Cytogenetic Relationship between *Allium fistulosum* L. and *A. schoenoprasum* L.

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Summary

Interspecific hybrids between *Allium fistulosum* L. ($2n=16$) and *A. schoenoprasum* L. ($2n=16$) which are classified to different sections of the *Allium* were investigated cytogenetically to elucidate their relationship. Hybrid plants ($2n=16$) were produced by reciprocal crossings through embryo or ovule cultures, but the number of hybrid plants derived per pollinated flower was much smaller in the combination using *A. fistulosum* as a seed parent. At meiotic metaphase-I, chromosome pairings of 16_1 or $1_{II}+14_1$ occurred frequently; tetrads were observed together with dyads and heptads at tetrad stage. The hybrid plants exhibited three types of anther development; a) fully developed form, b) aborted form or c) having both forms. Unreduced spherical pollen grains were observed in fully developed anthers. Pollen stainability ranged from 13 to 65%. No plant was obtained in the backcross with *A. fistulosum*.

Chromosome doubled plants were produced through colchicine treatment of hybrid plants. In the chromosome doubled plant derived from the hybrid plant with fully developed anthers, pollen stainability was 64%. No seed was obtained through open pollination and crossing with *A. fistulosum* as a pollen parent. In the chromosome doubled plant derived from the hybrid plant with aborted anthers, anthers were aborted and were pollen-sterile.

These results indicate that the homology between the genomes of *A. fistulosum* and *A. schoenoprasum* is low and that they are distantly related to each other cytogenetically.

Key Words: *Allium schoenoprasum*, *Allium fistulosum*, interspecific relationship, interspecific hybrid, meiosis.

Introduction

Japanese bunching onion, *Allium fistulosum*, has been bred through intraspecific crossing or selection (Ford-Lloyd and Armstrong, 1993). To obtain interspecific hybrid plants of *A. fistulosum* and expand its germ-plasm, *A. schoenoprasum* was selected as a potential parental species. *A. schoenoprasum* (chives and asatsuki) plants which are grown as vegetables or herbs for tender green fistulous leaves or etiolated sheath, have many nutritive components and fine qualities compared with other species of the genus *Allium*.

According to Hanelt (1990)'s classification of cultivated species in the genus *Allium*, *A. fistulosum* is systematically classified to the section *Cepa*, whereas *A. schoenoprasum* belongs to the section *Schoenoprasum*, of the same subgenus *Rhizirideum*. Hanelt (1990) stated that delimitation between the above two sections is not necessarily clear.

Crossings between the above two species were performed in *A. fistulosum* $\times$ *A. ledebourianum* (Yamaura,

1955) (asatsuki was classified as *A. ledebourianum* by the author) and *A. fistulosum* $\times$ *A. schoenoprasum* (Gonzalez and Ford-Lloyd, 1987). In the former, seedlings were obtained *in vivo* and were confirmed to be hybrids by observing somatic chromosomes. In the latter, it was only reported that seedlings were obtained through embryo rescue method. Attempt at crossing between *A. schoenoprasum* and *A. cepa* was unsuccessful (Gonzalez and Ford-Lloyd, 1987). Cytologically, these two species differ in their nuclear DNA content (Jones and Rees, 1968) and their karyotypes at mitotic metaphase (Ved Brat, 1965). Their cross-compatibility and the genetic behavior of their progenies have not been studied.

Section *Cepa* species including *A. fistulosum* are the most closely related to *A. schoenoprasum* among the examined species and sections based on morphological, cytological and chemical studies (El-Gadi and Elkington, 1977), RFLP analysis of chloroplast DNA (Havey, 1991), RAPD analysis (Wilkie et al., 1993) and dot blot analysis with RAPD probe (Dubouzet et al., 1997).

The purpose of this study was to estimate the relationship between these two species by producing F_1 hybrids and examining their chromosome behavior, and obtaining chromosome doubled plants to restore fertility of F_1 hybrids as a first step for the improvement of *A.*

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fistulosum.

Materials and Methods

A. fistulosum cv. Kujyo and a Swedish commercial strain of chives, *A. schoenoprasum* were crossed reciprocally. Embryos or ovules were cultured 9–29 days after pollination on the modified Nitsch medium (1951) in which Fe-EDTA was substituted for FeSO_4 , containing $30 \text{ g} \cdot \text{liter}^{-1}$ sucrose and $7.5 \text{ g} \cdot \text{liter}^{-1}$ agar. Plantlets were transferred to sterilized vermiculite in pots.

To produce chromosome doubled plants, stem tips of hybrid plants were cultured on the modified MS medium (Murashige and Skoog, 1962) containing 0.2% colchicine for 4 to 8 days and then subcultured on the modified MS medium containing $0.5 \text{ mg} \cdot \text{liter}^{-1}$ NAA and $2 \text{ mg} \cdot \text{liter}^{-1}$ kinetin. The modified MS medium consisted of a half strength of MS macro nutrient salts, substituted Fe-EDTA for FeSO_4 and MS micro nutrient salts. Shoots were cultured for rooting on a commercial nutrient medium (N: P: K = 7: 6: 19 mg%). All media contained $30 \text{ g} \cdot \text{liter}^{-1}$ sucrose and $7.5 \text{ g} \cdot \text{liter}^{-1}$ agar.

Karyotype, meiosis in pollen mother cell (PMC), pollen mitosis and pollen stainability were examined according to Inada and Endo (1994).

Results

1. Cross-compatibility between *A. fistulosum* and *A. schoenoprasum*

Hybrid plants were obtained by reciprocal crossings (Table 1), but the number of plants per pollinated flower was much smaller in *A. fistulosum* $\times$ *A. schoenoprasum* (0.005) than in *A. schoenoprasum* $\times$ *A. fistulosum* (0.11). Nine hybrid plants that matured and flowered were used for cytological observation (shown in Table 2, except one, s3f6, from *A. schoenoprasum* $\times$ *A. fistulosum*).

2. Cytology of F_1 hybrid plants

1) Karyotype

The parent species and all hybrid plants had 16 somatic chromosomes (Figs. 1a, 1b, 1c). Hybrid plants had two types of J-shaped chromosomes characteristic of the parent species and their hybridity was confirmed.

2) Meiosis

Meioses progressed regularly in both parent plants. Seven reciprocal hybrid plants observed showed chromosome pairings of $(1-0)_{III}$ (trivalent) + $(1-5)_{II}$ (bivalents) + $(1-16)_I$ (univalents) at meiotic metaphase-I with the highest frequency of 16_I (or $16_I + 1$ chromosome fragment) [9/25 PMCs (36.0%)–67/107 PMCs (62.6%), 5 plants] or $1_{II} + 14_I$ [14/42 PMCs (33.3%)–25/55 PMCs (45.5%), 2 plants] (Table 2). Bivalents were mostly rod-shaped with one subterminal chiasma or one chiasma at the distal region (Figs. 2a, 2b). One trivalent was observed in 2 plants. Chromosome fragments were observed in 3.7–10.0% of PMCs examined. There were PMCs with less than 15 chromosomes. At anaphase- and telophase-II monads were observed with dyads (Fig. 2c). At tetrad stage 2 to 7 microspores were observed with 63.1–85.4% being tetrads and 8.5 to 24.6% dyads, including ones with a micronucleus or some micronuclei.

3) Pollen stainability and seed fertility

Pollen fertilities of both parent plants were more than 90%. Hybrid plants exhibited three types of anther development at anthesis; a) most anthers fully developed and dehiscent, releasing pollen in 3 plants, s3f11-1, s3f11-2 and s3f12, b) nearly all anthers shrunken in 5 plants, s2f1, s2f2, s3f1, s3f3 and s3f6, and c) filled and shrunken anthers in one plant, f5s1. Fully developed anthers contained aceto-carmin-stainable, spherical and binucleate pollen grains (Fig. 3a). In 7 to 15 anthers on each of 4 plants, pollen stainability varied, ranging from 13.0 to 65.4% (Table 2). Pollen grains with 16 chromosomes were observed at pollen mitotic metaphase (Fig. 3b), and are apparently unreduced ones; they would have developed from cells of $n=16$ which did not divide at first meiosis and divided into dyads at second meiosis (Fig. 2c). Pollen grains germinated on an agar medium. No seed was obtained by selfing (238 flowers) and crossing (316 flowers) with *A. fistulosum* cv. Kujyo as a pollen parent in 3 plants (s3f11-1, s3f11-2, f5s1). Crossing (36 flowers) with *A. fistulosum* cv. Kujyo as a seed parent produced abortive seeds in one plant (s3f11-1).

3. Cytology of chromosome doubled plants

Table 1. Results of reciprocal crossings between *A. fistulosum* and *A. schoenoprasum* through embryo or ovule culture.

Cross-combination ²	No. of flowers pollinated (1)	No. of embryos or ovules cultured	No. of embryos or ovules that germinated	No. of plants potted (2)	(2) / (1)	No. of plants that matured and flowered
<i>A. fistulosum</i> $\times$ <i>A. schoenoprasum</i>	194	25	2	1	0.005	1
<i>A. schoenoprasum</i> $\times$ <i>A. fistulosum</i>	132	25	20	15	0.11	8

² Parents used: *A. fistulosum*, cv. Kujyo; *A. schoenoprasum*, a Swedish commercial strain of chives.

Fig. 1. Somatic metaphase chromosomes of *Allium schoenoprasum* (1a), *A. fistulosum* (1b), their hybrid plant (1c) and its chromosome doubled plant (1d). 1a, 1b, 1c; $2n=16$, 1d; $2n=32$. Arrowheads and arrows indicate J-shaped chromosomes of *A. schoenoprasum* and *A. fistulosum*, respectively. Bar=10 μ m.

Fig. 2. Chromosome pairing at meiotic metaphase-I (2a, 2b) and anaphase-II (2c) in PMCs of hybrid plants derived from *A. schoenoprasum* $\times$ *A. fistulosum*. 2a; 16_{I} , 2b; $2_{\text{II}}+12_{\text{I}}$, 2c; dyad cell (lower) and monad cell (upper). Bar=10 μ m.

Fig. 3. Pollen grains (3a) and pollen mitotic metaphase (3b) of a hybrid plant, s3f11-1, of *A. schoenoprasum* $\times$ *A. fistulosum*. 3a; spherical stainable pollen grains are observed with sterile ones, bar=100 μ m. 3b; $n=16$, bar=10 μ m.

Fig. 4. Chromosome pairing at meiotic metaphase-I in a PMC (4a) and pollen mitotic metaphase (4b) in a chromosome doubled plant, 4x-s3f11-2, resulting from *A. schoenoprasum* $\times$ *A. fistulosum*. 4a; $15_{\text{II}}+2_{\text{I}}$, 4b; cells of $n=16$ (left) and $n=16+$ one fragment (right). Bar=10 μ m.

1) Karyotype

Chromosome doubled plants were obtained from two hybrid plants, s3f11-2 with fully developed anthers and s2f1 with aborted anthers. They had 32 somatic chromosomes including 4 characteristic J-shaped chromosomes derived from both parents of hybrid plants (Fig. 1d).

2) Meiosis

In 4x-s3f11-2, derived from s3f11-2, chromosome pairing was $(16-14)_{\text{II}}+(0-4)_{\text{I}}$; that with 16_{II} occurred most frequently at meiotic metaphase-I of PMCs (Table 3, Fig. 4a). No unequal bivalent was recognized in any PMCs. PMCs with 1 to 2 chromosome bridges or 1 to 2 lagging chromosomes occurred in 83/229 cells (36.2%) at telophase-I.

Table 2. Chromosome pairing at meiotic metaphase-I in PMCs and pollen stainability of parents and F₁ hybrid plants between *A. fistulosum* and *A. schoenoprasum*.

Parents and hybrid plants	Number of PMCs observed	Number of PMCs ^z											Average frequency of chromosome pairing	Pollen stainability (%)
		16 _I	1 _{II} +14 _I	2 _{II} +12 _I	3 _{II} +10 _I	4 _{II} +8 _I	5 _{II} +6 _I	6 _{II} +4 _I	7 _{II} +2 _I	8 _{II}	1 _{III} +13 _I	1 _{III} +1 _I +11 _I		
<i>A. fistulosum</i> ^y	189	0	0	0	0	0	0	0	0	189	0	0	8 _{II}	94.8
<i>A. schoenoprasum</i> ^y	61	0	0	0	0	0	0	0	0	61	0	0	8 _{II}	95.9
<i>A. fistulosum</i> × <i>A. schoenoprasum</i>														
f5s1	55	18	25	9	2	0	1	0	0	0	0	0	0.98 _{II} +14.04 _I	11.0 65.4 ^x
<i>A. schoenoprasum</i> × <i>A. fistulosum</i>														
s2f1	25	9	8	5	2	1	0	0	0	0	0	0	1.12 _{II} +13.76 _I	0
s2f2	72	29 (3)	27	11	4	0	0	0	0	0	0	1	0.013 _{III} +0.86 _{II} +14.24 _I	0-0.9 ^x
s3f1	80	39 (4)	22 (4)	13 (1)	4	2	0	0	0	0	0	0	0.85 _{II} +14.3 _I	0
s3f3	42	7	14	11	8	1	1	0	0	0	0	0	1.64 _{II} +12.72 _I	0
s3f11-2	74	37	31	5	1	0	0	0	0	0	0	0	0.59 _{II} +14.81 _I	0 27.5 ^x
s3f12	107	67 (2)	33 (2)	4	1	0	0	0	0	0	2	0	0.019 _{III} +0.41 _{II} +15.12 _I	0 13.0 ^x
s3f11-1	—	—	—	—	—	—	—	—	—	—	—	—	—	0.8-26.2 ^x

^z Numeral in parenthesis indicates number of PMCs containing one chromosome fragment.^y Parents used are shown in Table 1.^x Range of values in the examined anthers.

Table 3. Chromosome pairing at meiotic metaphase-I of chromosome doubled plants derived from *A. schoenoprasum* × *A. fistulosum* hybrid plants.

Plant number	Number of PMCs observed (%)	Number of PMCs (%)						Pollen stainability (%)
		Chromosome pairing						
		16 _{II}	15 _{II} +2 _I	14 _{II} +4 _I	13 _{II} +6 _I	1 _{III} +14 _{II} +1 _I	1 _{III} +13 _{II} +3 _I	
4x-s3f11-2	74 (100)	51 (68.9)	15 (20.3)	8 (10.8)	0 (0)	0 (0)	0 (0)	64.3
4x-s2f1	88 (100)	66 (2) ^z (75.0)	16 (2) ^z (18.2)	3 (3.4)	1 (1.1)	1 (1.1)	1 (1.1)	0

^z Number of PMCs containing one chromosome fragment.**Table 4.** Chromosome number of microspores at pollen mitotic metaphase in a chromosome doubled plant of *A. schoenoprasum* × *A. fistulosum* hybrid plant.

Plant number	Number of microspores observed (%)	Number of microspores (%)			
		Chromosome number (n)			
		15	16	17	18
4x-s3f11-2	38 (100)	5 (13.2)	27 ^z (71.0)	4 (10.5)	2 (5.3)

^z Only one microspore contained 16 chromosomes and one chromosome fragment.

In 4x-s2f1, derived from s2f1, chromosome pairing was (1-0)_{III} + (13-16)_{II} + (1-6)_I at meiotic metaphase-I (Table 3). PMCs with 16_{II} occurred in 75.0%, including 2 with a chromosome fragment. Two unequal bivalents were present in 17 out of 88 PMCs (17.0%). Division from anaphase- to telophase-II seemed to be normal, forming dyads and daughter nuclei of almost similar sizes at both poles in 129 of 156 PMCs (82.7%), and micronucleus, chromosome bridge and minicromosome present in the remaining PMCs.

3) Pollen stainability and seed fertility

In 4x-s3f11-2, chromosome number of cells at pollen mitotic metaphase ranged from 15 to 18 with 16 in 71.0% of the cells including some with a chromosome fragment (Table 4, Fig. 4b), and 2 J-shaped chromosomes characteristic of both parent plants were observed. Pollen stainability was 64.3% with a variation of pollen grain size (Table 4). No seed was obtained from 135 open-pollinated flowers and 29 cross-pollinated ones with *A. fistulosum* cv. Kujyo as a pollen parent; 16 empty seeds set in 123 selfed flowers. In 4x-s2f1, anthers were shrunken, degenerated and contained no stainable pollen grain.

Discussion

Frequency of germination of embryos or ovules after *in vitro* culture was considerably lower in *A. fistulosum* × *A. schoenoprasum* than in the reciprocal one. Thus, the number of hybrid plants per pollinated flower differed. It is possible that embryos or ovules in the former may have stopped developing when they were cultured, but the reason for this is obscure. It is also not

clear whether our result indicates the difference in reciprocal cross-compatibility.

The number of hybrid plants per pollinated flower resulting from *A. fistulosum* × *A. schoenoprasum* was much smaller in this study (0.005) than the 0.20 and 0.33 reported by Gonzalez and Ford-Lloyd (1987) for two accessions of *A. fistulosum*; they did not examine the hybridity of their progenies. The data between these two studies might be attributed to the difference in embryo rescue method, such as the incubation stages of ovule and embryo after pollination, the culture medium and strains used as parent plants.

Interspecific hybrid plants have been previously produced *in vivo* between *A. fistulosum* and species of the section *Cepa* and *A. roylei*. On cytological examination the frequency of bivalents at meiotic metaphase-I in PMCs of the above hybrid plants (2n=16) was 7.98-8.0 in *A. fistulosum* × *A. altaicum* (Nishitani, 1987; Inada and Endo, 1994); 3.1-7.86 in *A. fistulosum* × *A. cepa* (and *A. fistulosum* × *A. ascalonicum*) (Cochran, 1950; Emsweller and Jones, 1945; Levan, 1936; Maeda, 1937, 1942; Kurita, 1959, *A. Bouddhae* var. *viviparum* × *A. cepa*; Tashiro, 1984); and 7.53 in *A. fistulosum* × *A. roylei* (McCollum, 1982). Emsweller and Jones (1945) stated that variability in frequency and type of bivalents formed in hybrid progenies between 10 cultivars of *A. cepa* and an inbred line of *A. fistulosum* indicates the existence of variability within *A. cepa*. In hybrid plants produced by embryo rescue method in *A. fistulosum* × *A. tuberosum* of the section *Rhizirideum*, pairing between chromosomes from both species could not be compared with chromosome pairing in our hybrid plants because two genomes from tetraploid *A. tuberosum*

formed bivalents and one genome from diploid *A. fistulosum* univalents ($8_{II}+8_I$) (Amagai et al., 1995).

The average frequency of bivalents of 0.41–1.64 formed in 7 hybrid plants in our study was much lower than those in the above interspecific hybrids between *A. fistulosum*, and *A. altaicum*, *A. cepa* and *A. roylei*. This result suggests that chromosomes of *A. fistulosum* have much lower homology to those of *A. schoenoprasum* than the above species. Van Raamsdonk et al. (1992) stated that 6 species of section *Cepa* including the above mentioned species and *A. roylei*, and *A. fistulosum* are so closely related as to produce *in vivo* their F_1 hybrid plants, and F_2 ones except 2 species. These data would indicate that *A. schoenoprasum* is distantly related to species within the section *Cepa* and *A. roylei*.

Meiotic irregularity occurred similarly in all hybrid plants, leading to pollen sterility. Among them some plants had almost normal anthers and others had degenerated ones. Unreduced fertile pollen grains were formed with sterile ones in the normal anthers, whereas they were not formed in the degenerated ones. We assume that abnormal development of anthers would have stopped the development of unreduced pollen grains. It is thought that degeneration of anthers would have been caused by genetic discordance between two species which showed low chromosome homology and indicated a distant relationship. On the other hand, Tatlioglu (1993) reported that chives have male-sterilizing cytoplasm and nuclear gene. When we used *A. schoenoprasum* (chives) of our study's material as a seed parent in the crossing experiment with *A. schoenoprasum* (asatsuki), male-sterile hybrid plants with degenerated anthers occurred (not published). Occurrence of male-sterility following anther abortion in hybrid plants between male-sterile *A. cepa* and its some closely related species was reported by McCollum (1974) and Saini and Davis (1967, 1969). Therefore, the cytoplasm and recessive fertility restoring gene may be a factor causing male-sterility of our hybrid plants of which anthers did not develop.

It suggests a possibility of expanding *A. fistulosum* germplasm that a chromosome doubled hybrid plant between *A. schoenoprasum* and *A. fistulosum* had pollen fertility, although it was seed-sterile. Further investigation is required to restore seed fertility of hybrid plants and chromosome doubled ones, to make clear morphological and ecological characteristics of these plants and to hybridize different strains both of two species.

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Allium fistulosum L. と *A. schoenoprasum* L. の類縁関係の細胞遺伝学的検討

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摘 要

Allium 属植物中、相互に近縁な異なる 2 節にそれぞれ分類される *A. fistulosum* L. と *A. schoenoprasum* L. の類縁関係を検討するため、2 種 (ともに $2n=16$) 間の F_1 雑種を作出し、細胞遺伝学的調査を行った。雑種個体 ($2n=16$) は両方向の相反交雑で胚または胚珠培養法により得られたが、*A. fistulosum* を子房親にした組合せではその獲得率が極めて低かった。雑種個体の花粉母細胞減数分裂第一分裂中期では 16_I または $1_{II} + 14_I$ の対合型が最高頻度であり、四分子期では四分子が最高頻度であったが、二～七分子も観察された。葯の発育については充実葯、退化葯およびこれら両方をもつ個体に

分かれた。充実葯をもつ個体では非還元性花粉が形成され、染色花粉率は 13–65% であった。*A. fistulosum* との戻交雑では次代植物は得られなかった。雑種個体の稔性回復を目的に染色体倍加個体を作成した。充実葯をもつ雑種個体由来の倍加個体では、染色花粉率は 64% であったが、放任受粉および *A. fistulosum* との戻交雑では次代植物は得られなかった。一方、葯が退化した雑種個体由来の倍加個体では、葯は退化し、花粉不稔性であった。以上の結果から、*A. fistulosum* と *A. schoenoprasum* はゲノムの相同性は非常に低く、類縁性の程度が小さいことが明らかになった。