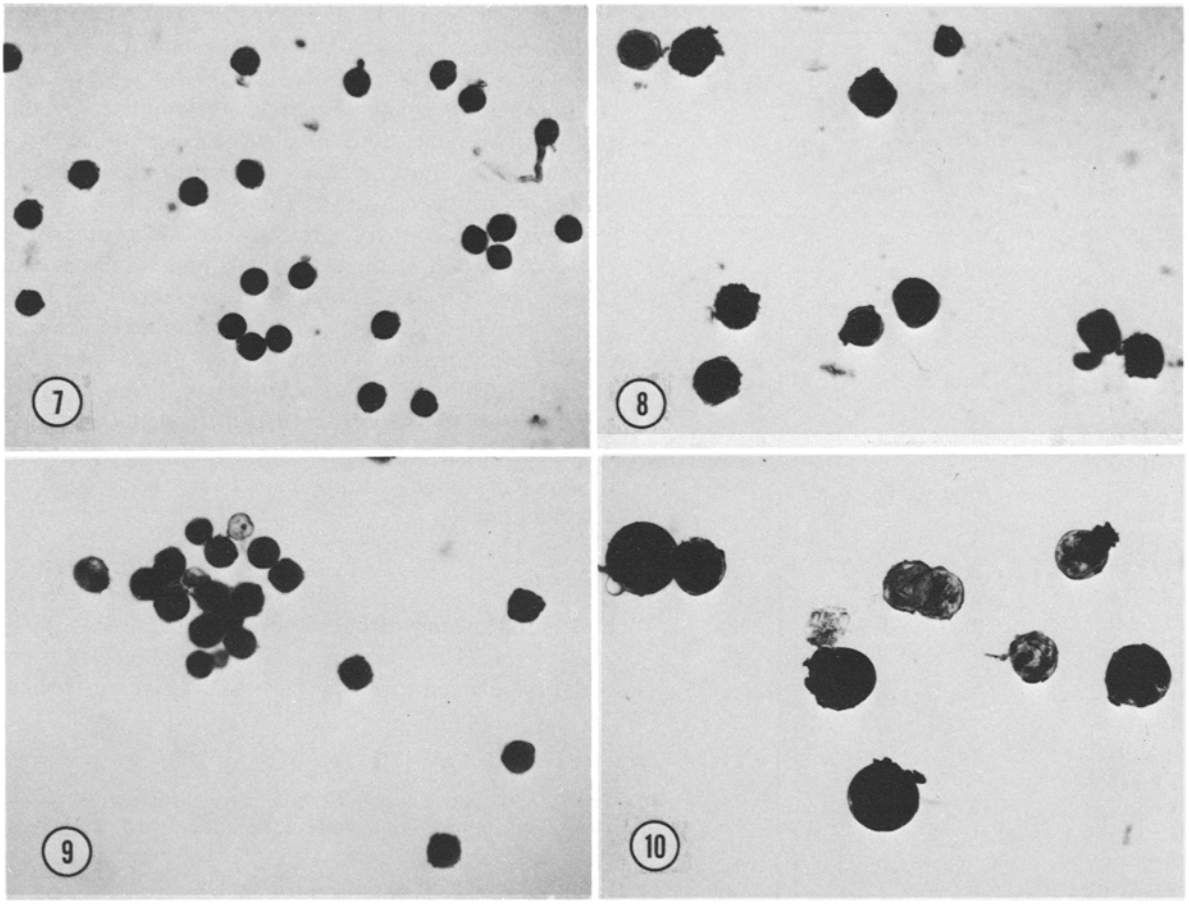


Fig. 7. Pollen from a male-fertile diploid plant. ×825

Fig. 8. Coenocytic microspores from a male-sterile diploid plant. ×825

Fig. 9. Pollen from a male-fertile triploid plant. ×825

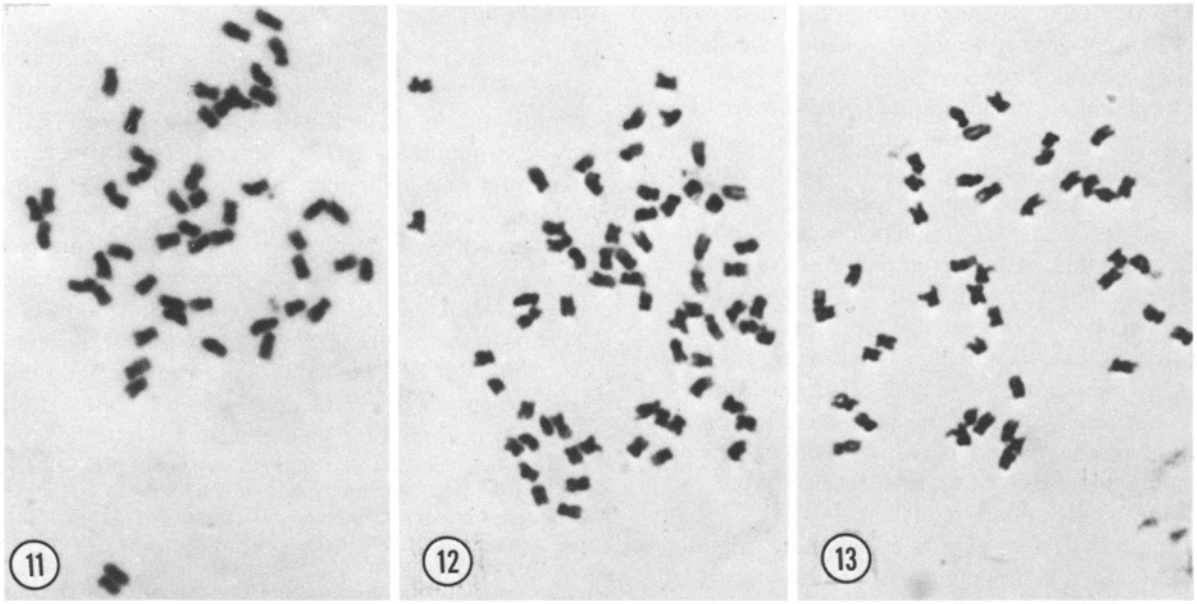
Fig. 10. Coenocytic microspores from a male-sterile triploid plant. ×825

diameters from diploid male-fertile and male-sterile plants were 19.2 ± 0.1 μm and 33.1 ± 0.4 μm, respectively. Pollen grain diameter from male-fertile triploid plants ranged from 19.0 to 33.3 μm, with an average of 23.8 ± 2.8 μm. Coenocytic microspore diameters from the male-sterile triploids varied from 28.6 to 47.6 μm with an average of 38.1 ± 3.8 μm.

In triploid male-fertile plants, four classes of pollen grains were noted: plump and fully stained; plasmolyzed and partially stained; darkly stained; and empty or aborted (unstained) (Fig. 9). The plump pollen grains represent the viable pollen grains. The plasmolyzed pollen grains suggest degeneration or deficiency. Pollen fertility in these male-fertile triploid plants varied from 57% to 82%, with an average of about 71%. A small portion (5%) of darkly stained pollen, similar to *ms1* pollen, also was observed. The percentage of darkly stained pollen grains in male-fertile plants varied from 0.8 to 9.3. This might be due to the incomplete penetrance of the *Ms1* allele, genotypic difference, or to dosage effect of *ms1*. Coenocytic microspores of male-sterile triploid plants were either darkly stained, plasmolyzed with partially dark stain, or aborted (Fig. 10). The frequencies of these types were 48%, 17%, and 35%, respectively.

Chromosome number

Number of seeds obtained from 32 fertile triploid plants varied from 1 to 13, whith an average of 4.4 per plant. Seeds from these male-fertile triploids were germinated and root tip chromosome number determined. A total of 140 viable progeny was obtained. Ninety-nine of these 140 progeny were grown to maturity.



Figs. 11–13. Mitotic chromosome number of some aneuploids obtained from triploids and their progenies. **11** 50-chromosome plant from a triploid progeny. ×2420; **12** 64-chromosome plant from a triploid progeny. ×2110; **13** 43-chromosome plant obtained from a 45-chromosome plant of a triploid progeny. ×1900

Table 3. Frequency and chromosome numbers from progenies of triploid soybean plants

Chromosome no.	No. of plants	%	Chromosome no.	No. of plants	%
40	2	1.4	58	10	7.1
44	1	0.7	60	26	18.6
45[a]	4	2.9	61	5	3.6
47	1	0.7	62	14	10.0
49	2	1.4	63	6	4.3
50	6	4.3	64	10	7.1
52	5	3.6	65	1	0.7
53[b]	5	3.6	66	10	7.1
54	6	4.3	67	2	1.4
55	5	3.6	68[c]	6	4.3
56	5	3.6	70	1	0.7
57	6	4.3	71[d]	1	0.7
			Total	140	

[a] One 45-chromosome plant set 23 seed of which 15 germinated; three progeny had 41 chromosomes; six had 42 chromosomes; 4 had 43 chromosomes, and 2 had 44 chromosomes

[b] One 53-chromosome plant gave one progeny with 50 chromosomes

[c] One 68-chromosome plant gave one progeny with 73 chromosomes

[d] The 71-chromosome plant gave four progeny, two with 72 chromosomes, and 2 with 74 chromosomes

Among these 99 plants, 23 were male sterile and 76 were male fertile. A chi-square test for a 3 : 1 segregation ratio was nonsignificant at the 5% level ($\chi^2 = 0.16$; $P = 0.50$–0.75), indicating that the male-fertile triploid parents were *Ms1 ms1 ms1*.

Chromosome numbers of the 140 progeny of these fertile triploid plants varied from 40 to 71, with a modal value around 60 (Figs. 11 and 12; Table 3). Only four aneuploid plants set seed and their progenies segregated for different chromosome numbers (Fig. 13; Table 3).

Discussion

Meiotic studies; secondary associations

Meiotic studies of male-fertile and male-sterile triploids revealed no distinguishable differences in chromosome associations at diakinesis or metaphase I. The numbers of trivalents observed varied from 0 to 20, with an average of near 17 (Table 1). Two enneavalents, associations of three trivalents, were observed in one cell. Several hexavalents, pentavalents, and quadrivalents also were noted in some cells at diakinesis or metaphase I. The occurrence of multivalents other than trivalents and the sum of groups of trivalents and bivalents not equivalent to the basic number 20 might be due to either 1) occurrence of nonhomologous association by chance, 2) close secondary association, 3) partial homology among the chromosomes associated, or 4) artifact of chromosome stickiness.

In our studies, about 9% of the pollen mother cells in diakinesis or metaphase I exhibited either multivalents or groups of trivalents + bivalents in excess of the basic number 20. This indicates that pairings could occur between nonhomologous chromosomes (Table 1, Figs. 3 and 4). Crane et al. (1982) described the occur-

rence of bivalents and secondary associations in haploid soybean (2n=20) derived from the genetic male-sterile (*ms1 ms1*) lines. They observed from 0 to 5 bivalents per cell at diakinesis or metaphase I. Our observation of from 0 to 3 hexavalents in triploids seems to be consistent with their finding of bivalents in haploid soybean. Cultivated soybean (*Glycine max*), which behaves cytogenetically and genetically as a diploid, has been suggested to be a tetraploid (Bernard and Weiss 1973; Hadley and Hymowitz 1973; Palmer 1976; Bingham et al. 1976; Crane et al. 1982; Lee and Verma 1984). However, no direct evidence has been provided. Recently, Jackson and Casey (1982) developed models to analyze meiotic configuration for classification of types of polyploidy. Nevertheless, we found it difficult to determine the exact chiasma frequency from our materials for the use of their model.

We believe that, if soybean is of polyploid origin or has a duplicated genome, the occasional occurrence of multivalents might be possible. Another indication is the occurrence of secondary chromosome associations. Secondary associations at meiosis have been interpreted as indicating distant relationships between different sets of chromosomes in allopolyploids (Darlington 1931; Lawrance 1931). This assumption has been proved to be accurate in wheat (*Triticum aestivum* [2n=42]) (Riley 1960; Kempanna and Riley 1964). Stebbins (1950) stated that, in most cases, secondary associations have been considered to be an indication of the polyploid nature of a species or genus; however, it might also be due to modification by segmental interchange, duplication of chromosomal segments, or other phenomena not at all related to polyploidy. In soybean, secondary association of three and two chromosomes were reported by Crane et al. (1982). In our studies, the maximum number of associations of three and two trivalents are two and six, respectively (Table 2). This also might correspond to the nonhomologous pairing observed in diakinesis or metaphase I.

Our finding of multivalents and secondary chromosome association in this study supports the allopolyploid or segmental allopolyploid origin of soybean. Complete verification of this hypothesis would be facilitated if certain genetic systems regulating specific pairing, such as the *Ph* locus in wheat (Sears and Okamoto 1958), were available in soybean.

Sorrells and Bingham (1979) pointed out that some *Ms1 ms1* plants produced restitution gametes in various stages of cytokinesis, although in the majority of plants microspore development seemed normal. In our study, most microspores in fertile triploids (*Ms1 ms1 ms1*) looked normal, whereas in sterile plants some restitution coenocytic microspores did occur. Thus, we believe that if restitution gametes did occur in fertile heterozygous *Ms1 ms1 ms1* plants the probability might be too low to be recognized in this study, or it might be affected by some other factors such as different genetic background or environmental conditions.

Pollen fertility

On the average, 71% of the pollen in male-fertile triploids is normally well stained; however, seed set was generally low in these triploids. Lin and Lee (1979), studying triploids in *Rhoeo,* observed an average of 45% normally stained pollen by using cotton blue stain; they found low seed set in these triploids. They suggested that the low fertility was due either to the fact that the cotton blue stain was probably not specific enough to differentiate between viable and nonviable pollen, or to the failure of zygote formation or development. Although I_2KI stainability did provide good differential between the *ms1* and non-*ms1* pollen, I_2KI stainability may not be a good indicator of fertility.

Schulz-Schaeffer (1980) pointed out that most of the gametes produced by autotriploid individuals do not have balanced chromosome complements and are not viable. Brink and Cooper (1947) noted that success of the embryo depends on the normal development of the endosperm in almost all species. Therefore, the low fertility in these triploids in our study could be attributed to 1) imbalance of gamete chromosome number, or 2) failure of zygotic development due to chromosome or genomic imbalance, or 3) failure of endosperm development.

Chromosome number

Both random and preferential chromosome segregations in meiosis were reported in triploid organisms (see Schulz-Schaeffer 1980). As shown in Table 3, the pattern of distribution in chromosome number in our selfed progeny of triploids seems very close to a random distribution with a majority (about 60%) falling between 56 and 65. The lack of chromosome numbers between 72 and 80 may be explained by 1) the chance of obtaining gametes with high hypodiploid or diploid chromosome number being lower than that of obtaining gametes with intermediate chromosome numbers, and 2) the competitive disadvantage of gametes with higher hypodiploid chromosome number being greater than that of hypermonoploid gametes.

Triploid progeny manifested 3:1 segregation for male fertility versus male sterility. This might be the result of random segregation of the chromosome involved in the male-sterile phenotype. Thus, it provides evidence to verify the genotype of the triploid *Ms1 ms1 ms1* plants that result from the fertilization of an *ms1 ms1* ovule by *Ms1* pollen. This is further supported by the finding of potential fusion of nuclei in female embryo sacs of *ms1 ms1* plants (Kennell 1984), providing some evidence for the formation of polyploids found in the homozygous recessive *ms1 ms1* progeny.

Most of the aneuploids produced from self progeny of these triploids had chromosome number higher than the diploid level, precluding their use in genetic studies. However, among the self progeny of a 45-chromosome plant were three plants with 41 chromosomes, six with

42, four with 43, and two with 44 chromosomes. These aneuploids could be used for establishing trisomic lines and in genetic studies. The possible random distribution of chromosome segregation observed in this study suggests that crosses of fertile diploids with these triploids might produce trisomic plants.

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