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Marker chromosomes commonly observed in the genus *Glycine*

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Summary. Soybean [*Glycine max* (L.) Merr.] chromosomes were analyzed using the chromosome image analyzing system, CHIAS, and seven groups, including subgroups, were identified based on morphological characteristics. Two pairs of chromosomes were conspicuous in their morphological traits. One pair of chromosomes, which had the largest arm ratio among all the chromosomes, was commonly observed in the species in all three subgenera of the genus *Glycine*. These chromosomes also displayed a unique pattern after N-banding and were detected as marker chromosomes. *G. soja,* which is considered to be the ancestor of *G. max,* has two types of marker chromosomes. The lines that carry the same type as *G. max* may be the ancestors of *G. max* among the lines of *G. soja*. The morphological differences of the marker chromosomes within the species in the subgenus *Soja* are discussed in relation to the domestication process of soybean.

Key words: Genus *Glycine* – Soybean – Karyotype – Marker chromosome – Image analysis

Introduction

Three subgenera have been classified within the genus *Glycine* – *Soja*, which consists of two species including soybean, *G. max*, has a basic chromosome number of 20 (Hymowitz and Newell 1981); *Glycine,* whose basic number is also 20, consists of seven species (Hymowitz and Newell 1981); and *Bracteata*, whose basic number is 11, consists of one species (Verdcourt 1966, 1970). There is a cross compatibility between the species within each subgenus, with a few exceptions (Newell and Hymowitz 1983). The species in the subgenus *Bracteata* differs from the species within the other two subgenera not only in the basic chromosome number, but also in various characteristics of the phenotypic traits of plants, geographic distribution, electrophoretic patterns of the storage protein, etc. Hymowitz and Newell (1981) removed the subgenus *Bracteata* from the genus *Glycine*. Buttery and Buzzell (1976) and Gurley et al. (1979) suggested that the basic chromosome number was 10 rather than 20, which would be extraordinarily large compared with other plant species, and that in subgenus *Bracteata* the basic number is 11.

Against this background it would be important from the viewpoint of taxonomy, cytology, genetics, and even breeding of soybean if the soybean chromosomes could be completely identified or if at least certain marker chromosomes were identified. However, there have hitherto been no reports on the chromosomes common to the three subgenera, nor has there been complete identification of soybean chromosomes (Sen and Vidyabhusan 1960; Ladizinsky et al. 1979; Ahmad et al. 1983), presumably due to the small size (ca. 1 μm) of the chromosomes at the mitotic mid-metaphase stage and to the large chromosome number, e.g., ranging from 40 (*G. max*) to 80 (*G. tabacina*). Fukui and Mukai (1988) succeeded in identifying all the chromosomes of *Atriplex rosea* L., which display approximately the same size as the soybean chromosomes at the mitotic metaphase. Fukui and Iijima (1991) and Iijima et al. (1991) also identified the rice chromosomes based on an image parameter, the condensation pattern (CP) using the chromosome image analyzing system, CHIAS (Fukui 1985).

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Table 1. Nineteen accessions of the genus *Glycine* currently used in this study

Subgenus	Species	Chromosome no.	Varieties or accessions
Soja	*G. max* (L.) Merr.	2n=40	Bonminori
		2n=40	EC114524
		2n=40	Matsuura
		2n=40	Mikuriyaao
		2n=40	Moshidou Gong 503
		2n=40	Toyosuzu
	G. soja Sieb. & Zucc.	2n=40	Gongzhuling wild soybean
		2n=40	Kamitondacho 1
		2n=40	Nakatsutsumi 2
		2n=40	No. 4 COL/IBARAKI/1983/WATANABE-2
		2n=40	No. 137 IBARAKI/NAGATA
Glycine	*G. canescens* F.J. Herm.	2n=40	White elifb
	G. clandestina Wendl.	2n=40	PI1233138
	G. falcata Benth.	2n=40	
	G. latifolia (Benth.) Newell & Hymowitz	2n=40	
	G. tabacina (LaGill.) Benth.	2n=80	Miyakozimatsurumame
	G. tomentella Hayata	2n=80	Lindeman
Bracteata	*G. wightii*	2n=22	Tinaroo
	(R. Grah. ex Wight and Arn.) Verdc.	2n=44	Soja perene

In this paper, we describe a marker chromosome that is commonly found in all three subgenera of the genus *Glycine* and the chromosomal characteristics revealed by the imaging and banding methods.

Materials and methods

Plant materials

Nineteen accessions of soybeans and their relatives in the genus *Glycine*, which were used as plant materials, are shown in Table 1. Seeds were sown on a wet filter paper in the petri dishes and germinated at 28 °C under continuous illumination. Root tips 2–3 cm in length were excised and used for the chromosome preparations.

Cytology

The revised enzymatic maceration method (Fukui et al. 1987) was employed. Root tips were pretreated with 0.01% colchicine for 3 h at 10 °C and fixed with the fixative (methanol:acetic acid = 3:1) for at least 3 days. Then they were macerated with an enzymatic mixture (2% Cellulase Onozuka RS, Yakult Honsha Co. Ltd., Tokyo; 1.5% Macerozyme R-200, Yakult Honsha Co. Ltd., Tokyo; 0.3% Pectolyase Y-23, Seishin Pharmaceutical Co. Ltd., Tokyo; 1 m*M* EDTA; pH was adjusted to 4.2) at 37 °C for 15 min in a humid chamber. After the mixture was thoroughly washed, distilled water was dropped onto the macerated root tips and removed with a piece of filter paper after 5 min. Then the root tips were chopped into thin pieces with fine forceps while adding the fixative. The glass slides were air-dried and stained with 2% Giemsa solution (E. Merck AG, Darmstadt, Germany). For the N-banding method, the following procedures (Funaki et al. 1975) were adopted. The chromosome samples were air-dried for more than 1 day after sample preparation. The glass slides were immersed in 1 *M* NaH_2PO_4 at 95 °C for 3 min and then they were stained with the 2% Giemsa solution.

Photographic procedures and image analyses

The pro-metaphase spreads were photographed using Neopan F (ISO 32, Fuji Photo Film Co. Ltd., Tokyo). Enlargement was carried out under two different conditions to obtain properly exposed prints and underexposed prints of the same pro-metaphase plate. Chromosomal parameters such as length, area, and condensation pattern were determined by using the chromosome image analyzing system, CHIAS (Fukui 1985, 1986, 1988). The CP was defined as a density profile along the mid-rib of each chromatid (Fukui 1989). The arm ratios of the chromosomes were also calculated.

Results

Characterization of soybean chromosomes

Figure 1 shows the soybean chromosomes at the pro-metaphase stage (Fig. 1 a) and the mid-metaphase stage (Fig. 1 b). Most of the chromosomes at the mid-metaphase stage were about 1 μm in length and their shape was very similar. They were totally contracted and no structural differentiation within each chromosome could be observed. All the chromosomes at the pro-metaphase stage, however, clearly showed an uneven condensation, most of them appearing more darkly stained at both proximal regions of the short and long arms than at the terminal regions. Two chromosomes showed a heavy condensation at the short arm only, as indicated by the solid arrowheads in the figure. Gaps in the interstitial regions of the chromosomal long arms were also detected in two chromosomes, as indicated by the open arrowheads. The unevenness of the chromosomal condensation along the mid-rib of the chromatid was

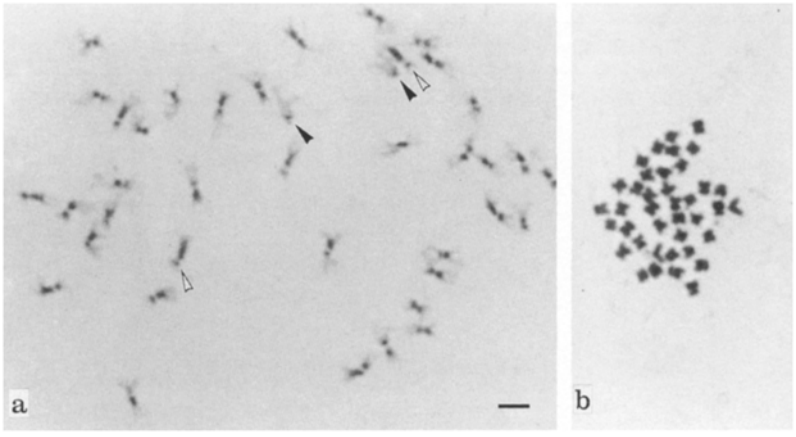

Fig. 1 a, b. Typical morphology of the soybean chromosomes at mitotic pro-metaphase (**a**) and mid-metaphase (**b**) stages. ▲ and △ show the chromosomes with the distinct characters. *Bar* indicates 3 μm

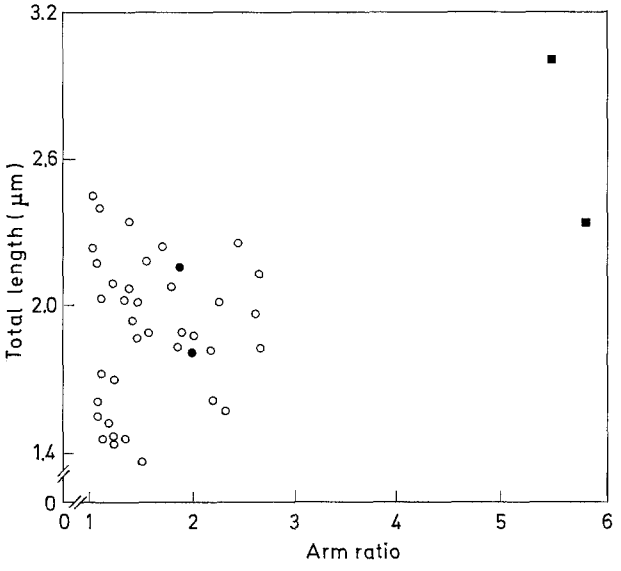

Fig. 2. Scattergram of the soybean chromosomal data relating to total length (vertical axis) and arm ratio (horizontal axis) from a pro-metaphase spread. The 40 chromosomes are indicated by ○, ●, and ■. ● and ■ show the chromosomes with the distinct characters as indicated in Fig. 1 a

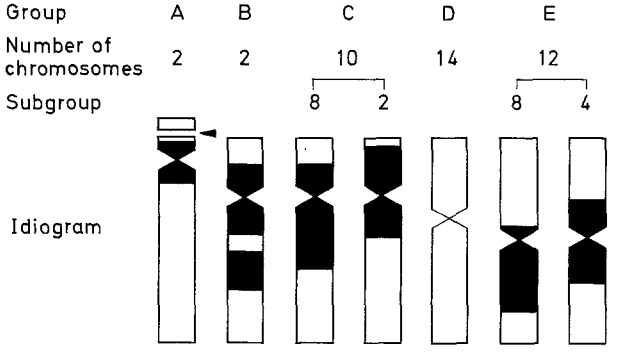

Fig. 3. Idiograms of the soybean chromosomes represented by the seven groups. ▲ shows nucleolar organizing region. Idiogrammatic representation of the condensed regions was not presented, since single patterns like the chromosomes in Group C or E were not defined among the chromosomes within Group D

digitally measured by using the CHIAS, and the respective lengths of the long and short arms were also measured simultaneously.

Figure 2 shows a scattergram of two parameters, namely, the total length (vertical axis) and the arm ratio (horizontal axis). Arm ratios of the pro-metaphase chromosomes ranged from 1.0 to 2.7, except for two chromosomes, which showed a value of 5.7. Total length ranged from 1.3 to 2.5 μm. Those two chromosomes with the exceptional arm ratios, as typically shown by one of the two chromosomes, had the longer length of 3 μm, as indicated by solid rectangles in Fig. 2. These chromosomes were so characteristic that they could be easily identified by visual inspection under the microscope. They usually had a long and non-condensed long arm at the pro-metaphase stage. The chromosomes with a single gap on the long arm did not show values as characteristic as those of the above-mentioned ones for these two numerical parameters, as shown by the solid circles in Fig. 2.

The CP was measured for every 80 chromatids of the 40 soybean chromosomes. Combination of the CP and the conventional numerical parameters made it possible to categorize the 40 soybean chromosomes into five groups with seven categories, including subgroups as shown in Fig. 3.

Group A corresponded to the telocentric two chromosomes with unique characteristics shown in Figs. 1 and 2. They exhibited a proximal condensation in both arms, and most of the regions of the short arm were apparently condensed. Satellites were sometimes observed in close proximity to the end of the short arm of the chromosomes. Other morphologically characteristic chromosomes (Group B) included the submedian chromosomes with a gap at the center of the long arm contraction. Thus, the chromosomes sometimes displayed a trimodal condensation pattern when the gap was clear. Group C consisted of ten chromosomes with an arm ratio larger than 1.6. These submedian chromosomes

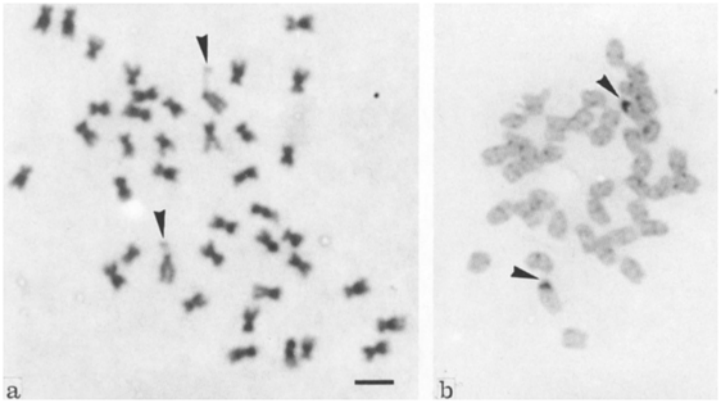

Fig. 4 a, b. Marker chromosomes of *G. max* indicated by *arrowheads* harboring the satellites at the end of the short arm (**a**) and clear large N-banding patterns (**b**). *Bar* indicates 3 μm

Table 2. Average data of the arm ratio and the total length of the chromosomes within each group

Group	Arm ratio		Total length		No. of chromosomes
	M*	SD**	M	SD	
A	7.22	2.13	2.29	0.47	2
B	2.23	0.29	2.01	0.17	2
C	2.37	0.38	1.95	0.26	10
D	1.56	0.20	2.00	0.39	14
E	1.17	0.08	1.89	0.33	12

* Mean value
** Standard deviation

were divided into two subgroups based on the characteristics of the CP. Eight chromosomes had a larger proximal condensed region in the long arm than in the short arm. Two chromosomes exhibited a reversed CP pattern, i.e., the condensed region in the proximal long arm region was smaller than that of the short arm, as typically shown in Fig. 3. Group E consisted of the 12 chromosomes whose arm ratios were smaller than 1.2. Twelve median chromosomes of Group E were also categorized into two subgroups, i.e., 8 chromosomes with a single large condensed region and 4 chromosomes with proximal condensed regions equally extended either on the short or long arm. Group D consisted of the remaining 14 chromosomes whose arm ratios were neither large nor small enough to assign the chromosomes into Group C or E. These chromosomes classified tentatively in Group D should be reexamined by methods other than just morphological. Thus, some chromosomes now assigned to Group D could be reclassified into either Group C, Group E, or other new groups. It was certain, however, that there was no interchange of chromosomes between Group C and Group E, since the scattergram of the 200 soybean chromosomes indicated a dispersed distribution or a gap of the distribution of the chromosomes around the arm ratio, 1.5.

Table 2 shows the average values and the standard deviation of the arm ratio and the total length of the chromosomes for each group based on 200 soybean chromosomes from five pro-metaphase spreads. The average values of the arm ratio and the total length of the chromosomes in Group A were the largest. Difficulties in the discrimination of the diffused end of the chromosomes in the long arm and the rapid contraction in the length with the progression of the mitotic stages resulted in the largest standard deviation.

Marker chromosomes of the genus Glycine

The chromosomes of Group A were conspicuously different in their morphology from the rest of the soybean chromosomes. A satellite was sometimes found attached to the end of the short arm of the chromosome or nearby (Fig. 4a). The results of the N-banding treatment also confirmed the peculiar characters of the chromosomes, as shown in Fig. 4b. All the chromosomes displayed paired small dots at the centromeric position, except for the two chromosomes of Group A. They showed clear large bands in the area covering their short arm and the nucleolar organizing regions (NOR). Thus, even for the markedly contracted chromosomes shown in Fig. 4b, the two chromosomes in Group A were easily identified by the N-banding method. The unique morphology at both the pro- and mid-metaphase stages (Fig. 1a, b) and the exceptional pattern in the N-band characterized the Group A chromosomes or marker chromosomes.

The observation of the 19 accessions from the three subgenera listed in Table 1 revealed the existence of chromosomes with similar characteristics to those of *G. max*. No morphological differentiation of the marker chromosomes was observed from those represented in Fig. 5a among the six varieties and lines of *G. max*. Morphological diversity was, however, clearly observed in the marker chromosomes among the five lines of *G. soja*, which also belonged to the same subgenus *Soja* as *G. max*. Two

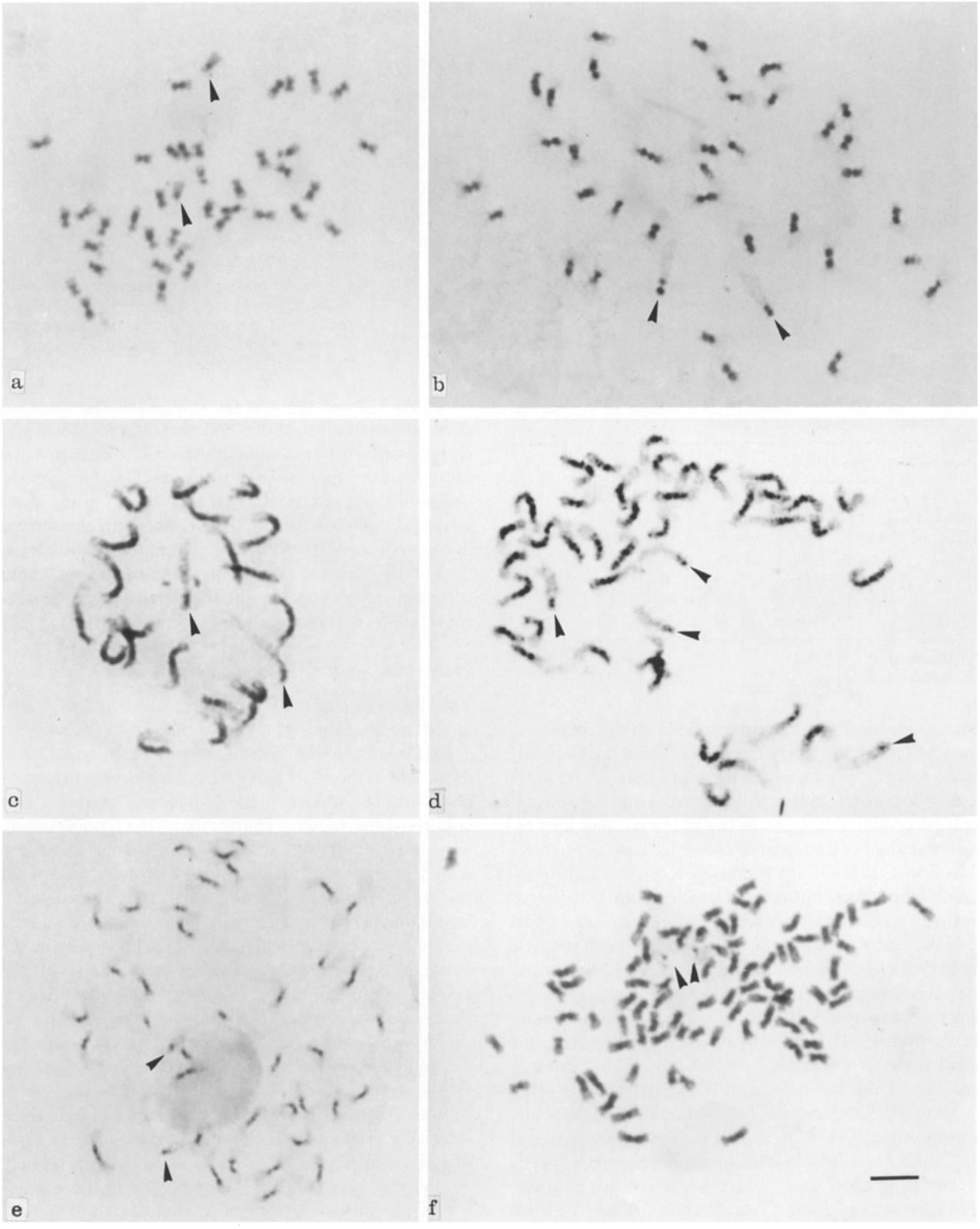

Fig. 5a–f. Several examples of the marker chromosomes commonly observed in the three subgenera of the genus *Glycine*. *Arrowheads* indicate the marker chromosomes of *G. soja*, M type (**a**); *G. soja*, S type (**b**); *G. wightii*, Tinaroo, chromosome number 22 (**c**); *G. wightii*, Soja perene, chromosome number 44 (**d**); *G. canescens* (**e**); *G. tomentella* (**f**). *Bar* indicates 5 μm

lines of Nakatsutsumi 2 and No. 137 which showed the same type of marker chromosomes as *G. max* were designated as M (max) type (Fig. 5a). The rest of the three lines – Gongzhuling wild soybean, No. 4, and Kamitondacho 1 – which showed a different type of marker chromosome with a larger short arm than the M type, were designated as S (soja) type (Fig. 5b). The average arm ratio in area of the ten chromosomes of M and S type was 8.26 and 5.61, respectively, and the difference between the values was significant at the 5% level. For the subgenus *Bracteata,* two lines in *G. wightii* were examined. One of the lines, Tinaroo, had a chromosome number of 22 and the presence of a pair of marker chromosomes was confirmed (Fig. 5c). The other line, Soja perene, had two pairs of marker chromosomes among the 44 chromosomes (Fig. 5 d). *G. wightii* consisted of at least two lines with different ploidy levels. Six species that were investigated in the subgenus *Glycine. G. canescens, G. clandestina, G. latifolia, G. falcata* had a pair of marker chromosomes among their 40 chromosomes, as typically indicated in Fig. 5e. The presence of at least one pair of marker chromosomes was confirmed in the two species of *G. tabacina, G. tomentella* (Fig. 5f) with 80 chromosomes. The marker chromosomes were found in all the subgenera of the genus *Glycine.*

Discussion

Many researchers have attempted to identify all the soybean chromosomes. Singh and Hymowitz (1988) established the idiogram based on the pachytene chromosomes of the soybean (*G. max* × *G. soja*) F_1 hybrid, whereas Sen and Vidyabhusan (1960) categorized the mitotic chromosomes into large, middle, and small chromosome groups according to their length with two pairs, 14 pairs and four pairs of chromosomes for the respective groups. Ladizinsky et al. (1979) classified them into four groups based on the C-banding pattern with the Giemsa staining. Ahmad et al. (1983) tried to distinguish them based on the values of the arm ratio and chromosome length. Among the 20 chromosomes of the haploid complement, 9 were eventually identified and described individually. The remaining 11 were characterized into two classes based on the values of the length and arm ratio. In all these reports since the mid-metaphase chromosomes were used for the analysis, the grouping was coarse, which may not be useful even for cytological studies of soybean. This condition was ascribed to the similarity in the shape and the small size of the soybean chromosomes at the mid-metaphase stage. Fukui (1989) defined an image parameter, CP, which would be useful for chromosome identification and characterization at the mitotic pro-metaphase stage. Plant chromosomes with small sizes like *Atriplex rosea* L. (Fukui and Mukai 1988) and *Oryza sativa* L. (Fukui and Iijima 1991; Iijima et al. 1991) were successfully identified by using the CP. The application of the imaging method for the measurement of the CPs for each of the soybean chromosomes made it possible to identify seven groups, including the subgroups.

All the image data have been digitized and the objectivity in the analytical processes was confirmed. The pair of chromosomes in Groups A and B showed characteristic morphological traits and could be easily distinguished from the rest of the chromosomes. The chromosomes in Group A, which showed a characteristic morphology and banding pattern, could thus be used as the marker chromosomes of the genus *Glycine,* since they were found in all the subgenera of the genus. The fact that they existed as a pair in the diploid species implies that soybean is not autotetraploid. The possibility of being either allotetraploid or diploid remains to be determined by further studies. The basic chromosome number of 20 is found only in the genus *Glycine* among the 51 genera of Phaseoleae (Lackey 1980). Thus, this author suggested that the original basic chromosome number of *Glycine,* which was 11, could be reduced to ten by aneuploidization. Then he assumed that polyploidization had taken place. Species in the subgenus *Bracteata* have the basic number of 11, but the possibility of introgression and integration of the individual chromosomes to *G. max* may be low, as the chromosomal morphology is different between the two subgenera.

The marker chromosome was also designated as a satellite chromosome, based on the morphological traits and the N-banding pattern. Although a pair of satellite chromosomes has been reported to occur in *G. max* (except for certain varieties) but could not be visualized by morphological observation (Oinuma 1952; Palmer and Heer 1973), we were able to determine the numbers of satellite chromosomes in the species of the three subgenera in this report.

The chromosomes in the species of the subgenus *Bracteata* are much larger than those in the species belonging to the subgenus *Glycine* and *Soja,* and the basic chromosome numbers are 11 and 20, respectively. Even though the characteristics of the satellite chromosomes are very similar in all the species in the three subgenera, the existence of two pairs of satellite chromosomes in the line Soja perene in *G. wightii,* with 44 chromosomes, suggests that the line could be an autotetraploid of a certain diploid line within the species, due to the duplication of the chromosome number. One pair of satellite chromosomes in the line with 44 chromosomes was usually attached to the short arm, suggesting the low activity at the NOR for a high ploidy level. This also may account for the fact that the presence of only one pair of satellite chromosomes has been confirmed by microscopic obser-

vation so far in the 80 chromosome species of the subgenus *Glycine*.

The differentiation of the short arm traits of the marker chromosomes was observed among the lines of *G. soja,* although no such differentiation was confirmed in the seven varieties of *G. max*. The M type marker chromosomes of *G. soja* are similar to those of *G. max* and the S-type marker chromosomes have significantly larger short arms than those of *G. max*. Moshidou Gong 503, which was once classified as another species *G. gracilis* (Skvortzow 1927) and now is included in *G. max* (Hermann 1962; Wang 1976; Broich and Palmer 1980), is a semiwild species scattered throughout China. The short arm of the marker chromosome is also of the M type and no morphological difference from the cultivated soybean chromosomes was detected. Skvortzow (1927) once suggested that *G. gracilis* was the intermediate type between the wild species and the cultivated soybean. It is generally recognized that the cultivated soybean was derived from certain lines of *G. soja* (Morse 1950; Williams 1950). Thus, it is suggested that certain M type lines of *G. soja* may be the ancestral species of the cultivated soybean. The accumulation of mutations and genetic recombinations, which have occurred in certain M type lines of *G. soja,* may be the main factors responsible for the formation of *G. max*. The individuals of the M type line in *G. soja* that have useful and favorable agronomic characters could be selected and the species of *G. gracilis* and *G. max* could be developed. The favorable agronomic characters, which include larger beans, seed retention, non-climbing plant, could arise by natural mutations occurring in *G. soja*. Ting (1946) discussed the fact that some characters of wild soybean show complete or partial dominance to those of the cultivated soybean. Although more information is obviously necessary to verify this hypothesis, the fact that the common trait of the marker chromosomes could be found in the intermediate type and in some of the wild lines of soybean may be an interesting clue to the analyses of the evolution and domestication of the soybean.

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