A new and distinctive male-sterile, female-fertile desynaptic mutant in soybean (*Glycine max*)

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A spontaneous desynaptic mutation, affecting only microsporogenesis and causing pollen sterility, has been detected in BR97-12986H, a line of the official Brazilian soybean breeding program. In this male-sterile, female-fertile mutant, up to metaphase II, the meiotic behavior was similar to that described for the *st* series of synaptic mutants previously reported in soybean. Besides many univalents, few or total absence of bivalents were recorded in diakinesis. Bivalents presented one or two terminal chiasmata, while univalents retained the sister chromatid cohesion. Bivalents and most univalents congregated at the equatorial metaphase plate, although univalents frequently migrated to the poles prematurely. Laggards resulting from delay in chiasmata terminalization were also recorded. Distinctly different in their behavior from *st* series soybean mutants, telophase I-originated micronuclei of different sizes organized their own spindle in the second division. This behavior contributed towards an increase in genome fractionation. Several microspores and microcytes of different sizes were recorded at the end of meiosis. Pollen sterility was estimated at 91.2 %. Segregation ratio for sterility in this line and its progenies reached 3:1. Allelism tests with *st* series of synaptic mutants are in progress. The importance of male-sterile, female-fertile mutations for soybean breeding programs is discussed.

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Meiosis is a complex process that includes cytogenetic events such as chromosome pairing, synaptonemal complex formation, recombination chromosome segregation, and the creation of gamete meiotic products. The precise sequence of meiosis in under genetic control (GOTTSCHALK and KAUL 1974; BAKER et al. 1976; GOLUBOVSKAYA 1979, 1989). Normal segregation of chromosomes during the first meiotic division in most eukaryotes to ensure haploid gametes depends on the prior success of homologous chromosome synapsis during the zygotene stage of prophase I. This success is necessary for the occurrence of crossing-over and chiasmata formation during the subsequent pachytene stage (GOLUBOVSKAYA et al. 1997). The phenomenon of synapsis, i.e. the homologous chromosomal pairing characteristic of normal meiosis, is gene controlled (KODURU and RAO 1981). Mutations or malfunctioning of genes controlling synapsis reduce or annul the pairing process. Whereas absence or failure of synapsis is termed asynapsis (*as*), the immediate separation of the homologues following normal pachytene pairing is specified as desynapsis (*ds*) (GOTTSCHALK and KAUL 1980a,b).

Due to the high frequency of univalents in both asynaptic and desynaptic mutants, later meiotic irregularities are more or less similar in both groups and lead towards sterility. The most frequently utilized stages for discerning the action of *as* and *ds* genes are diakinesis and metaphase I, from which conclusions may be drawn with regard to chromosomal behavior during the earlier stages. However, as the phenotypic effects of *as* and *ds* genes do not differ in these stages, it is not easy to differentiate asynapsis from desynapsis. Analysis of the pachytene phase is thus essential. Unfortunately, early meiotic stages are not amenable for cytological analysis in most plant species. These difficulties are the main source of confusion to the effect that many cases of meiotic irregularities documented as due to *as* genes may have been caused by *ds* genes (GOTTSCHALK and KAUL 1980a,b). For a solution of this problem, RILEY and LAW (1965) proposed the term ''synaptic mutants'' to describe the lack of prophase I chromosome pairing.

Synaptic mutants are common in the plant kingdom. They occur in about 20 higher plant families, consisting of 50 genera and approximately 70 species (KODURU and RAO 1981), with most taxa belonging to the family Poaceae (SINGH 1993). Several male-sterile and female-sterile lines of synaptic mutants in soybean have been described. These mutants were named *st*, and a series from *st2* to *st8* has been genetically and cytogenetically reported (PALMER and HORNER 2000). In this paper the cytology of a

spontaneous male-sterile, female-fertile desynaptic mutant found in the breeding program developed at Embrapa–Soybean National Research Center is provided.

MATERIALS AND METHODS

Soybean male-sterile plants (MS) have been recorded in the breeding program carried out by Embrapa Soybean in Londrina-PR, Brazil. The male-sterile plants could not be distinguished from fertile ones until pod formation, when a few pods, probably resulted from bees pollination, or their total absence were observed on green plants that retained their leaves at maturity. In 1996, we observed several plants segregating for male-sterility in a F_5-progeny-row from back-cross BR5(6) × Parnaíba. Male-fertile plants from this progeny-row were selected and evaluated for segregation to be used in the following year. They were denominated BR97-12986. Within the segregating families, a ratio of a 3 male-fertile: 1 male-sterile plants was found, which is indicative of segregation of a single recessive gene. The heterozygous form (BR97-12986H) is maintained in the Soybean Germplasm Collection by Embrapa Soybean, Londrina-PR, Brazil. So that the sterility-segregating heterozygous plants could be identified, plant progeny tests were conducted in a greenhouse. About 12 seeds of normal plants were grown in pots and progenies with fertile and male-sterile plants were considered heterozygotes. The remaining seeds from heterozygotes for the MS character were once more sown in pots. The first flowers were tested for pollen viability and 0.5 % propionic carmine was used for staining. The sterile plants were identified, flower buds were collected between 9:00 and 12:00 a.m. in an ideal stage for meiotic analysis and fixed in a mixture of 95 % ethanol, chloroform, and propionic acid (6:3:2 v/v) for 24 h, after which they were transferred to 70 % alcohol and stored at 4°C until use. Microsporocytes were prepared by squashing and stained with 1 % propionic carmine. Ten male-sterile plants were cytologically analyzed. The number of microsporocytes analyzed per plant ranged from 328 to 434, comprising the stages from diakinesis to tetrad. A number of 1000 pollen grains were scored at random in each plant for the estimation of pollen viability. Plump, well-stained pollen grains were considered viable.

RESULTS

Conventional cytological analysis of the meiotic behavior in ten sterile plants taken from the line BR97-12986H revealed the mutant as a desynaptic phenotype. While fertile plants presented totally regular meiosis and pollen fertility, the sterile ones had high levels of meiotic abnormalities and pollen sterility. Table 1 shows the frequency of abnormalities for each plant in each meiotic phase from diakinesis to the tetrad stage. Frequency of abnormalities varied among phases and plants. The phase with the least number of abnormalities was metaphase II, whereas diakinesis had the most abnormalities. Average meiotic abnormalities of the ten plants reached 91.6 % with pollen sterility averaging 91.2 %.

Zygotene, pachytene, and diplotene stages in BR97-12986H were not amenable for accurate analysis. Meiotic figures, with one or two terminal chiasmata, were found in all diakinesis events from fertile plants (Fig. 1a); while, in sterile plants, univalent chromosomes were predominant (Fig. 1b). A few bivalents, with one or two terminal chiasmata, were observed at this stage in some microsporocytes (Fig. 1c). Sister chromatid cohesion in this mutant was perfect. Sister chromatids underwent separation only in anaphase II. Although bivalents and most univalents congregated at the equatorial metaphase plate in metaphase I (Fig. 1d), univalents frequently migrated precociously to the poles. The number of univalents in precocious ascension varied among cells (Fig. 1d and 1e) and between poles also (Fig. 1e). Since bivalents had one or two chiasmata, delay in chiasma terminalization (Fig. 1e) promoted the occurrence of laggard chromosomes in anaphase I (Fig. 1f). Owing to irregular chromosome segregation in metaphase I and anaphase I, many micronuclei occurred at the end of the first meiotic division (Fig. 1g). In the second division, the meiotic behavior differed from that of other species. Micronuclei formed in telophase I remained in prophase II and metaphase II (Fig. 1h). Micronuclei organized their own spindles which fractionated the genome in anaphase II (Fig. 1i). As a result of high levels of irregular chromosome segregation, many micronuclei were observed in telophase II (Fig. 1j). Cytokinesis divided the main nuclei and micronuclei into several different-sized microspores and microcytes (Fig. 1l). Moreover, sterile pollen grains in mutant plants were not of the same size (Fig. 1m).

DISCUSSION

A unique feature of meiosis I is that the homologous chromosomes, each containing two sister chromatids, segregate away from each other. For the success of the process at least one chiasma must be present in the bivalent. When a chiasma is not present, the resulting univalents are free to segregate randomly and may arrive at the same pole. MAGUIRE (1993,

Table 1. *Percentage of cells with meiotic abnormalities in each phase of meiosis and pollen sterility*

Plant	Number of cells/plant	Phases of meiosis							Means/ plant	% pollen sterility
		Diakinesis	Metaphase I	Anaphase I	Telophase I	Metaphase II	Anaphase II	Telophase II	Tetrads	
1	328	100.0	96.15	100.0	82.60	78.26	71.43	84.70	86.67	85.64	96.00
2	434	100.0	95.00	100.0	92.15	84.28	91.83	94.91	100.0	94.47	91.24
3	391	100.0	96.66	100.0	96.87	82.14	100.0	94.23	91.81	94.12	92.82
4	424	100.0	96.15	100.0	96.15	78.87	86.66	87.80	95.65	91.04	90.66
5	346	100.0	100.0	100.0	83.78	90.47	90.90	82.43	86.84	90.17	90.44
6	350	100.0	94.83	94.74	93.48	91.67	91.89	93.75	90.00	90.57	95.76
7	425	100.0	94.59	100.0	90.28	80.59	93.15	90.57	82.79	91.53	92.70
8	402	100.0	97.87	100.0	93.22	85.91	95.45	92.45	98.21	91.79	86.52
9	418	100.0	92.45	100.0	84.13	77.77	89.09	84.21	87.18	93.54	84.09
10	357	100.0	100.0	100.0	89.47	88.57	97.06	93.75	91.43	93.56	92.00
Means/phase	387.5	100.0	96.37	99.47	90.21	83.85	90.75	89.88	91.06	91.64	91.22

1995) has emphasized that recombination is insufficient to hold the chiasma in place. Additional factors, located either at the chiasmata or between sister chromatids, are required to maintain chiasmata. Study of desynaptic mutants is a potentially important source of information on the chiasma maintenance mechanism. While crossing-over is essential for chiasma formation, the maintenance of these chiasmata requires additional genetic factors. The latter seem to rely on the activity of the synaptonemal complex (SC) central region. Recent studies demonstrating that desynaptic plants have a defective synaptonemal complex have led MAGUIRE et al. (1991, 1993) to suggest that the substance binding sister chromatids is derived from the SC. A multisubunit complex of conserved proteins, called cohesin, is thought to provide longitudinal links along chromatids and maintaining the chiasma in place (BHATT et al. 1999; NASMYTH et al. 2000).

Desynaptic mutants, reported in some species, including animals, do not always display the same meiotic behavior with regard to univalents. In most desynaptic mutants, univalents maintain the sister chromatid cohesion until anaphase II for proper segregation (GOTTSCHALK and KAUL 1980a,b; KODURU and RAO 1981), whereas rare desynaptic mutants are unable to maintain sister chromatid cohesion up to this phase. Premature separation of sister chromatids in these mutants occurs prior to metaphase I (MIYAZAKI and ORR-WEAVER 1994). The desynaptic mutations found in BR97-12986 affect only chiasma maintenance. Univalents appeared just after SC disruption, but sister chromatid cohesion remained perfect till anaphase II. This fact suggests that the mutation failed to affect proteins (cohesins) involved in the sister chromatid cohesiveness. BASCOM-SLACK et al. (1997) analyzed some desynaptic mutants and asked why some exchanges were less effective to ensure disjunction. They hypothesized that exchanges themselves might be inadequate to enhance disjunction. Exchanges initiated or resolved at inappropriate times or mediated by different enzymes from those used to establish meiotic recombination nodules and chiasmata may be unable to influence segregation. The failure of exchanges close to telomeres to ensure disjunction is consistent with the model that the chiasma binder is less effectively established near telomeres. This is also consistent with the model that the capacity of sister-chromatid cohesion to hold a chiasma in place is proportional to the distance between the exchange and the telomere, where the greater distance results in higher cohesion (MOORE et al. 1994). In this context, the cause of desynapsis in BR97-12986 could be

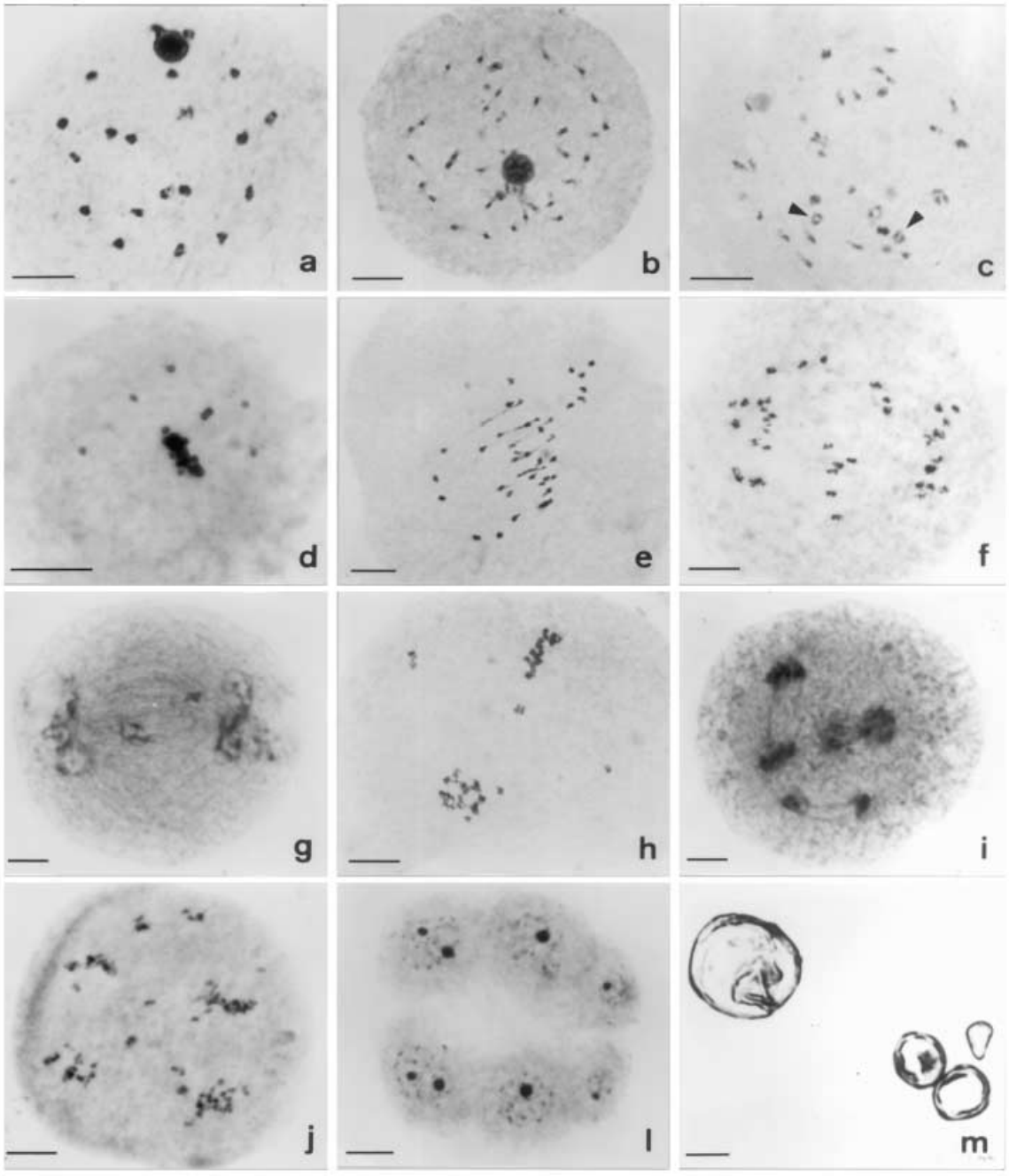

Fig. 1. Aspects of both meiosis I and II in the mutant BR97-12986H. **a)** Normal diakinesis in fertile plants where 20 small bivalents show one or two terminal chiasmata. **b,c)** Diakinesis in the mutant showing 40 univalents in **b**, and some bivalents with one or two terminal chiasmata in **c** (arrowheads). **d)** Metaphase I with some chromosomes migrating precociously to the poles. **e)** Early anaphase I with bivalents yet attached by chiasmata. Note the different amount of chromosomes migrating precously to the poles in **d** and **e,f)** Late anaphase I with many laggards. **g)** Telophase I with two micronuclei. **h)** Metaphase II with micronuclei. Observe both sister chromatids in the univalents. **i)** Early anaphase II with three multipolar spindles. **j)** Early telophase II with many micronuclei. **l)** Tetrad with two microcytes. **m)** Sterile pollen grains of different sizes. Bars = 1 μm.

attributed to chiasmata localization. In our study, the few bivalents detected in diakinesis always showed terminal chiasmata.

An additional role for chiasmata in plants is to ensure proper meiotic spindle assembly. In synaptic mutants, with disruption of recombination or chi-

asma maintenance, a general failure in bipolar spindle formation has been observed (KODURU and RAO 1981). The effects of univalents in meiosis I may range from small extra minispindles to tripolars or quadripolars, whereas multiple spindle aberrations are a secondary effect caused by unpaired chromosomes (DAWE 1998). According to DAWE and CANDE (1995), the simplest explanation for these findings is that unpaired chromosomes disrupt the spindle owing to their single functional kinetochore. The meiotic behavior of univalents found in BR97-12986H differed from that reported for most synaptic mutants of several species, and also from other *st* soybean synaptic mutants. The univalents and bivalents in this line congregated in a single metaphase plate and a normal bipolar spindle assembly was reported in the first division, similar to other *st* synaptic soybean mutants (HADLEY and STARNES 1964; PALMER 1974a,b; PALMER and KAUL 1983; ILARSLAN et al. 1997; PALMER and HORNER 2000). Whereas multiple spindles in soybean mutants have never been reported in the second division, in the present line, the single chromosome or group of chromosomes of telophase I micronuclei organized its own spindle. Thus, multiple spindles of different sizes were observed in the same cell. In the second division, the mutant's peculiar behavior contributed towards an increase in genome fractionation, leading to meiotic products with many microcytes and microspores of variable sizes. Pollen sterility was estimated at 91.2 %. The *st* synaptic mutants of soybean, from *st2* to *st8*, always showed more than 90 % sterile pollen grains. Due to the fact that most synaptic mutants also affected female fertility, PEIRSON et al. (1997) suggested that a set of genes controlled homologous chromosome pairing and recombination in both anthers and ovules. All *st* soybean mutant series were reported to be also male-sterile and female-sterile. Contrastingly, line BR97-12986H presented high seed production when cross-pollinated by bees or man, indicating that the mutation affected only microsporogenesis, thus the mutant is characterized as male-sterile, female-fertile.

PRAKKEN (1943) classified desynaptic mutants according to chromosome dissociation, or rather, into weak, medium-strong and complete. Plants of the first group are not very different from normal ones. In the second group, some chromosomes may remain paired till metaphase I, but in the third no bivalents are extant. Most known desynaptics are of the first two types and only a few are of the third type. Taking into consideration the frequency of bivalents found in diakinesis and metaphase I, line BR97-12986H could be classified as a medium-strong desynaptic mutant. Activity of desynaptic genes differs from plant to plant, even from cell to cell, possibly the result of environmental factors. According to RAY and SHERMAN (1988), the manifestation of the desynaptic expression might fluctuate as a result of seasonal variations, including high and low temperatures. In BR97-12986H both levels of variations have been reported, i.e. frequency of bivalents among cells within plants and of abnormal cells among plants was variable. Such variations might be the result of temperature changes in the non-controlled glasshouse where the plants were grown. Temperature has been reported as having more influence on phenotypic level of partial male sterility (*msp*) systems than any other environment factor. Effects of temperature on *msp* soybean mutants have been described by STELLY and PALMER (1980a,b) and CARLSON and WILLIAMS (1985).

Gamete imbalance may be one of the major consequences of synaptic mutations, especially when they are incomplete and may lead to various forms of aneuploidy in later generations (KHUSH 1973). In soybean, aneuploids have been reported among the progeny of synaptic mutants (HADLEY and HYMOWITZ 1973; PALMER 1974a,b). The *st2* and *st3* soybean mutants produced mostly tetraploid progenies (PALMER 1974b), while the *st4* had more aneuploid plants among its progeny (PALMER and HEER 1976). On the other hand, *st5* with chromosome abnormalities similar to those reported in *st4*, failed to generate more self- or cross-pollinated seed. Although the capacity of BR97-12986H to generate aneuploids has not been tested, the high frequency of meiotic abnormalities increased by multiple spindle formation in the second division suggests its unsuitability for such purposes.

A segregation that fits the 3:1 ratio has been observed in the original BR97-12986H and in the progeny-row from heterozygous fertile plants after selfing. This suggests that the mutation is caused by a single recessive gene. Preliminary studies on allelism tests with the soybean *ms* series of alleles, from *ms1* to *ms6*, for male sterile/female-fertile plants indicated that the gene in the sister line of BR97-12986H is not allelic to any of the *ms* genes already studied (A. Seifert, Embrapa Soybean; pers. comm.). Allelism tests with some *st* soybean mutant series from the Soybean Genetic Type Collection (USDA/ARS) are in progress. Some phenotypic characteristics of the BR97-12986H mutant are similar to those of *st2* and *st3* asynaptic/desynaptic (HADLEY and STARNES 1964) and *st4* desynaptic (PALMER 1974a) soybean mutants. In this case, late in the season, fertile plants were mature and the sterile ones were green and vigorous. Based on their cytology, since they have multiple spindle assemblies in the second division,

and on the fact that this mutation caused only male-sterility, the mutant might represent a new mutation in the gene that controls chromosome pairing and chromosome segregation only during microsporogenesis.

Cytological data indicate that this mutant is different from the seven male-sterile and female-sterile soybean synaptic mutants reported in soybean. Male-sterile, female-fertile mutants are considered a powerful tool in hybridization breeding programs, mainly in soybean where the major obstacle in F_1 hybrid seed production is the intensive hand-labor requirements for large number of pollinations. According to JIN et al. (1997), in spite of its wide range of possible uses in breeding programs, it has not been used as yet for commercial production of hybrid seed. This is due to the fact that large quantities of hybrid seed cannot be produced at present. Such mutations have been used in breeding programs to facilitate crossing experiments and increase the number of novel recombinant genotypes available for testing by breeders, to generate random mating populations for use in recurrent selection programs (BRIM and STUBER 1973; GRAYBOSCH and PALMER 1988; LEWERS et al. 1996; LEWERS and PALMER 1997) and to test the feasibility of commercial production of hybrid soybean seed.

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