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The frequency of polyembryonic seedlings and polyploids from ms_1 soybean *

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Summary. Seed from homozygous recessive ms_1 genetic male-sterile soybean (*Glycine max* (L.) Merr.) plants was studied for frequencies of polyembryonic seedlings and different levels of polyploidy among abnormal seedlings from six different source populations: Ames ms_1 (Ams), North Carolina ms_1 (NCms), Tonica ms_1 (Tms), Urbana ms_1 (Ums), and F_4 generation seed obtained from crosses of ms_1 to two chromosome interchange lines (Ams × Clark T/T and Ums × KS-172-11-3). Frequencies of polyembryony observed in Tms, Ums, Ams, NCms, F_4 seed from Ams × Clark T/T, and F_4 seed from Ums × KS-172-11-3 were 3.6%, 2.4%, 3.1%, 2.5%, 2.2% and 0.1%, respectively. Frequencies of abnormal seedlings from these six sources varied from 1.7% (Ums × KS-172-11-3) to 16.8% (Ams × Clark T/T). Frequencies of polyploids among the abnormal seedlings ranged from 6.8% in Ums × Ks-172-11-3 to 66.7% in Tms. On average, the frequency of polyploid individuals from monoembryonic seedlings was 1.22%. Chromosome number of these seedlings varied from 20 to 200. Variation of the frequencies of polyembryonic seedlings and polyploid progeny among abnormal seedlings suggested that the mechanism(s) controlling the characters of polyembryony and formation of polyploids was associated with the ms_1 gene and was affected by other gene(s) or environmental factors.

Key words: Soybean – *Glycine max* (L.) Merr. – Male sterile – Polyploidy – Polyembryony

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Introduction

The first report of male-sterile, female-sterile soybean (*Glycine max* (L.) Merr.) plants was by Owen (1928).

Synaptic male-sterile mutants were reported by Hadley and Starnes (1964); Palmer (1974), and Palmer and Kaul (1983). Partial male-sterility systems are known: Arkansas partial male-sterile (Caviness et al. 1970) and *msp* (Stelly and Palmer 1980a, b). Completely male-sterile, female-fertile mutants are ms_1 (Brim and Young 1971; Palmer et al. 1978; Yee and Jian 1983), ms_2 (Graybosch et al. 1984), ms_3 (Palmer et al. 1980) and ms_4 (Delannay and Palmer 1982). A structural male-sterile mutant $fs_1 fs_2$ was described by Johns and Palmer (1982). Within the ms_1 and ms_4 sterile systems, the formation of coenocytic microspores is due to the failure of cytokinesis after telophase II of meiosis. In ms_4 there is either early degeneration of coenocytic microspores or further division of the microspore (Delannay and Palmer 1982), whereas in ms_1 most coenocytic microspores do not undergo complete cell division, but differentiate into large grains (Albertsen 1976; Albertsen and Palmer 1979). Similar phenomena also were noted in two male-sterile lines by Rubaihayo and Gumisiriza (1978).

In addition to the formation of coenocytic microspores, homozygous recessive $ms_1 ms_1$ plants also were associated with the production of polyembryonic seedlings, haploids, and polyploids in their progenies (Kenworthy et al. 1973; Cutter and Bingham 1977; Beversdorf and Bingham 1977; Crane et al. 1982). Polyembryony, haploidy, and polyploidy, as explained by Cutter and Bingham (1977), result from abnormal embryo-sac development, producing supernumerary nuclei and restitution of these extra nuclei before fertilization.

On the average, the frequency of polyembryony reported among progeny of homozygous recessive $ms_1 ms_1$ plants is 4.0%, 2.3%, and 2.2%, respectively (Kenworthy et al. 1973, Beversdorf and Bingham 1977; Sorrells and Bingham 1979). The seed for these three studies, however, all came from North Carolina ms_1 (Brim and Young 1971). There are at least five independent mutations at the ms_1 locus in soybean. Four mutants, designated the North Carolina, Urbana, Tonica, and Ames male steriles, arose spontaneously and independently of each other in the United States (Palmer et al. 1978). Another

mutation at the ms_1 locus is the Shennong male sterile recently reported in China (Yee and Jian 1983).

Occurrence of twin seedlings from non-male-sterile soybeans was reported by Owen (1928b) in the study of inheritance of cotyledon colors in a Chinese variety; the frequency of double-embryo seeds was 0.44%. Shorter and Byth (1975) reported relatively high frequencies (6.3% to 13.0%) of twin seedlings in three Australian cultivars. However, from their limited number of chromosome counts, all twin seedlings examined were diploid-diploid except for one diploid-haploid.

The objective of our study was to examine the relationships among polyembryonic seedlings, polyploids, haploids, and male sterility. To provide more genetic information on the action of the ms_1 gene, we report frequencies of polyembryonic seedlings and polyploids from $ms_1\,ms_1$ male-sterile progeny among different seed-source populations. The samples examined were from four independent source populations and two derived populations.

Materials and methods

Seed harvested from homozygous recessive $ms_1\,ms_1$ plants was obtained from six different source populations: North Carolina ms_1 (NCms) T260, Urbana ms_1 (Ums) T266, Tonica ms_1 (Tms) T267, Ames ms_1 (Ams) T268, and F_4 seeds from the cross of ms_1 to two homozygous chromosome interchange lines (Ams × Clark T/T and Ums × KS-172-11-3). Seed from T260 were obtained from Dr. C. A. Brim, North Carolina State University. Seed from the other populations were grown at Ames, Iowa. The T number refers to the Soybean Genetic Type Collection number.

The origin of the four independent ms_1 mutants was as follows: North Carolina ms_1 was found in a farmer's field by inspectors from the North Carolina Certified Seed Growers' Association in 1966 (Brim and Young 1971). Urbana ms_1 was found in an F_3 row from the cross of 'Clark-*S*' × SRF 300 at Urbana, Illinois, 1971 (Boerma and Cooper 1978). Tonica ms_1 was found in a field of 'Harosoy' by a farmer at Tonica, Illinois in 1955 (Palmer et al. 1978). Ames ms_1 was found in a row segregating for desynaptic mutant st_4 at Ames, Iowa, in 1970 (Palmer et al. 1978).

The two interchange lines used for crosses with ms_1 lines were: Clark T/T, a near-isogenic cultivar 'Clark' with an interchange from PI 101404B (a *Glycine soja* accession from Northeastern China) and KS-172-11-3, an interchange involving the satellite chromosome from an irradiated population of the cultivar 'Hodgson' (Sadanaga and Newhouse 1982). The derived populations (Ams × Clark T/T and Ums × KS-172-11-3) have trisomic segregation for white flower (w_1) and ms_1 both of Linkage Group 8.

Seed were germinated and chromosome number determined by use of the procedure of Palmer and Heer (1973).

Frequencies of polyembryonic and abnormal seedlings and of polyploids among the polyembryonic seedlings, the abnormal seedlings and total number of seed planted from the six source populations were tested for homogeneity by the formula: $X^2 = (\Sigma\, p_i\, a_i - \bar{p}\, A)/\bar{p}\,\bar{q}$. Differences among populations were tested, on the basis of

$$Z = \frac{P_1 - P_2}{\sqrt{\bar{p}\,\bar{q}\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$ (Snedecor and Cochran 1980)

Where

$\bar{p}$ = frequency of events over all seed sources;
$\bar{q} = (1 - \bar{p})$;
P_i = frequency of events in i source;
a_i = number of events in i source;
n_i = number of observations in i source; and
A = total number of events over all sources.

Results and discussion

A total of 159 sets of polyembryonic seedlings (146 twins, 12 triplets, and a quadruplet) was found among 9,153 seed planted from the six sources (Table 1). Chromosome numbers of the twins included diploid-diploid, haploid-diploid, diploid-triploid, diploid-tetraploid, triploid-triploid, triploid-tetraploid, and tetraploid-tetraploid. Figure 1 shows chromosomes of a 2n = 20 plant (a haploid) as one member of a twin. From the 12 triplets, only one set showed a triploid-triploid-unknown, while all others manifested 2n = 40. The quadruplet had a chromosome number of 100 in each individual seedling. In this study, the majority of the twins were at the diploid chromosome level, which agrees with the findings of Beversdorf and Bingham (1977) and Cutter and Bingham (1977).

Seed that were slow in germinating usually were either very small or very large and seedlings hat visibly abnormal

Fig. 1. Mitotic chromosomes of a haploid (2n = 20) seedling obtained from progeny of Ames ms_1 source, A75-1187 sterile plant (× 1,950)

Fig. 2. Mitotic chromosomes of a diploid (2n = 40) seedling obtained from Ames ms_1 source, A75-1180 sterile plant (× 1,100)

Fig. 3. Mitotic chromosomes of a triploid (2n = 60) seedling from progeny of Tonica ms_1 source, P327-1 sterile plant (× 1,950)

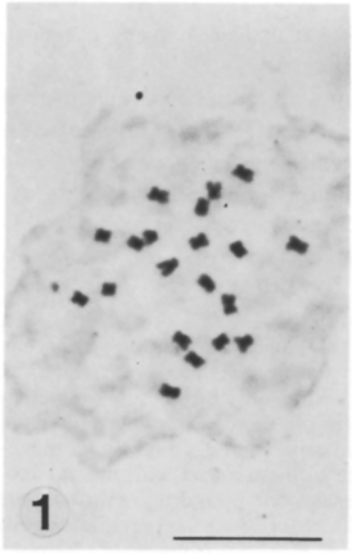
Fig. 4. Mitotic chromosomes of a tetraploid (2n = 80) seedling from progeny of Tonica ms_1 source, P13 sterile plant (× 1,950)

Fig. 5. Mitotic chromosomes of a hexaploid (2n = 120) seedling from progeny of Tonica ms_1 source, P8 sterile plant (× 1,950)

Fig. 6. Mitotic chromosomes of a pentaploid (2n = 100) seedling from progeny of Ames ms_1 source, A75-1187 sterile plant (× 1,950)

Fig. 7. Mitotic chromosomes of an octoploid (2n = 160) seedling from progeny of North Carolina ms_1 source, A77-336-16 sterile plant (× 1,100)

Fig. 8. Mitotic chromosomes of a decaploid (2n = 200) seedling from progeny of Tonica ms_1 source, A75-1189 sterile plant (× 1,200)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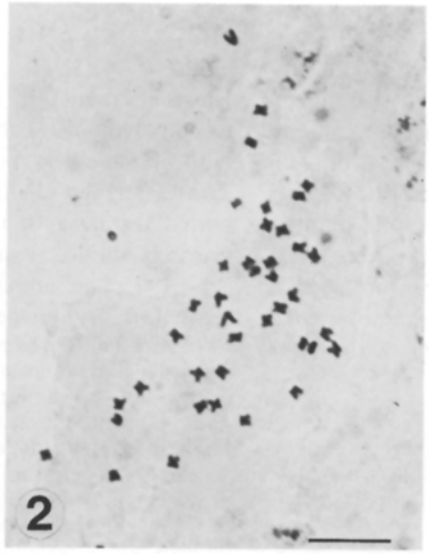
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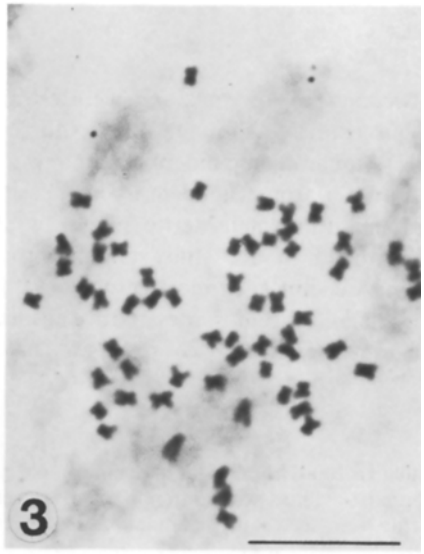
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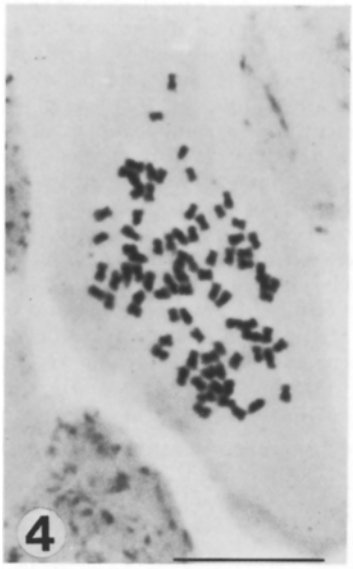
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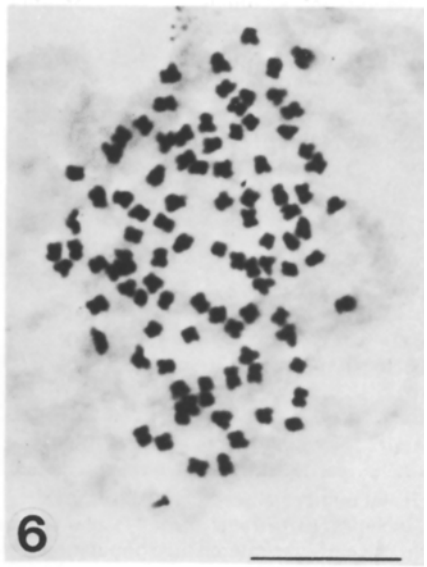
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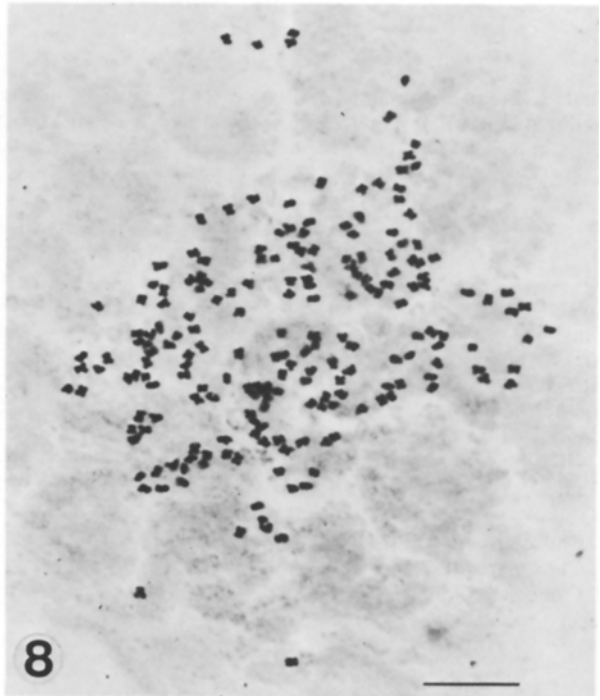
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cotyledons and/or roots and were classified as abnormal seedlings. Although Beversdorf and Bingham (1977) found a haploid plant among a population of 800 plants from monoembryonic seed produced by early-maturing male-sterile plants, no haploid plants were found in our study among progeny from abnormal seedlings. In most cases, these abnormal seedlings had 40 chromosomes and we suspect the observed abnormalities were the result of natural variation.

Table 1. Total number of polyembryonic seedlings and abnormal seedlings with different ploidy levels from six male-sterile (ms_1) seed source populations in soybean[a]

Polyembryonic seedlings		Abnormal seedlings	
Chromosome no.	No. of sets observed	Chromosome no.	No. of plants observed
40-40	113	20	0
20-40	5	40	264[b]
40-60	19	60	35
40-80	3	80	24
60-60	1	100	6
60-80	3	120	8
80-80	2	140	15
40-40-40	11	160	12
60-60-?	1	180	2
100-100-100-100	1	200	2
		?[c]	8
Total	159	Total	376

[a] Total number of seed planted was 9,153
[b] Includes 10 trisomic (2n=41) plants segregating from the two chromosome interchange populations
[c] Chromosome number unconfirmed, but above diploid level

However, about 30% of the abnormal seedlings proved to be polyploids (Tables 1 and 3). Chromosome numbers of these ms_1 progenies varied from 2n = 40 to 2n = 200 (Figs. 2–8). This is the highest ploidy reported from ms_1 homozygous recessive progenies. In previous studies, Palmer and Heer (1976) reported a 2n = 180 plant among the progeny of Tonica male-sterile (ms_1 ms_1) soybean plants.

Cutter and Bingham (1977) suggested that polyembryony and polyploidy in ms_1 ms_1 progenies resulted from abnormal embryo sac development, with subsequent supernumerary nuclei and the restitution of these extra nuclei before fertilization. Haploids could arise from egg sacs by parthenogenetic development of one of these nuclei with the gametophytic chromosome number or perhaps androgenetically. Sorrells and Bingham (1979) reported the predominance of diploids and of polyploids in F_1 plants from crosses between ms_1 haploids and diploids. Only 4 of 67 F_1 plants proved to be trisomics (2n = 41). They suggested that the restitution gamete production associated with the ms_1 allele carried by the haploid reduced the efficiency of isolating aneuploids. In our studies, the ploidy levels are multiples of 20 instead of 40, i.e., the multiple of the gametic, not the sporophytic, chromosome number. Albertsen and Palmer (1979) reported that male sterility in the various ms_1 mutants was caused by the failure of cytokinesis following telophase II of meiosis. The four nuclei become enclosed in a single-celled structure, followed by either degeneration or the occasional development of extensions resembling pollen tubes. Whether these pollen-like tubes can effect fertilization and/or occurrence of polyploidy is not known. Sterile ms_1 ms_1 plants occasionally produced seed in the greenhouse where pollinating vectors seemed to be absent (Cutter 1975; Palmer and Heer 1976).

The frequency of polyembryonic seedlings was 2 to 4% for five male-sterile source populations (Table 2) which agrees with the results of Kenworthy et al. (1973), Sorrells and Bingham (1979), and Beversdorf and Bingham (1977). The F_4 seed from Ums × KS-172-11-3 gave an extremely low frequency (0.1%)

Table 2. Frequency of polyembryonic seedlings and number of diploid seedlings vs. non-diploid seedlings in polyembryonic seedlings from six male-sterile (ms_1) seed source populations in soybean

Seed source	No. of seed planted	Polyembryony sets		No. of polyembryonic individuals			
		No.	%[a]	Total	Diploid	Non diploid	% of Non diploid[b]
Tms	1,051	38	3.6[ac*]	79	64	15	19.0
Ums	905	22	2.4[b]	45	39	6	13.3
Ams	784	24	3.1[ab]	52	45	7	13.5
NCms	2,474	61	2.5[b]	127	115	12	9.4
Ams × Clark T/T	464	10	2.2[bc]	20	15	5	25.0
Ums × KS-172-11-3	3,475	4	0.1[d]	8	8	0	0.0
Total	9,153	159	1.7	331	286	45	13.8

[a] Chi-square (df=5) for homogeneity = 98.01 P<0.01
[b] Chi-square (df=5) for homogeneity = 6.43 P=0.50–0.25
* Frequencies followed by the same letter are not significantly different from one another at the 5% level

Table 3. Frequency of abnormal seedlings and number of diploids and polyploids among the abnormal seedlings from six male-sterile (ms_1) seed source populations in soybean

Seed source	No. of seed planted	Abnormal seedlings				% polyploid among no. of seed planted[b]
		No.	%[a]	No. of polyploids	% polyploid[b]	
Tms	1,051	54	5.1[b*]	36	66.7[a*]	3.43[b*]
Ums	905	33	3.6[b]	10	30.3[bc]	1.11[c]
Ams	784	42	5.4[b]	10	23.8[cd]	1.28[c]
NCms	2,474	110	4.4[b]	16	14.5[cd]	0.65[c]
Ams × Clark T/T	464	78	16.8[a]	36	46.2[b]	7.76[a]
Ums × KS-172-11-3	3,475	59	1.7[c]	4	6.8[d]	0.12[d]
Total	9,153	376	4.1	112	29.8	1.22

[a] Chi-square (df = 5) for homogeneity of frequency of abnormal seedlings = 249.66; $P < 0.01$
[b] Chi-square (df = 5) for homogeneity of frequency of polyploids among abnormal seedlings and among number of seed planted are 72.89 and 248.26, respectively; $P < 0.01$
* Frequencies followed by the same letter are not significantly different from one another at the 5% level

of polyembryonic seedlings. Incidence of seedlings with chromosome number other than the diploid level among polyembryonic seedlings was 19.0%, 13.3%, 13.5%, 9.4%, 25.0%, and 0% in Tms, Ums, Ams, NCms, F_4 seed of Ams × Clark T/T, and F_4 seed of Ums × KS-172-11-3, respectively.

Frequencies of abnormal seedlings among male-sterile progeny were much more uniform among the four original ms_1 seed-source populations [Ams (5.4%), Tms (5.1%), NCms (4.4%), and Ums, (3.6%)] than between F_4 seed of the two interchange crosses Ams × Clark T/T (16.8%) and Ums × KS-172-11-3 (1.7%) (Table 3).

The percentage of polyploids found among these abnormal ms_1 progenies varied with seed source (Table 3). Tonica ms_1 had the highest percentage (66.7%) of polyploidy among abnormal seedlings, and F_4 seed of Ums × KS-172-11-3 had the lowest (6.8%). However, when the frequency of polyploidy among the total number of seed planted is considered, Ams × Clark T/T had the highest frequency (7.76%) and the F_4 seed of Ums × KS-172-11-3 had the lowest frequency (0.12%). This is a more conservative estimation of polyploidy because polyploids also were observed among normal-appearing seedlings but records were not made.

From our unpublished data, progenies of Ams × Clark T/T and Ums × KS-172-11-3 had trisomic inheritance for w_1 (white flower) and ms_1. In this study, three trisomic plants were found in abnormal seedlings from F_4 seed of Ams × Clark T/T and seven in Ums × KS-172-11-3.

Statistical tests on homogeneity are presented in Tables 2 and 3. Only the frequency of non-diploid ploidy levels among the polyembryonic progenies was homogeneous. The other parameters showed a heterogeneity among the six source populations. Thus, differences between each two source populations for the frequency of polyembryonic seedlings, abnormal seedlings, and polyploidy among the abnormal seedlings and among total number of seed planted were compared. Results indicated that F_4 seed of crosses of Ums × KS-172-11-3 had a significantly lower frequency than the other five seed sources in the occurrence of abnormal seedlings and polyploid progeny. Progeny of Tonica ms_1 differ in frequency of polyembryonic seedlings from Ums, NCms, and Ums × KS-172-11-3 (Table 2) and from all five other sources in frequency of polyploids from their abnormal seedlings (Table 3). No significant differences in frequency of polyploidy among total number of seed planted were found among the Ums, Ams, and NCms (Table 3). However, when each of the above three sources was compared with the other three populations respectively, the difference is statistically significant (Table 3).

Genetic control of the occurrence of polyembryonic seedlings in soybean is not clearly understood. Owen (1928b) found a frequency of 0.44% of twins in 5000 seed of a Chinese cultivar; he found no twins in similar examination of a number of other cultivars. The same tendency toward twinning also was found among F_2 seed and F_4 seed from crosses between the Chinese cultivar and other cultivars. Shorter and Byth (1975) reported that frequencies of twin seedlings from three Australian cultivars were 13.0%, 12.0%, and 6.3%. They observed twin seedlings among progenies of both normal plants and twin plants, but the frequency varied

when seed were produced in different environments. Only diploid-diploid twins and one haploid-diploid twin were found.

Beversdorf and Bingham (1977) also detected a lower frequency (0.7% in 800 seed planted) of polyembryony from maturity group I in male-sterile (ms_1) progeny than from later maturity groups. Boerma and Cooper (1978) reported that sterile plants from Ums tended to have a higher seed set and greater frequency of 2- and 3-seeded pods than did NCms sterile plants, which had predominantly 1-seeded pods. This suggested that Ums, on the basis of its female fertility, was phenotypically distinct from NCms, and they suggested either that Ums is a different allele from NCms or that Ums had closely linked modifier gene(s) that affect female fertility. Therefore, it is not known whether the genetic control of polyembryonic seedlings from non-male-sterile sources was the same as that of male-sterile sources.

In this study, measurement of differences in the frequency of polyembryonic seedlings and polyploids among different ms_1 seed source populations provided some evidence on the effect of different genetic background on the action of the ms_1 gene. Use of two derived populations (crosses of two ms_1 lines with two chromosome interchange lines) enabled us to see if any linked factors involved with ms_1, resulting from the interchange, could have an effect on the occurrence of polyembryony and polyploidy.

This study showed that variation occurred in frequencies of polyploidy and polyembryony when different source populations were used (Tables 2 and 3). Although the difference in frequency of polyembryony between F_4 seed of Ams × Clark T/T and the original Ams populations was not significant, a substantial decline in frequency was observed when comparing the F_4 seed of Ums × KS-172-11-3 to the Ums populations (Table 2). In comparing the two original ms_1 populations with the F_4-seed-derived ms_1 populations, the occurrence of polyploids is either increased (F_4 seed of Ams × Clark T/T vs. Ams) or decreased (F_4 seed of Ums × KS-172-11-3 vs. Ums) (Table 3). Therefore, the change of frequency of polyembryony and (or) polyploidy associated with the male-sterility (ms_1) character could be either intensified or reduced when different genetic background materials are introduced. This could be explained by a linkage of ms_1 with modifying genes.

The occurrence of polyembryony and polyploidy from all six ms_1 populations in this study confirmed the pleiotropic effects of the ms_1 gene on the frequency of polyembryony and polyploidy. As previously mentioned, frequency of polyembryonic seedlings was reported to vary when seed was produced in different environments (Shorter and Byth 1975). The NCms population was grown in North Carolina while the other five populations were grown in Iowa. Therefore, the variation in frequency of polyembryony and polyploidy displayed by the different sources of the ms_1 gene suggests that the action of the ms_1 gene on polyembryony and polyploidy might be modified by some other gene(s) when different genetic backgrounds were used, and might be affected by environmental conditions where the plants were grown.

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