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The genomic relationship between *Glycine max* (L.) Merr. and *G. soja* Sieb. and Zucc. as revealed by pachytene chromosome analysis*

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Summary. This study was conducted with the objective of determining the genomic relationship between cultivated soybean (*Glycine max*) and wild soybean (*G. soja*) of the subgenus *Soja*, genus *Glycine*. Observations on crossability rate, hybrid viability, meiotic chromosome pairing, and pollen fertility in F_1 hybrids of *G. max* × *G. soja* and reciprocals elucidated that both species hybridized readily and set mature putative hybrid pods, generated vigorous F_1 plants, had a majority of sporocytes that showed 18II + 1IV chromosome association at diakinesis and metaphase I, and had a pollen fertility that ranged from 49.2% to 53.3%. A quadrivalent was often associated with the nucleolus, suggesting that one of the chromosomes involved in the interchange is a satellited chromosome. Thus, *G. max* and *G. soja* genetic stocks used in this study have been differentiated by a reciprocal translocation. Pachytene analysis of F_1 hybrids helped construct chromosome maps based on chromosome length and euchromatin and heterochromatin distribution. Chromosomes were numbered in descending order of 1–20. Pachytene chromosomes in soybean showed heterochromatin distribution on either side of the centromeres. Pachytene analysis revealed small structural differences for chromosomes 6 and 11 which were not detected at diakinesis and metaphase I. This study suggests that *G. max* and *G. soja* carry similar genomes and validates the previously assigned genome symbol GG.

Key words: *Glycine max* – *Glycine soja* – Interspecific hybrid – Pachytene karyotype

Introduction

The subgenus *Soja* (Moench) F. I. Herm. of the genus *Glycine* Willd. contains the soybean [*G. max* (L.) Merr.] and its wild annual progenitor, *G. soja* Sieb. and Zucc. As both species carry the chromosome number $2n = 40$, hybridize rather easily, generate viable fertile hybrids, and differ only by a reciprocal translocation or by a paracentric inversion (see Hadley and Hymowitz 1973; Ahmad et al. 1977; Palmer et al. 1987), Singh and Hymowitz (1985) and Singh et al. (1988) proposed the genome symbol GG for *G. max* and *G. soja*. However, Ahmad et al. (1984) reported the total length of the chromosome complement of *G. soja* to be about 6–7% smaller than that of *G. max*. Kozak (1986) found ". . . the absence of identity of the genomes" in *G. max* × *G. soja*. These contradictory results prompted us to re-examine the genomic relationship between *G. max* and *G. soja*.

In this paper, we report on crossability rate, hybrid viability meiotic chromosome pairing, and pollen fertility in the interspecific hybrid of *G. max* × *G. soja*. Since the mitotic metaphase chromosomes of *G. max* and *G. soja* are small and morphologically similar to each other (Sen and Vidyabhusan 1960; Ahmad et al. 1983, 1984), attempts were made to conduct pachytene chromosome analysis of the F_1 hybrids. All 20 hybrid pachytene chromosome pairs were identified by chromosome lengths, arm ratios and differentiation of euchromatic and heterochromatic segments. A standard pachytene karyotype of *G. max* and *G. soja* is presented for the first time.

Materials and methods

The seeds of two soybean cultivars ('Bonus', 'Essex') and an accession (PI 81762) of *G. soja* were kindly supplied by R.L. Bernard, USDA/ARS, Urbana/IL, *Glycine soja* accession

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PI 81762 was originally collected from the USSR. The parent and F_1 plants were grown in the greenhouse in 15 cm clay pots containing a 3:1:2 mixture of clay loam:peat:sand, and fertilized every week with a standard greenhouse mixture. In the winter months (October–May), the temperature of the greenhouse was maintained at approximately 25°–27°C, and the plants were given a 14 h photoperiod under metal halide lights; in the summer months (June–September), the plants were grown in pots outdoors.

Flower buds were emasculated 1–2 days before anthesis and pollinated simultaneously from newly opened flowers. If crosses were successful, pods matured on the plants. Five seeds from each hybrid combination were germinated on moist filter paper in a petri dish, and two hybrid seedlings were transferred to pots in the greenhouse.

Hybrid morphology was compared with that of the parents to confirm hybridity. Flower buds were fixed in a freshly prepared mixture of 3:1 absolute ethanol:propionic acid. Ferric chloride (1 g/100 ml fixative) was added to the fixative to intensify the staining of chromosomes. Buds were washed twice with 70% ethanol after 48 h of fixation and stored in 70% ethanol under refrigeration. One anther from a bud was used to determine the meiotic stages. Once an appropriate meiotic stage was observed, the remaining anthers were stained in 1.5% propiono-carmine (1.5 g carmine dissolved in 100 ml 45% propionic acid) for 1 week under refrigeration. One stained anther was placed on a clean slide in a drop of 45% acetic acid, and a cover slip was then placed over the anther. The slide was gently heated 3–4 times (not to be boiled), 2–3 s each, over an alcohol flame. The cover slip was then tapped gently twice with a scalpel to release pollen mother cells from the anther. A piece of blotting paper was placed over the cover slip, and gentle thumb pressure was applied.

Microsporocytes with 1–3 separated bivalents at pachynema were studied for chromosome length, centromere position, and distribution of euchromatin and heterochromatin. Photomicrographs were taken under 100× oil plan objective of a Nikon EFM microscope using Kodak Technical Pan film 2415-059-121. Photomicrographs were enlarged to ×2,400 and printed on Kodak Polycontrast Rapid II RC NM Paper. Individual pachytene chromosome lengths and arm ratios were determined by measuring sketched drawings of the photomicrographs. Each pachytene chromosome was given a number based on its total length, from longest (chromosome 1) to shortest (chromosome 20). In describing the centromere positions on the chromosomes, the nomenclature of Levan et al. (1964) was followed.

Meiotic chromosome association was also examined at diakinesis. Chromosome migration at anaphase I was studied for chromatin bridges and fragments. The pollen fertility of parents and F_1 hybrids was ascertained by counting about 1,000 pollen grains stained in 1.5% propiono-carmine.

Results

Crossability

Crossability barriers were not observed in *G. max* × *G. soja* nor in the reciprocal crosses. In each cross, some mature pods developed. However, reciprocal cross differences were observed (Table 1): pod sets were lower (1.8%–6%) in *G. soja* × *G. max* than in *G. max* × *G. soja* (8.7%–11.1).

Table 1. Crossability rate in *G. max* ($2n=40$) and *G. soja* ($2n=40$) interspecific crosses

Crosses	No. of florets pollinated	Pod set	Crossability rate (%)
Bonus[a] × PI 81762[b]	18	2	11.1
PI 81762 × Bonus	110	2	1.8
Essex[a] × PI 81762	46	4	8.7
PI 81762 × Essex	159	9	6.0

[a] *Glycine max*
[b] *G. soja*

Table 2. Meiotic chromosome configuration at diakinesis and pollen fertility (%) in *G. max* × *G. soja* and in its reciprocal crosses

Hybrids	2*n*	II	IV	Total PMC	Pollen fertility (%)
Bonus[a] × PI 81762[b]	40	18.3	0.9	38	49.2
PI 81762 × Bonus	40	18.2	0.9	25	52.0
Essex[a] × PI 81762	40	18.2	0.9	48	53.3
PI 81762 × Essex	40	18.4	0.8	25	51.2

[a] *Glycine max*
[b] *G. soja*

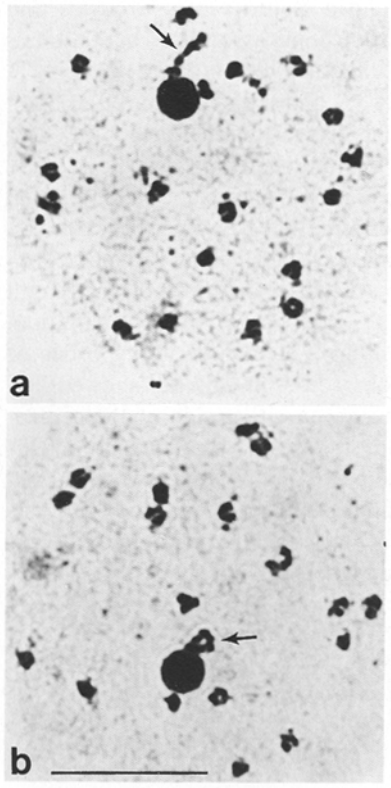

Fig. 1a and b. Chromosome association at diakinesis in *G. max* × *G. soja* F_1 hybrids showing 18 II + 1 IV. *Arrows* show a quadrivalent associated with the nucleolus. *Bar* represents 10 μ

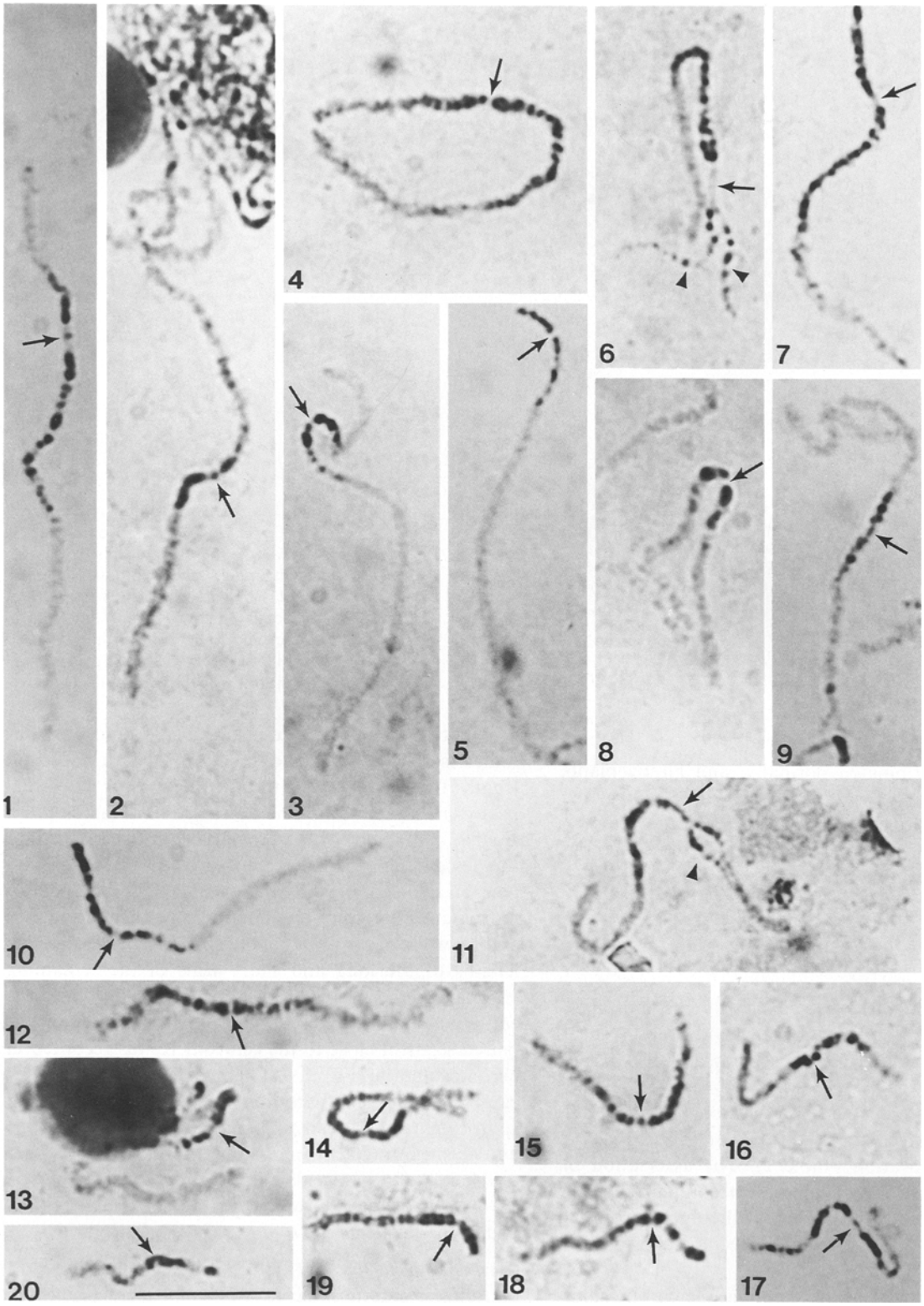

Fig. 2. Photomicrographs of the pachytene chromosome complement of *G. max* × *G. soja* F_1 hybrids. Each figure shows a different chromosome. For example, Fig. 2; 1, chromosome 1; Fig. 2; 20, chromosome 20. *Arrows* indicate centromere locations. *Arrow heads* in chromosomes 6 and 11 show heteromorphic regions. *Bar* represents 10 μ

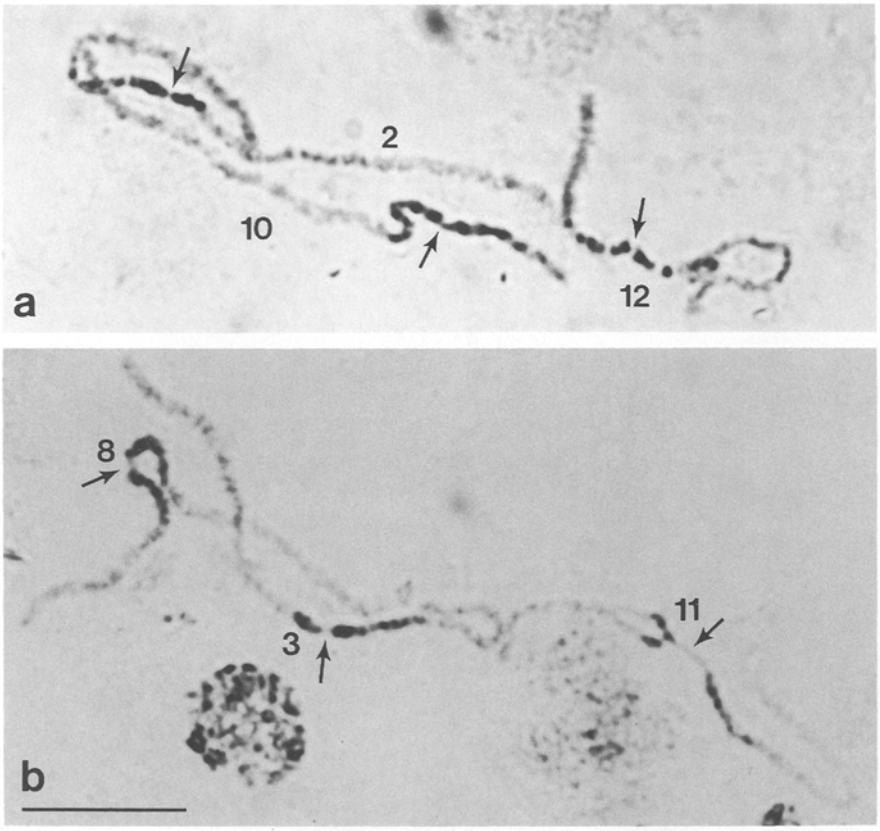

Fig. 3a and b. Photomicrographs of the pachytene chromosomes of *G. max* × *G. soja* F_1 hybrids. **a** A cell with 3 pachytene chromosomes: 2, 10 and 12; **b** a cell with 3 pachytene chromosomes: 3, 8 and 11. Note a heteromorphic pairing in chromosome 11. *Arrows* show centromere positions. *Bar* represents 10 μ

Morphology

Hybrid seeds germinated normally, and all F_1 plants were vigorous in their vegetative growth. They carried twinning, pod shattering, and black pod traits from *G. soja*, PI 81762, and were intermediate between the parents in leaf, flower, and pod and seed sizes.

Meiosis

All F_1 plants had the expected $2n=40$ chromosomes. The chromosome configuration 18II + 1IV observed at diakinesis in a majority of sporocytes and the partial pollen fertility (49.2%–53.3%) found in all F_1 plants suggest that the studied *G. soja* accession, PI 81762, differs from *G. max* cultivars, 'Bonus' and 'Essex', by a reciprocal translocation (Table 2). The association of four chromosomes in a quadrivalent configuration involving the nucleolus indicates that the nucleolus organizer chromosome is involved in the reciprocal translocation (Fig. 1a and b).

Another approach for determining the chromosome homology between *G. max* and *G. soja* is to analyze the chromosome pairing of F_1 hybrids at pachynema. Since it was impossible to trace all 20 chromosome pairs in a cell, attempts were made to isolate 1–3 bivalents (Figs. 2 and 3). Pronounced euchromatin and heterochromatin differentiation and measurements of chromosome parameters such as long and short arm length and total length (Table 3) facilitated the identification of individual pachytene bivalents and the construction of an idiogram (Fig. 4). All 20 bivalents were numbered from 1 to 20 in the descending order of their lengths. Of the 20 pachytene bivalents of *G. max* × *G. soja* F_1 hybrids, heteromorphic regions were observed only in chromosomes 6 and 11, while pairing was completely normal all along the lengths of the long and short arms of the remaining chromosome pairs. In chromosome 6, the short arm was entirely unpaired (Fig. 2, *6*). On the other hand, an unpaired segment close to the centromere was recorded in chromosome 11 (Fig. 2, *11*). This is not an artifact because the same configuration was observed in several sporocytes (Fig. 3b). At anaphase I, no chromatin bridge and acentric fragment were seen. Therefore, there is no evidence that a paracentric inversion is involved.

The following are salient features of the individual pachytene bivalents in *G. max* × *G. soja* F_1 hybrids:

Chromosome 1 (Fig. 2, *1*): 39.79 μ long; submedian and the longest chromosome in the complement (Table 3). The long arm consists of an 11.25 μ heterochromatic region, while the short arm carries a small heterochromatic zone proximal to the centromere. The distal segments of the long and short arms are completely euchromatic.

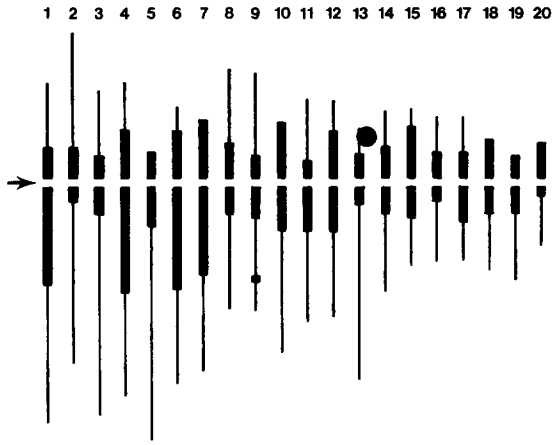

Fig. 4. Proposed idiogram, based on Fig. 2 and 3, of the pachytene chromosomes of the soybean. *Arrow* indicates centromere location. ×2,400

Table 3. Measurements (μ) of pachytene chromosomes of *G. max* × *G. soja* F_1 hybrid

Chromosome no.	Long arm (L)	Short arm (S)	Total length (L+S)	Arm ratio (L/S)	Centromere position[a]	Heterochromatic length		
						L	S	Total
1	28.33	11.46	39.79	2.47	sm	11.25	3.75	15.00
2	20.83	17.29	38.12	1.20	m	1.67	3.75	5.42
3	27.29	10.42	37.71	2.62	sm	3.13	2.71	5.84
4	25.21	11.46	36.67	2.20	sm	12.50	5.83	18.33
5	30.42	2.92	33.34	10.42	t	4.58	2.92	7.50
6	23.54	8.33	31.87	2.83	sm	12.08	5.83	17.91
7	22.08	6.67	28.75	3.31	st	10.42	6.67	17.09
8	14.58	13.13	27.71	1.11	m	3.13	4.17	7.30
9	14.58	12.50	27.08	1.17	m	4.58	2.71	7.29
10	20.00	6.67	26.67	3.00	sm	5.00	6.67	11.67
11	16.25	9.17	25.42	1.77	sm	5.00	2.08	7.08
12	15.63	9.17	24.80	1.70	sm	5.00	5.83	10.83
13	21.67	1.88	23.55	11.53	t	2.08	1.88	3.96
14	12.50	7.71	20.21	1.62	m	3.13	3.75	6.88
15	9.17	8.33	17.50	1.10	m	3.75	6.25	10.00
16	8.75	7.08	15.83	1.24	m	1.67	3.13	4.80
17	8.75	7.08	15.83	1.24	m	4.17	3.13	7.30
18	9.79	4.58	14.37	2.14	sm	3.13	4.58	7.71
19	11.04	2.50	13.54	4.42	st	3.13	2.50	5.63
20	6.67	3.96	10.63	1.68	sm	1.04	3.96	5.00

[a] sm, submedian; m, median; t, terminal; st, subterminal

Chromosome 2 (Fig. 2, *2*): 38.12 μ long; median. This chromosome carries the least heterochromatin – only the centromere is flanked by sharply defined chromomeres.

Chromosome 3 (Fig. 2, *3*): 37.71 μ long. Submedian centromere position and sharply defined centromeric heterochromatin in the long and short arms make this chromosome easy to distinguish from chromosome 2.

Chromosome 4 (Fig. 2, *4*): 36.67 μ long; submedian. About 50% of the long and short arms proximal to the centromere are heterochromatic; this distinguishes it from chromosome 1.

Chromosome 5 (Fig. 2, *5*): 33.34 μ long. This chromosome carries a nearly terminal centromere with the short arm (2.92 μ) entirely heterochromatic. The long arm has three pronounced, large, deeply-staining chromomeres covering 4.58 μ of the centromeric region; the rest of the long arm is euchromatic.

Chromosome 6 (Fig. 2, *6*): 31.87 μ long; submedian with the heteromorphic short arm. About half of the long arm proximal to the centromere is heterochromatic.

Chromosome 7 (Fig. 2, *7*): 28.75 μ long; has a subterminal centromere with the short arm entirely heterochromatic, and 47% of the long arm proximal to the centromere is heterochromatic. Thus, chromosome 7 is the most heterochromatic chromosome in the complement.

Chromosome 8 (Fig. 2, *8*): 27.71 μ long; median. Both arms carry a short heterochromatic zone proximal to the centromere. Chromosome length distinguishes it from chromosome 2 (38.12 μ).

Chromosome 9 (Fig. 2, *9*): 27.08 μ long; median. Centromeric regions of the long and short arms are flanked by heterochromatin. The long arm contains a dark-staining chromomere about 3.3 μ from the telemere. This feature makes distinguishing chromosome 9 from chromosome 8 rather easy.

Chromosome 10 (Fig. 2, *10*): 26.67 μ long; submedian. The short arm of this chromosome is completely heterochromatic and is similar to the short arm of chromosome 7. Only 25% of the long arm proximal to the centromere is heterochromatic, and this distinguishes it from chromosome 7.

Chromosome 11 (Fig. 2, *11*): 25.42 μ long; submedian with centromeric heterochromatin on both arms. The heteromorphic short arm of chromosome 11 distinguishes it from chromosomes 8 and 9.

Chromosome 12 (Fig. 2, *12*): 24.80 μ long; submedian and consists of almost equal length heterochromatic zones proximal to the centromere on the long and short arms.

Chromosome 13 (Fig. 2, *13*): 23.55 μ long. This chromosome is the nucleolus organizing, or satellited chromosome. Part of the long arm is associated with the nucleolus. The short arm is heterochromatic, and this chromosome carries a nearly terminal centromere. The

nucleolus-organizing feature of chromosome 13 distinguishes it from chromosome 5.

Chromosome 14 (Fig. 2, *14*): 20.21 μ long; median. The centromeric region is stained deeply while the distal segments of both arms are euchromatic.

Chromosome 15 (Fig. 2, *15*): 17.50 μ long; median. The long and short arms are almost equal (arm ratio = 1.10). The short arm of this chromosome is 75% heterochromatic.

Chromosome 16 (Fig. 2, *16*): 15.83 μ long; median. This chromosome is one of the four chromosomes 14–17 carrying median centromeres, but the distribution of the heterochromatic segments permits an easy identification.

Chromosome 17 (Fig. 2, *17*): 15.83 μ long; median. This chromosome is similar to chromosome 16 in gross morphology, but the distribution of deeply-staining centromeric heterochromatin distinguishes one from the other. The long arm of chromosome 17 carries a 4.17 μ heterochromatic zone while the corresponding arm of chromosome 16 has a 1.67 μ heterochromatic segment.

Chromosome 18 (Fig. 2, *18*): 14.37 μ long; submedian. The short arm consists of three large, distinct chromomeres.

Chromosome 19 (Fig. 2, *19*): 13.54 μ long. The subterminal centromere distinguishes this chromosome from chromosomes 18 and 20. The short arm is completely heterochromatic.

Chromosome 20 (Fig. 2, *20*): 10.63 μ long. The fact that this is the shortest chromosome of the complement makes it possible to distinguish it from chromosomes 18 and 19. The short arm is heterochromatic, and there is a large chromomere proximal to the centromere on the long arm.

The above distinguishing traits of individual pachytene chromosomes were utilizing to construct a standard chromosome (cytological) map of the soybean (Fig. 4). All the pachytene bivalents carried heterochromatin, deeply-stained with propiono-carmine, proximal to and on either side of the centromere on the long and short arms.

Furthermore, the short arms of six (chromosomes 5, 7, 10, 18–20) of the 20 bivalents were completely heterochromatic. It should be noted that 35.84% of the soybean genome was found to be heterochromatic; this is higher that that observed (28.72%) for tomato (Barton 1950). The least heterochromatic segment was recorded for chromosome 2 (14.2%), while chromosome 7 carried the maximum (59.4%) heterochromatin. It is evident from chromosome parameters, though single pachytene chromosomes were measured, that chromosome 1 is about four times longer than chromosome 20 (Table 3).

Discussion

Based on classical taxonomy, the cultivated soybean (*G. max*) and its annual progenitor, wild soybean (*G. soja*), belong to the subgenus *Soja* of the genus *Glycine*. The information on crossability rate, hybrid viability, meiotic chromosome pairing, and pollen fertility in interspecific hybrids of *G. max* and *G. soja* that was obtained in this study demonstrates that the two species hybridize readily, generate viable vigorous F_1 hybrids, and differ by a reciprocal translocation. This confirms earlier observations (Hadley and Hymowitz 1973; Palmer et al. 1987), but contradicts the findings of Kozak (1986) who reported the absence of genome identity between *G. max* and *G. soja*. Thus, the genome symbol GG assigned to *G. soja* and *G. max* by Singh and Hymowitz (1985) and Singh et al. (1988) is valid.

The chromosome homology between *G. max* and *G. soja* can be determined precisely by analyzing the pachytene chromosomes of their F_1 hybrids. Pachytene chromosomes have not been utilized so far to construct chromosome maps in species of the *Glycine*. According to Palmer and Kilen (1987), "no reliable techniques are known that consistently produce a high degree of success with squash preparations of soybean meiocytes". However, we obtained reproducible results by utilizing the cytological techniques described in this study. On the other hand, the published results on karyotype analysis based on somatic chromosomes of *G. max* and *G. soja* is not very conclusive (Ladizinsky et al. 1979; Ahmad et al. 1984). Because of a high chromosome number (2n = 40), small and similar chromosome sizes (1.42–2.84 μ) (Sen and Vidyabhusan 1960), median to submedian centromere positions, and the lack of morphological landmarks, individual somatic chromosomes of the soybean have not been clearly distinguishable.

It was not possible to trace all 20 pachytene chromosome bivalents in a single cell. The isolation of 1–3 bivalents, observations on chromosome measurements and a euchromatin and heterochromatin differentiation (Figs. 2 and 3; Table 3) facilitated the identification and construction of pachytene chromosome maps (1–20) of the soybean for the first time (Fig. 4). The heterochromatin was distributed proximal to and on either side of the centromeres on the long and short arms, and 6 of the 20 short arms were totally heterochromatic. This latter feature makes soybean pachytene chromosomes rather unique. This pattern resembles that of maize (McClintock 1929; Rhoades 1950), tomato (Barton 1950), *Brassica* (Röbbelen 1960), alfalfa (Gillies 1968), *Ricinus*

(Jelenkovic and Harrington 1973; Paris et al. 1978); diploid potato (Ramanna and Wagenvoort 1976) and pigeon pea (Dundas et al. 1983). Furthermore, soybean pachytene chromosome have better euchromatin and heterochromatin differentiation than that observed for the pachytene chromosomes of rice (Shastry et al. 1960; Khush et al. 1984) sugarbeet (Yu 1977; Nakamura and Tsuchiya 1982) and barley (Sarvella et al. 1958; Singh and Tsuchiya 1975).

At diakinesis or metaphase I in *G. max* × *G. soja* F_1 hybrids, the only gross chromosome structural change seen was a quadrivalent configuration apparently due to a reciprocal translocation (Fig. 1 a and b, Table 2). However, pachytene chromosome analysis revealed heteromorphic chromosome pairing for chromosomes 6 and 11, while 18 bivalents synapsed normally (Fig. 2). Such associations may be due to cryptic structural differences (Stebbins 1950). Similar results have been reported in F_1 hybrids of indica-japonica rices (Shastry and Misra 1961).

Soybean cytogenetics has lagged far behind maize, barley, wheat, tomato, and rice. Of the 20 linkage groups expected in soybean, 13 have only been suggested. The majority of the linkage groups carry 2 or 3 loosely associated genes. Furthermore, their independence has not been tested in primary trisomics. In soybean, three primary trisomics (Tri A, Tri B, Tri C) and six interchanges have been reported (Palmer and Kilen 1987). The proposed chromosome numbering system based on pachytene analysis may help identification of the available aneuploid lines. However, there is an urgent need to isolate all the possible primary trisomics and to assemble and identify interchanges in soybean.

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References

Ahmad QN, Britten EJ, Byth DE (1977) Inversion bridges and meiotic behavior in species hybrids of soybean. J Hered 68:360–364

Ahmad QN, Britten EJ, Byth DE (1983) A quantitative method of karyotypic analysis applied to the soybean, *Glycine max*. Cytologia 48:879–892

Ahmad QN, Britten EJ, Byth DE (1984) The karyotype of *Glycine soja* and its relationship to that of the soybean, *Glycine max*. Cytologia 49:645–658

Barton DW (1950) Pachytene morphology of the tomato chromosome complement. Am J Bot 37:639–643

Dundas IS, Britten EJ, Byth DE (1983) Pachytene chromosome identification by a key based on chromomeres in the pigeonpea. J Hered 74:461–464

Gillies CB (1968) The pachytene chromosomes of a diploid *Medicago sativa*. Can J Genet Cytol 10:788–793

Hadley HH, Hymowitz T (1973) Speciation and cytogenetics. In: Caldwell BE (ed) Soybeans: improvement, production, and uses. Agronomy no. 16, Agronomy Inc/WI, pp 97–116

Jelenkovic G, Harrington E (1973) Chromosome complement of *Ricinus communis* at pachytene and early diplotene. J Hered 64:137–142

Kush GS, Singh RJ, Sur SC, Librojo AL (1984) Primary trisomics of rice: origin, morphology, cytology and use in linkage mapping. Genetics 107:141–163

Kozak MF (1986) Cytological analysis of meiosis in microsporogenesis in interspecific soybean hybrids. Cytol Genet 20:49–51

Ladizinsky G, Newell CA, Hymowitz T (1979) Giemsa staining of soybean chromosomes. J Hered 70:415–416

Levan A, Fredga K, Sandberg AA (1964) Nomenclature for centromeric position on chromosomes. Hereditas 52: 201–220

McClintock B (1929) Chromosome morphology in *Zea mays*. Science 69:629

Nakamura C, Tsuchiya T (1982) Pachytene chromosome morphology in diploid sugarbeet, *Beta vulgaris*. Z Pflanzenzücht 89:229–244

Palmer RG, Kilen TC (1987) Qualitative genetics and cytogenetics. In: Wilcox JR (ed) Soybeans: improvement, production, and uses, 2nd edn. Agronomy no. 16, Agronomy Inc WI, pp 135–209

Palmer RG, Newhouse KE, Graybosch RA, Delannay X (1987) Chromosome structure of the wild soybean accessions from China and the Soviet Union of *Glycine soja* Sieb. & Zucc. J Hered 78:243–247

Paris HS, Shifriss O, Jelenkovic G (1978) Idiogram of *Ricinus communis* L. J Hered 69:191–196

Ramanna MS, Wagenvoort M (1976) Identification of the trisomic series in diploid *Solanum tuberosum* L., group tuberosum. 1. Chromosome identification. Euphytica 25: 233–240

Rhoades MM (1950) Meiosis in maize. J Hered 41:59–67

Röbbelen G (1960) Beiträge zur Analyse des *Brassica* – genoms. Chromosoma 11:205–228

Sarvella P, Holmgren JB, Nilan RA (1958) Analysis of barley pachytene chromosomes. Nucleus 1:183–204

Sen NK, Vidyabhusan RV (1960) Tetraploid soybean. Euphytica 9:317–322

Shastry SVS, Misra RN (1961) Pachytene analysis in *Oryza* II. Sterility in japonica-indica rice hybrids. Chromosoma 12: 248–271

Shastry SVS, Ranga Rao DR, Misra RN (1960) Pachytene analysis in *Oryza*-I. Chromosome morphology in *Oryza sativa*. Indian J Genet Plant Breed 20:15–21

Singh RJ, Hymowitz T (1985) The genomic relationships among six wild perennial species of the genus *Glycine* subgenus *Glycine* Willd. Theor Appl Genet 71:221–230

Singh RJ, Tsuchiya T (1975) Pachytene chromosomes of barley. J Hered 66:165–167

Singh RJ, Kollipara KP, Hymowitz T (1988) Further data on the genomic relationships among wild perennial species ($2n=40$) of the genus *Glycine* Willd. Genome 30:166–176

Stebbins GL (1950) Variation and evolution in plants. Columbia University Press, New York

Yu MH (1977) Preliminary study of pachytene morphology in a homozygous line of sugarbeet. Crop Sci 17:833–836