Journal of Plant Biology, December 2004, 47(4) : 322-329

Geographical Distribution of Cytotypes and Genomic Structures in Natural Populations of the *Scilla scilloides* Complex in Korea

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Cytotype distribution, B-chromosome frequency, and genomic constitution in the natural populations of the *Scilla scilloides* complex in Korea were analyzed. Plants with various cytotypes were found: AA (2n=16), BB (18), AAB (25), ABB (26), ABB (34), ABBB (35), BBBB (36), AABBB (43), AAABBB (51) and AAAABBBB (68). Allotetraploid AABB plants predominated with a frequency of 68.3%, and were found to distribute all over the Korean peninsula and Cheju-do. In diploids, the type AA plants distributed throughout the Korean midwest, while the type BB plants were limited to Cheju-do. Two other cytotypes, ABBB and AABBB, were found only in the southern part of the Korean peninsula including Cheju-do. Chromosomal variations, aneuploidy, and centromeric shifts were also found in the natural populations. The cytotypes AAB and AAAABBBB are reported here for the first time. B-chromosomes were found in 149 (85.6%) of 174 populations, the highest frequency being 81.8% in BB populations. The number of B-chromosomes per plant ranged from 1 to 31, and 1B plants predominated (21.0%). Subtypes, with respect to the number and composition of B-chromosomes, indicated that sexual reproduction is still prevalent in AABB populations.

Keywords: autosome, B-chromosome, cytotype, genome, *Scilla scilloides*, subtype

The *Scilla scilloides* complex, a bulbous plant of the family Liliaceae, is widely distributed in Far East Asia including mainland China, Korea and Japan (Haga and Noda, 1976; Araki, 1985; Yu and Araki, 1991). The chromosomal complements of this species comprise two differentiated genomes, A (x = 8) and B (x = 9). On the basis of combination of two basic genomes, various cytogenetic types have been found in the natural populations: AA (2n = 16), AB (17), BB (2n = 18), ABB (2n = 26), BBB (2n = 27), AAAA (32), AABB (2n = 34), ABBB (2n = 35), BBBB (2n = 36), AABBB (2n = 43), and AAABBB (2n = 51) (Morinaga, 1932; Okabe, 1938; Sato, 1942; Araki, 1972a, 1972b, 1975, 1985; Araki et al., 1976; Noda and Lee, 1980; Choi and Bang, 1990; Yu and Araki, 1991; Ding et al., 1998).

This species complex is an exemplary model for the study of genome differentiation and evolution. The relationship between the A and B genomes was analyzed by observing chromosome-pairing patterns in F1 hybrids of AA × BB plants (Araki, 1971; Noda, 1974a). Recently, molecular and cytogenetic approaches have been employed in order to elucidate the relationship between the two genomes (Hizume and Araki, 1994; Choi et al., 1997; Hizume and Araki, 1997; Hizume and Shibata, 2001). Numerical and structural chromosomal polymorphisms have been found in the natural populations of this species (Araki, 1972a, 1975; Araki et al., 1976; Uchino and Hayafuchi, 1983; Uchino and Tanaka, 1988).

The B-chromosome is an extra chromosome, and has been detected in more than 1,000 plant species (Jones and Rees, 1982). The number of B-chromosomes can be increased or decreased by non-disjunction during cell division. The B-chromosome also exhibits non-Mendelian transmission. The genetic effects of B-chromosomes have been studied in a few species (Ruiz Rejón et al., 1980), and their origins remain unclear. Numerical and structural B-chromosome variation has been previously studied in the Japanese populations (Haga and Noda, 1956; Haga, 1961).

In Korean natural populations of *S. scilloides*, however, only five cytotypes, AA, AABB, ABBB, AABBB, and AAABBB, have thus far been reported (Araki, 1972b, 1985; Noda and Lee, 1980). Due to the relative scarcity of sampling sites, not enough survey data exists to adequately explain cytotype distribution in the Korean populations. In this work, we investigated the geographical distribution of cytotypes in the Korean natural populations of *S. scilloides*. Chromosomal variation and B-chromosome frequency were

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also investigated.

MATERIALS AND METHODS

Bulbs of *S. scilloides* were collected from 174 natural populations in Korea (Fig. 1). They were transplanted, and are currently growing in the experimental garden at the School of Bioscience and Biotechnology, Chungnam National University. Actively growing root tips were pretreated with saturated 1-bromonaphthalene solution for 4 hr, fixed in acetic acid/alcohol (1:3, v/v) and squashed using a drop of 1% acetocarmine, after Feulgen staining.

Cytotypes were identified on the basis of genomic constitutions as previously described (Choi and Bang, 1990). B-chromosomes were classified into two types, metacentric isochromosomal (F) or minute telocentric (f). Subtypes, in terms of number and composition of B-chromosomes, were also investigated.

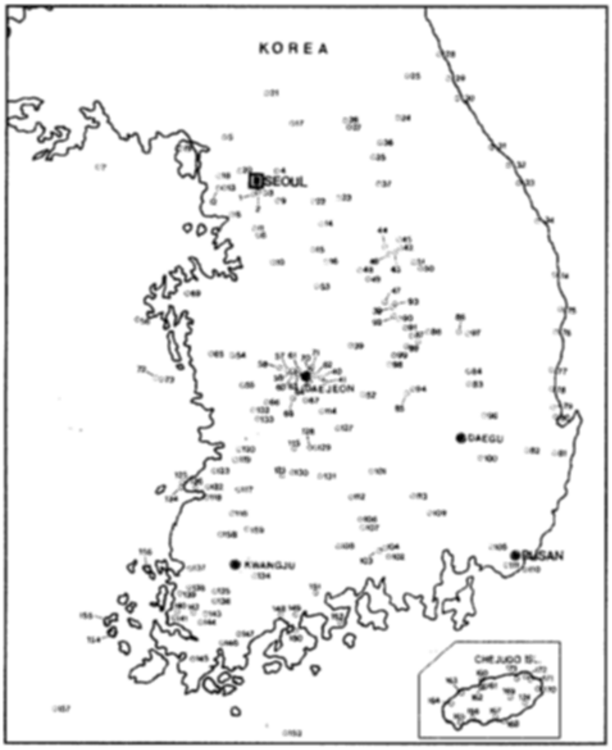

Figure 1. A map of Korea showing collection sites.

RESULTS

Cytogenetic Diversity and Geographical Distribution

A total of 2,439 *S. scilloides* plants from 174 natural populations in Korea were cytologically examined (Table 1). Cytotypes were easily identified by marker chromosome a1, which is the largest metacentric chromosome (Fig. 2).

Ten cytotypes ranging from diploid to octoploid were found in *S. scilloides* populations in Korea: AA (11.6%), BB (4.5%), AAB (0.04%), ABB (0.04%), AABB (68.4%), ABBB (11.3%), BBBB (0.4%), AABBB (3.5%), AAABBB (0.1%), and AAAABBBB (0.04%) (Table 1). Tetraploid AABB plants were found throughout the Korean peninsula and Cheju-do (130 populations), and predominated with a frequency of 68.4%. Triploid AAB (Fig. 2C) and octoploid AAAABBBB (Fig. 2J) plants were also detected for the first time in this study.

Geographical distribution of cytotypes of *S. scilloides* showed considerable differences, depending on genomic constitution. Furthermore, pure or mixed populations, with one to three cytotypes, were found in natural populations (Table 2). AA plants were found in 24 diploid populations, and limited to the mid-western regions of the peninsula (Fig. 2A and 3A), while type BB plants were found in only 2 populations of Cheju-do (Fig. 2B and 3A). AABB plants were found in 130 populations (110 pure and 20 mixed populations), and were found to encompass the vast majority of the Korean peninsula and Cheju-do (Table 2 and Fig. 3B), while type ABBB plants were found in only 28 populations, and were only found in the southern part of the peninsula and Cheju-do (Fig. 3C). Autotetraploid BBBB plants were found in a southwestern population (Fig. 3C). AABBB plants were found in 11 populations (1 pure and 10 mixed

Table 1. Frequency of cytotypes in natural populations of *S. scilloides* in Korea.

Cytotype	AA	BB	AAB	ABB	AABB	ABBB	BBBB	AABBB	AAABBB	AAAABBBB	Total
No. of plants	283	110	1	1	1688	276	10	86	3	1	2439
(%)	11.60	4.51	0.04	0.04	68.39	11.32	0.41	3.53	0.12	0.04	100.00

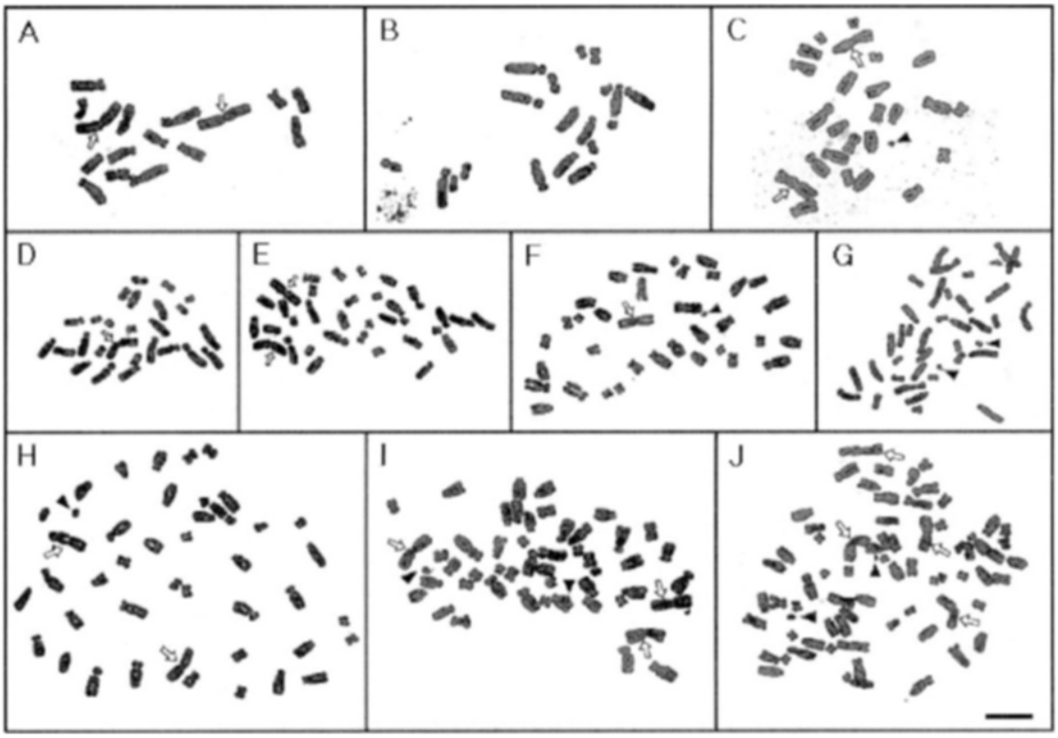

Figure 2. Cytotypes found in natural populations of *S. scilloides* in Korea. **A**, AA (2n = 16); **B**, BB (2n = 18); **C**, AAB (2n = 25+1f); **D**, ABB (2n = 26), **E**, AABB (2n = 34); **F**, ABBB (2n = 35+1f); **G**, BBBB (2n = 36+1F+1f); **H**, AABBB (2n = 43+1F); **I**, AAABBB (2n = 51+1F+1f); **J**, AAAABBBB (2n = 68+1F+1f). Arrows indicate a1 chromosomes. Dark triangles mark B-chromosomes. Bars, 10 μm.

Table 2. Genome constitution in natural populations of *S. scilloides* in Korea.

Type	Genome constitutions	No. of populations	(%)
1	AA	15	(8.6)
2	BB	1	(0.6)
3	AABB	110	(63.2)
4	ABBB	17	(9.8)
5	BBBB	1	(0.6)
6	AABBB	3	(1.7)
7	AA+AAB	1	(0.6)
8	AA+AABB	8	(4.6)
9	ABB+AABB	1	(0.6)
10	AABB+ABBB	5	(2.8)
11	AABB+AABBB	3	(1.7)
12	AABB+AAABBB	1	(0.6)
13	AABB+AAAABBBB	1	(0.6)
14	ABBB+AABBB	5	(2.8)
15	BB+ABBB+AABBB	1	(0.6)
16	AABB+AABBB+AAABBB	1	(0.6)
Total		174	(100.0)

populations). The other types, AAB, ABB, AAABBB and AAAABBBB were found only in one or two populations, either inland or on Cheju-do (Fig. 3D).

The structures of natural populations could be classified into 16 types, depending on the composition of cytotypes. Most of the populations (84.5%) were composed of one type, while the others were mixtures of two or three cytotypes, such as AABB+ABBB or BB+ABBB+AABBB (Table 2).

Chromosomal Variation in Natural Populations

Numerical chromosomal variations were found, with a frequency of 0.4%, in type AA and AABB plants. Two type AA plants were trisomics of the a1 or a4 chromosomes (Fig. 4A and B). Nine AABB plants were either monosomic (deletion of chromosome b1) or trisomic (chromosome a4) (data not shown).

Centromeric shift was found, with a frequency of 0.7%, in AA, BB, AABB, and ABBB plants (data not shown). In one AABB population (Fig. 1, site no. 51), 10 out of 12 plants carried chromosomes with centromeric shifts.

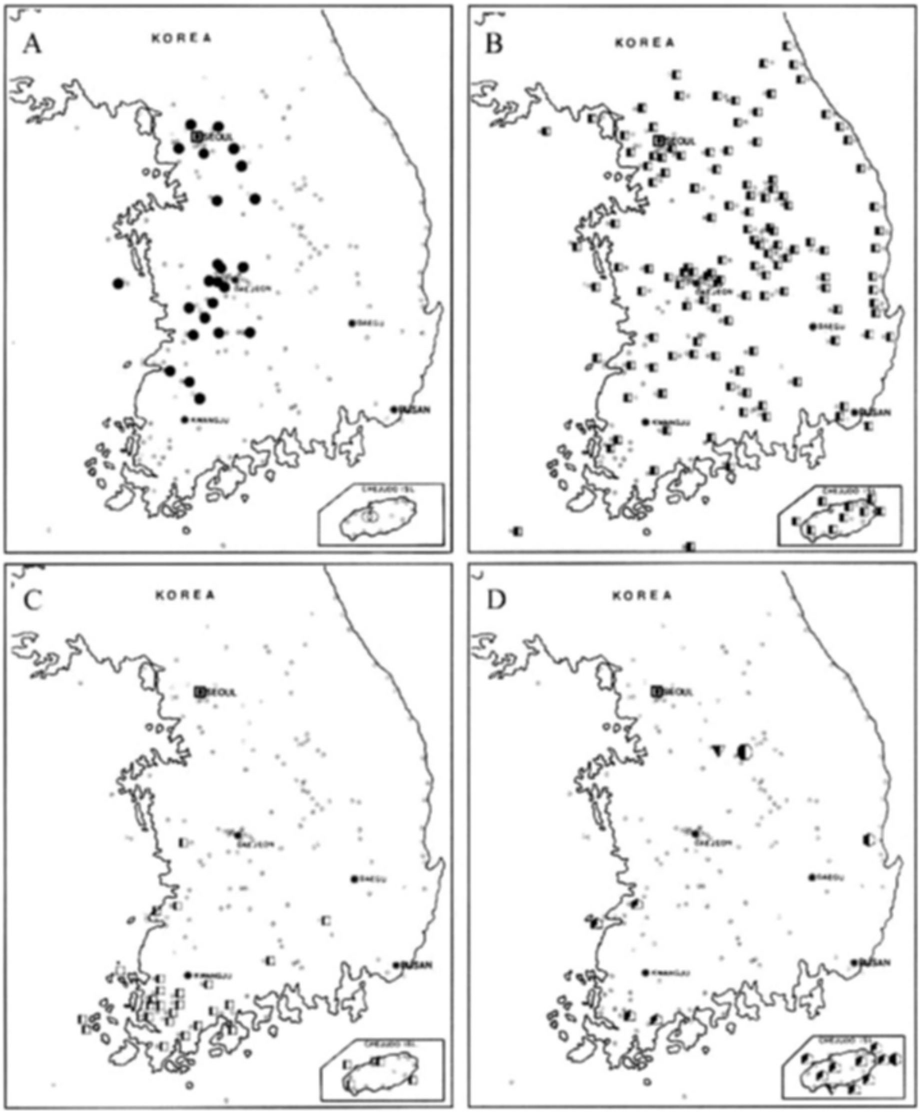

Figure 3. Geographical distribution of cytotypes of *S. scilloides*. **A**, AA (•) and BB (○); **B**, AABB (◧); **C**, ABBB (◨) and BBBB (□); **D**, AAB (▼), ABB (▽), AABBB (◭), AAABBB (◐) and AAAABBBB (◑).

Table 3. Frequency of B-chromosomes in natural populations of *S. scilloides* in Korea.

No. of populations		No. of plants			No. of B-chromosome	
0B (%)	Bs (%)	0B (%)	Bs (%)	Total	Total	Mean no./ plant
25 (14.4)	149 (85.6)	1,196 (49.0)	1,243 (51.0)	2,439 (100.0)	3,687	1.5

0B, without B-chromosome; Bs, with B-chromosome

B-Chromosomal Polymorphisms and Subtypes

B-Chromosomes were found in all cytotypes of *S. scilloides*, with the exception of type ABB. The average number of B-chromosomes per plant was 1.5 (Table 3). Most of the populations (149: 85.6%), and more than half of the plants (1,243: 51.0%) carried B-chromosomes. The B-chromosomes were classified

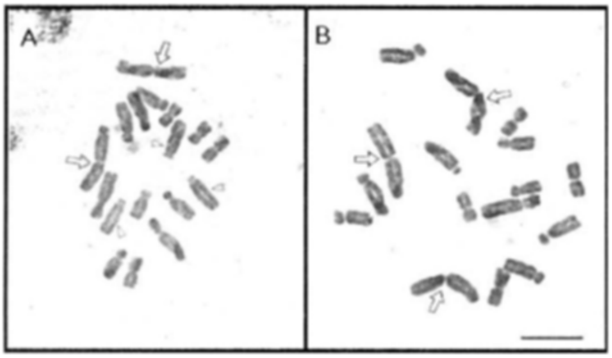

Figure 4. Somatic metaphase chromosomes with aneuploids in *S. scilloides*. **A**, AA (2n = 17) with trisomy of a4 chromosomes (triangles); **B**, AA (2n = 16) with trisomy of a1 and deletion of a2 chromosome. Arrows indicate a1 chromosomes. Bars, 10 µm.

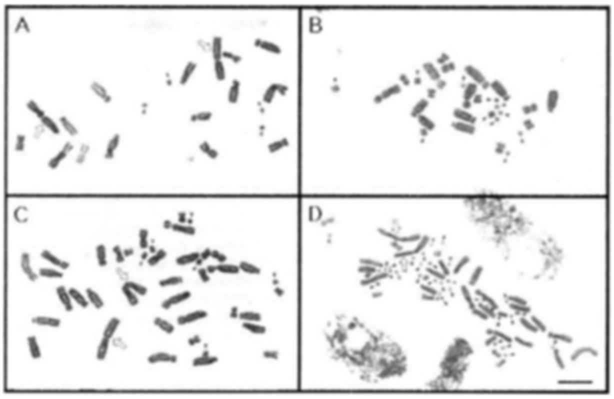

Figure 5. Somatic metaphase chromosomes with B-chromosomes in *S. scilloides* **A**, AA+4B (2n = 16+4f); **B**, BB+11B (2n = 4F+7f); **C**, AABB+6B (2n = 34+6F); **D**, AABB+31B (2n = 34+31f). Arrows indicate a1 chromosomes. Dark triangles mark B-chromosomes. Bars, 10 µm.

into two types, small isochromosome (F) with centromere and minute telocentric (f) which was half the size of F. Number, type, frequency, and distribution variations of the B-chromosome were found. With the exception of cytotype AA plants, which were all found to be f type, B-chromosomes exhibited compositional polymorphisms such as F, f and F+f. Figure 5 shows B-chromosomal variations in the number and composition: an AA plant with 2n = 16+4f (A), a BB plant with 2n = 18+4F+7f (B) and AABB plants with 2n = 34+6F (C). In the populations with large numbers of B-chromosomes, f type was more frequent than F type (data not shown). For example, the largest number of B-chromosomes per plant was 31, in an allotetraploid AABB population with a composition of 2n = 34+31f (Fig. 1 and 5D, site no. 20). The B-chromosome frequency was highest in type BB (81.8%) and 1B plants were prevalent, with a frequency of 21.0%.

In addition, many subtypes related to the number and the composition of B-chromosomes were observed in the natural populations of *S. scilloides* in Korea. In AABB populations, remarkable diversity among subtypes was discovered. For example, 14 different subtypes were counted out of 15 plants in an AABB population (Table 4).

DISCUSSION

There have been a number of studies on the cytogeographical distributions of *S. scilloides* (Araki et al., 1976; Haga and Noda, 1976; Noda and Lee, 1980; Araki, 1985; Yu and Araki, 1991; Ding et al., 1998). So far, seven cytotypes including BB, BBB, ABB, AABB, ABBB, BBBB and AABBB, have been found in

Table 4. Number of subtypes according to the B-chromosomes (F and f) in an AABB population (site no. 34) of *S. scilloides*.

No. of f / No. of F	0	1	2	3	4	5	6	No. of plants	No. of plants
0	-	-	1	-	-	-	-	1	1
1	-	1	1	1	1	-	1	5	5
2	1	-	2	-	1	-	-	4	3
3	-	1	-	-	-	-	-	1	1
4	1	-	-	-	-	-	-	1	1
5	-	1	-	-	-	-	-	1	1
6	-	-	-	-	-	-	-	0	0
7	-	-	1	-	-	-	-	1	1
8	1	-	-	-	-	-	-	1	1
Total	3	3	5	1	2	0	1	15	14

Japanese populations of *S. scilloides* with allotetraploid AABB predominating (Ihara, 1977). In Mainland China, three cytotypes, AA, AAAA and AABB, were reported in northern China (Yu and Araki, 1991), while BB plants were found only in the southern part of China (Yang and Zhu, 1987; Fu and Hong, 1989). More recently, Ding et al. (1998) reported six cytotypes, AA, AB, BB, AAA, BBB, and AABB, in only 45 natural populations from central, eastem, and southern China. Although type AA and AABB plants were predominant, more intensive cytogeographical study is needed in Chinese populations. The survey data showed that at least seven cytotypes were distributed throughout Mainland China.

In Korean peninsula, only five cytotypes of *S. scilloides*, AA, AABB, ABBB, AABBB, and AAABBB, have been reported to date (Araki, 1972b; Noda and Lee, 1980; Araki, 1985). In our survey, however, we found that ten cytotypes with enormous ploidy variation and diversified genomic constitutions existed in Korea: These include AA, BB, AAB, ABB, AABB, ABBB, BBBB, AABBB, AAABBB and AAAABBBB. Of the 10 cytotypes, AABB plants were the most predominant (68.4%). Differences between our data and these of previous reports might be attributable to our larger number of sampling sites throughout the Korean peninsula and Cheju-do (Araki, 1972b; Noda and Lee, 1980; Araki, 1985). The type BB and BBBB plants were reported for the first time in Korean populations. With respect to the introduction and distribution of this species, it was suggested that the sterile type ABBB and AABBB plants had been introduced to Korea from Japan (Araki, 1985), because BB and/or ABB plants, which could play an important role in forming ABBB and AABBB plants, have not yet been detected in Korean populations. However, various cytotypes including BB, ABB, AABB, ABBB, BBBB, AABBB and AAABBB were found in the southern part of the Korean peninsula and Cheju-do, and it is possible that natural hybridization is taking place in Korean populations.

It has been suggested that *S. scilloides* originated in China, and was introduced to Korea and Japan by human activities associated with agricultural cultivation (Maekawa, 1944; Haga and Noda, 1976; Araki, 1985). Therefore, Korea is a cytogeographical transition route between China and Japan, through which the plants may have been transferred. Interestingly, most of these plants are found in mountainous regions of high altitude in China, whereas all of the plants in Korea and Japan were found in agricultural fields, along roadsides, and in graveyards.

Two characteristic cytotypes of *S. scilloides*, AAB and AAAABBBB, are reported for the first time here, and the BB and BBBB plants, which had been known only in China and Japan, were also found for the first time in Korean natural populations. The occurrence of various cytotypes demonstrates that the Korean populations of *S. scilloides* are much more diversified than these of other regions. The diploid plants, AA and BB, showed geographically different distribution patterns. The AA genome plants were restricted to the midwestern part of the Korean peninsula (Fig. 2A), while the BB genome plants were found only in Cheju-do (Fig. 3A). In contrast, allotetraploid AABB plants were distributed throughout the Korean peninsula including Cheju-do (Fig. 3B). Interestingly, the type AA plants were found throughout China (Ding et al., 1998) and also in western Korea, but there have been no reports of AA plants in Japanese natural populations to date. The type BB plants were also abundant in eastern and southern China (Yang and Zhu, 1987; Fu and Hong, 1989; Ding et al., 1998). These data could provide a clue for the geographical relationship between the A and B genomes of *S. scilloides* occurring in China, Korea, and Japan. For example, it could be surmised that the AA plant, although widely distributed in China and Korea, has simply not yet been transferred to Japan. Conversely, the BB plant has been transferred to Japan from China via Korea. Interestingly, the AA genome is distributed only sparsely in the northern parts of China and Korea, while the BB genome has a transition route that more likely passed through the southern parts of China, Korea, and Japan. The AABB plant is the most common type in China, Korea, and Japan. It is thought that the AABB type is, cytogenetically, the most stable type in Korean populations of *S. scilloides*, since this cytotype occupies the widest area and has the highest frequency as compared to other regions. The ABBB and AABBB plants were limited to the southern part of Korea (Fig. 3C), but were frequently found in Japanese populations (Araki et al., 1976; Haga and Noda, 1976). However, our data do not cover the northern part of the Korean peninsula. Once the survey includes this area, the introduction and transition route of this species to Korea and Japan can be elucidated more clearly.

The chromosomal pairing pattern in F1 hybrids (AB, $2n = 17$) of *S. scilloides* from AA × BB showed that two genomes, A ($x = 8$) and B ($x = 9$), are partially homologous, although they are karyotypically well differentiated. It was proposed that the A genome is derived from the B genome, through translocation, inversion and the loss of the centromere (Araki, 1971). Secondary constrictions with NOR were found in the a2 chromosome of type AA, and the b1 chromosome of type BB, but not in the a2 chromosome of allotetraploid AABB plants (Araki, 1971; Haga and Noda, 1976; Ihara, 1977; Hizume and Araki, 1994; Choi et al., 1997). It was suggested that NOR in the A genome was suppressed in AABB plants by the strong NOR activity of the B genome (Sato, 1940, 1941). In *S. autumnalis*, NOR was also not detected in the allotetraploid AAB7B7 cytotype (Parker et al., 1991; Vaughan et al., 1993). Various cytotypes in *S. autumnalis* have been also reported in the natural populations (Hong, 1982; Parker et al., 1991).

Chromosomal variations were observed in natural populations of *S. scilloides*. Aneuploids were found at a percentage of 0.4% in AA and AABB plants. It was interesting that numerical chromosomal variations were detected only in the chromosomes of the A genome. Aneuploidal plants were frequently produced from asynapsis between homologous chromosomes during meiosis (Uchinio and Hayahuchi, 1983). In a Japanese population of *S. scilloides* consisting of types BB, BBB, ABB, AABB and ABBB, aneuploids were also found only in the chromosomes of the A genome (Araki, 1975). Chromosomes a1 and a4 in the A genome, in particular, were likely to be responsible for the production of aneuploids (Fig. 4). Aneuploids were found in sexually unstable ABB plants produced by vegetative propagation (Noda, 1975). Araki (1977) sampled some plants in a Japanese population of *S. scilloides* twice in order to study the structure of the population, and found that the frequency of aneuploidy changed from 6.8% to 23.0% in ten years. He proposed that new cytogenetic types occurred through aneuploidal plants in a population of this species. Consequently, it is likely that the production of aneuploids can make a population more complex, and that it also plays an important role in increasing cytogenetic diversity in this species.

Another chromosomal polymorphism, centromeric shift, was found in some plants of *S. scilloides*. Noda (1974b) analyzed meiotic chromosome b2 in type BB plants in a Japanese population, and described this structural variation as pericentric inversion, in which submetacentric chromosomes were converted into subtelocentrics by inversion involving a centromere. Type BB, AA, AABB, and ABBB plants in Korean populations were also found to have undergone centromeric shift (data not shown). Except for chromosome a6 in type AA, centromeric shift was detected only in chromosome b2.

The B-chromosomes of *S. scilloides* were classified into two types, F and f (Haga and Noda, 1956). However, four types (F, f, fs, and fl) were also reported based on the B-chromosome's morphology (Noda and Lee, 1980). The B-chromosomes showed considerable variation in the number and composition depending on the cytotypes, individuals, and populations. Among 10 cytotypes of *S. scilloides*, AABB plants had the most diversity with respect to number and composition of B-chromosomes. Polymorphic B-chromosomes were also reported in other plants: four types of *Allium schoenoprasum* (Bougoured and Parker, 1975) and three types of *S. autumnalis* (Parker et al., 1991). The largest number of B-chromosomes was $2n = 34+31f$ in an AABB plant (Fig. 5D). The highest B-chromosome frequency was detected in the type BB population (81.8%). The AA plants carried only type f, not F or F+f. Our data showed that Korean populations of *S. scilloides* had a much larger number of B-chromosomes than did other areas. In a previous survey, the B-chromosome frequencies of AA and AABB plants in the Korean populations of *S. scilloides* were 22.1% and 43.9%, respectively (Noda and Lee, 1980). In the present study, however, their frequencies in AA and AABB populations were found to be 31.8% and 48.4%, respectively. Many subtypes were observed in AABB populations, characterized by variations in chromosomal number and composition. Most of these populations appeared to be maintained by sexual propagation. It was demonstrated that the predominance of this cytotype is probably closely related to the prevalence of sexual reproduction. In contrast, in sterile types ABBB and AABBB, only one or two subtypes were counted in most populations of *S. scilloides* (Choi, 1996), and these populations might be maintained by vegetative propagation.

ACKNOWLEDGEMENT

This research was partly supported by a grant (code #: PF0300210-00, PI Jae-Wook Bang) from Plant Diversity Research Center of 21st Century Frontier Research Program funded by MOST, Korea.

Received June 30, 2004; accepted August 31, 2004.

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