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Cytological analysis of tetraploid hybrids between sweet potato and diploid *Ipomoea trifida* (H. B. K.) Don.

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Summary. Tetraploid F_1 hybrids between *Ipomoea batatas*, sweet potato (2n = 6x = ca. 90), and diploid (2n = 2x = 30) *I. trifida* (H. B. K.) Don. showed various degrees of fertility reduction. The present study aimed to clarify its causes by cytological analysis of meiotic chromosome behavior in the diploid and sweet potato parents and their tetraploid hybrids. The diploid parents showed exclusively 15 bivalents, and the sweet potato parents exhibited almost perfect chromosome pairing along with predominant multivalent formation. Their hybrids (2n = 4x = 57–63) formed 2.6–5.0 quadrivalents per cell, supporting the autotetraploid nature. The meiotic aberratios of the hybrids were characterized by the formation of univalents, micronuclei, and abnormal sporads (monad, dyad, triad, and polyad). The causes underlying these aberrations were attributed in part to the multivalent formation, and in part to a disturbance in the spindle function. Three hybrids showing serious meiotic aberrations were very low in fertility. The utilization of the sweet potato-diploid *I. trifida* hybrids for sweet potato improvement is described and, further, the role of interploidy hybridization in the study of the sweet potato evolution is discussed.

Key words: Sweet potato – *Ipomoea trifida* – Polyploidy – Interspecific hybrids – Unreduced gametes

Introduction

The efforts in utilizing wild *Ipomoea* species to diversify and improve sweet potato germ plasms have shed some light on the interspecific relationship between the wild species and cultivated sweet potato. Nishiyama et al. (1975) and Teramura (1979) classified the wild species into two or three groups on the basis of crossability. Of these, one group contains the species which are hybridized directly or indirectly with the sweet potato; these are *I. leucantha* Jacq. (2n = 2x = 30), *I. littoralis* Bl. (2n = 4x = 60), and *I. trifida* (H. B. K.) Don. (2n = 6x = 90).

The wild plants belonging to this group have aroused particular attention in genetic and breeding research of the sweet potato, and many of these plants were collected in the area from Mexico to Ecuador (Muramatsu and Shiotani 1974; Shiotani 1983; Kobayashi 1984). Kobayashi (1984), working with these accessions, emphasized a continuous morphological variation among them and presented the term '*I. trifida* complex' to the wild plants of this group. There has been controversy over his view, and different proposals for their taxonomical treatment have been reported (Austin 1978, 1983, 1988; Nishiyama 1971, 1982). Kobayashi's concept of the *I. trifida* complex, however, has been adopted by one of the authors, Shiotani; we use the names diploid *I. trifida* (= *I. leucantha*), tetraploid *I. trifida* (= *I. littoralis*), and hexaploid *I. trifida* (= previously *I. trifida*) in this report.

The genomic formula $B_1B_1B_2B_2B_2B_2$ was proposed for sweet potato (2n = 6x = 90) from the cytological study of the hexaploids synthesized by using diploid and tetraploid *I. trifida* and also their hybrids with sweet potato (Shiotani and Kawase 1987). Further, from the subsequent study of inter- and intraploidy hybrids within the *I. trifida* complex, Shiotani (1988) and Shiotani and Kawase (1989) concluded that the genomes B_1 and B_2

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are homologous and, hence, the sweet potato and polyploid *I. trifida* are autopolyploid, consisting of the genome B of diploid *I. trifida*.

In this study, tetraploid F_1 hybrids were produced between sweet potato and diploid *I. trifida*. These hybrids showed various degrees of fertility reduction. To clarify the causes of the fertility reduction, meiotic behavior was studied in the diploid *I. trifida* and sweet potato parents and their tetraploid hybrids. In addition, two highly fertile tetraploid *I. trifida* strains, used as the parents to evaluate cross-fertility of the hybrids, were also examined. Further, the potential use of the germ plasm of the *I. trifida* complex in sweet potato improvement and a possible origin of the cultuvated sweet potato are discussed.

Materials and methods

Six clonal strains (2288-02, -11, -30, -31, -36, and -64) of diploid *I. trifida* were produced from seeds collected at Salina Cruz, Oaxaca, Mexico, and two clonal strains (2232-33 and -34) of tetraploid *I. trifida* were obtained from seeds collected at Santa Elena, Peten, Guatemala. These seed materials belong to the collection of the Scientific Expedition to Latin America, 1972–1973, Kyoto University, Japan (Muramatsu and Shiotani 1974). The sweet potato cultivars used are 'Tamayutaka' (TY), 'Minamiyutaka' (MY), and 'Kyukei 15-2120' (K15-2120). TY is a cultivar derived from an intercultivar cross. MY is a cultivar produced by backcrossing a sweet potato × hexaploid *I. trifida* hybrid twice with other sweet potato cultivars (Sakamoto 1976). The breeding line, K15-2120, is an F_1 hybrid between a sweet potato cultivar and hexaploid *I. trifida* strain.

Meiotic chromosome behavior was studied in pollen mother cells (PMCs) of the two diploid *I. trifida* (2288-36 and 2288-64) and of two sweet potato parents (TY and MY), as well as of ten tetraploid F_1 hybrids, two from the 2x × 6x cross and eight from the 6x × 2x cross (Table 1). In addition, two naturally occurring tetraploid *I. trifida* strains (2232-33 and 2232-34) were examined.

Buds were fixed in modified Newcomer's fixative, a 12:5 Newcomer's fluid-glacial acetic acid mixture, and hydrolyzed in 0.7-*N* hydrochloric acid for 10 min at 42 °C. The materials were then rinsed in distilled water for a few minutes and transferred to Schiff's reagent. Slides were prepared using the iron-aceto-carmine squash technique. Chromosome counts in root-tip cells were made by the methods described by Shiotani and Kawase (1987).

For sporad analysis, appropriate buds were fixed in modified Newcomer's fixative for at least 30 min. The anthers were rinsed briefly in distilled water, squashed in 0.5% lacto-phenol cotton blue and left overnight prior to observation. Data were based on 120 sporads for each hybrid and a minimum of 500 sporads for each natural tetraploid. The frequency of unreduced (2n) pollen grains was estimated using the equation $(2X_2 + X_3)/(2X_2 + 3X_3 + 4X_4)$, where X_2, X_3, and X_4 are the number of dyads, triads, and tetrads, respectively. To investigate the development of sporads, more than 1,000 pollen grains taken from buds 2 days before anthesis were examined.

The crossing experiment was conducted to estimate the degrees of seed fertility (%) of the hybrids. Prior to the crossing, self-incompatibility and cross-incompatibility were determined by examining in vitro pollen germination on the stigma (Kowyama et al. 1980). Therefore, fertility data were restricted to the cross between the clones, which are cross-compatible with each other. For a comparison of fertility of the hybrids, the highly fertile natural tetraploid strains, 2232-33 and -34, were used as the female or male in crossing with the hybrids. Fertility data was recorded as seed set (%) where 25% is equivalent to one seed per four-ovulate flower pollinated.

Table 1. Tetraploid F_1 hybrids between sweet potato and diploid *I. trifida*

Hybrid	Cross combination
2x *I. trifida* × sweet potato F_1	
A48	2x *I. trifida* 2288-30 × MY[a]
A65	2x *I. trifida* 2288-64 × MY
Sweet potato × 2x *I. trifida* F_1	
A100	MY × 2x *I. trifida* 2288-36
A101	MY × 2x *I. trifida* 2288-36
A106	TY[b] × 2x *I. trifida* 2288-36
A110	MY × 2x *I. trifida* 2288-31
A111	MY × 2x *I. trifida* 2288-02
A112	TY × 2x *I. trifida* 2288-11
A113	TY × 2x *I. trifida* 2288-02
A115	K15-2120[c] × 2x *I. trifida* 2288-31

[a] Sweet potato cultivar 'Minamiyutaka'
[b] Sweet potato cultivar 'Tamayutaka'
[c] A breeding line 'Kyukei 15-2120'

Table 2. Mean chromosome configurations in diploid *I. trifida* and sweet potato parents

Clone	2n	No. of PMCs observed	Chromosome configuration at metaphase I[a]					
			Univalent	Bivalent	Trivalent	Quadrivalent	Pentavalent	Hexavalent
2x *I. trifida*								
2288-36	30	10	–	15	–	–	–	–
2288-64	30	8	–	15	–	–	–	–
Sweet potato								
'Tamayutaka'	90	20	1.0 (0–3)	25.0 (17–34)	0.1 (0–1)	4.4 (2–6)	0.1 (0–1)	3.5 (2–6)
'Minamiyutaka'	88	20	1.3 (0–4	23.8 (13–30)	0.1 (0–1)	4.5 (2–8)	0.2 (0–1)	3.4 (2–6)

[a] Range is given in parentheses

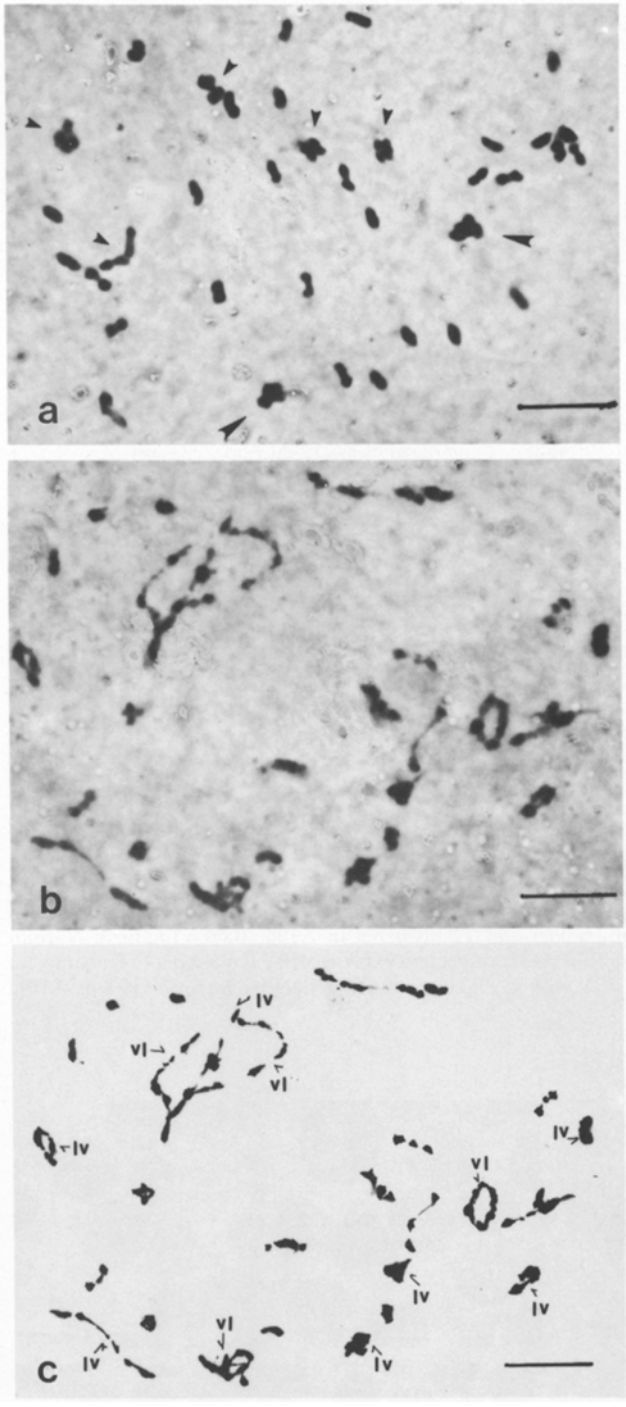

Fig. 1a–c. Chromosome configurations in the sweet potato cultivar 'Tamayutaka'. **a** Metaphase I showing two hexavalents (*large arrowheads*), five quadrivalents (*small arrowheads*), and 29 bivalents. **b** Early metaphase I. **c** Sketch of **b**, showing four hexavalent (*VI*), seven quadrivalents (*IV*), and 19 bivalents. Bars = 10 μm

Table 3. Mean chromosome configurations in sweet potato × diploid *I. trifida* F_1 hybrids and tetraploid *I. trifida*

Hybrid or clone	2n	No. of PMCs observed	Chromosome configuration at metaphase I[a]			
			Univalent	Bivalent	Trivalent	Quadrivalent
2x *I. trifida* × sweet potato F_1						
A48	60	18	3.8 (0–6)	20.9 (15–25)	–	3.6 (2–6)
A65	60	30	2.6 (0–8)	18.8 (13–24)	0.2 (0–2)	4.8 (3–7)
Sweet potato × 2x *I. trifida* F_1						
A100	60	62	0.4 (0.6)	20.4 (12–26)	0.1 (0–2)	4.6 (2–9)
A101	62	37	0.7 (0–4)	21.1 (13–27)	0.1 (0–2)	4.7 (2–9)
A106	60	25	0.4 (0–2)	24.0 (18–30)	0.4 (0–1)	2.6 (0–5)
A110	60	52	–	23.6 (18–30)	–	3.2 (0–6)
A111	57	36	0.7 (0–4)	20.4 (17–24)	0.3 (0–1)	3.7 (2–5)
A112	59	29	0.4 (0–1)	22.4 (13–29)	0.6 (0–1)	3.0 (0–8)
A113	61	23	0.04 (0–1)	19.1 (15–25)	1.0 (0–1)	5.0 (2–7)
A115	63	35	5.8 (3–9)	19.8 (15–23)	0.5 (0–2)	4.0 (2–5)
4x *I. trifida*						
2232-33	60	35	0.1 (0–2)	24.1 (20–28)	–	2.9 (1–5)
2232-34	60	46	–	23.2 (20–26)	–	3.4 (2–5)

[a] Range is given in parentheses

Results

Cytological analysis

Two diploid *I. trifida* strains showed regular chromosome pairing with 15 bivalents at metaphase I (MI). Two sweet potato cultivars, TY (2n = 90) and MY (2n = 88), indicated nearly complete chromosome pairing with only a few chromosomes unpaired (Table 2). Due to the small size of the meiotic chromosomes (a bivalent at MI is about 2.0–2.5 μm in length), multiple chromosome associations at early MI were easier to analyze than those in full contraction at mid-metaphase I. Both quadrivalent and hexavalent chromosomes at early metaphase appeared as a ring or loosely paired chain (Fig. 1a–c). The meiotic chromosome configurations characterized by predominant multivalent formation suggested the existence of the homologous chromosomes in duplication in the hexaploid sweet potato.

Tetraploid hybrids formed 18.8–24.0 bivalents and 2.6–5.0 quadrivalents per PMC and a few trivalents

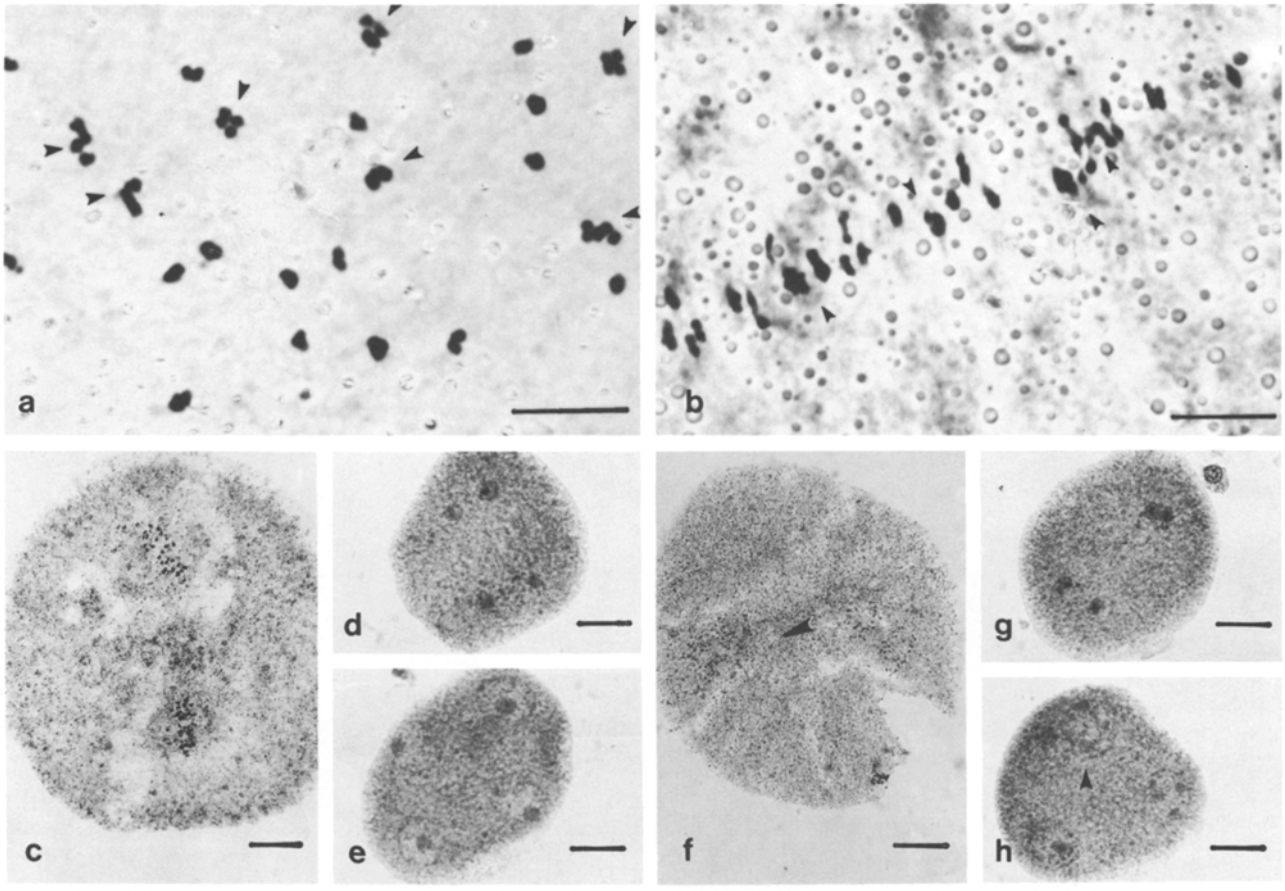

Fig. 2a–h. Meiosis in sweet potato × diploid *I. trifida* hybrids. **a** Metaphase I showing seven quadrivalents (*arrowheads*) and 17 bivalents in A101. **b** Metaphase I showing four quadrivalents (*arrowheads*) and 22 bivalents in A106. Bars = 10 μm. **c** Normal metaphase II in A101. **d** and **e** Early and late stage of normal telophase II in A101, respectively. **f** Anaphase II showing the incomplete separation of chromatids (*arrowhead*) in A101. **g** and **h** Telophase II with a single restitution nucleus (*arrowheads*) in A101. Bars = 25 μm

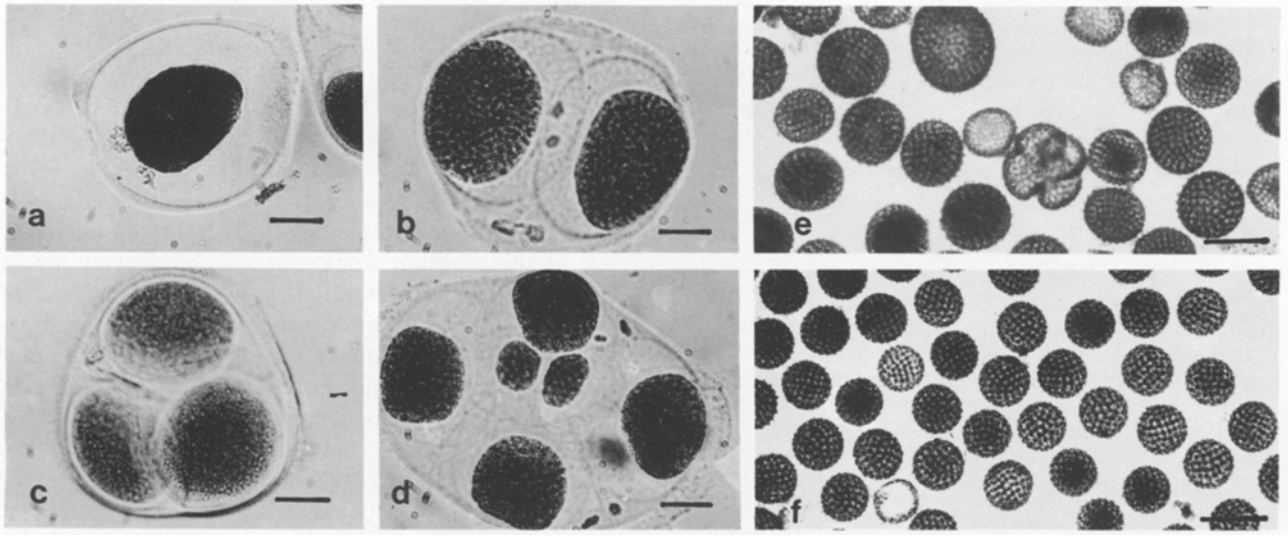

Fig. 3a–f. Sporads and pollen grains in sweet potato × diploid *I. trifida* hybrids and tetraploid *I. trifida*. **a** Monad in A101. **b** Dyad in A48. **c** Triad in A101. **d** Tetrad with micronuclei in A48. Bars = 25 μm. **e** Pollen grains in A65. **f** Pollen grains in the natural tetraploid 2232-33. Bar = 100 μm

Table 4. Frequencies (%) of tetrads, monads, dyads, triads, and polyads, number of micronuclei per tetrad, and frequency (%) of unreduced pollen in sweet potato × diploid *I. trifida* F_1 hybrids and tetraploid *I. trifida*

Hybrid or clone	Tetrad without micronuclei	Tetrad with micronuclei	No. of micronuclei per tetrad	Monad	Dyad	Triad	Polyad	Unreduced (2n) pollen
2x *I. trifida* × sweet potato F_1								
A48	36.7	45.8	1.26	–	6.7	10.8	–	6.4
A65	46.7	25.0	0.52	21.6	0.8	4.2	1.7	1.9
Sweet potato × 2x *I. trifida* F_1								
A100	23.3	67.5	2.14	1.7	–	6.7	0.8	1.8
A101	57.5	20.8	0.80	10.8	3.3	6.7	0.8	3.9
A106	20.8	71.7	2.52	–	–	0.8	6.7	0.2
A110	89.2	4.2	0.09	4.2	–	1.7	0.8	0.5
A111	98.3	1.7	0.03	–	–	–	–	0
A112	96.7	3.3	0.01	–	–	–	–	0
A113	85.8	10.0	0.01	2.5	–	0.8	0.8	0.2
A115	56.7	38.3	1.51	–	–	5.0	–	1.3
4x *I. trifida*								
2232-33	97.1	2.9	0.04	–	–	–	–	0
2232-34	98.9	1.1	0.01	–	–	–	–	0

(Table 3, Fig. 2a, b). Of the ten hybrids, three hybrids, A48 and A65 (both 2n = 60) and A115 (2n = 63), showed relatively high frequencies of univalents. The two natural *I. trifida* tetraploids (both 2n = 60) also formed quadrivalents with means of 2.9 and 3.4, respectively. There was no noticeable difference in chromosome configuration between the hybrids from the reciprocal crosses or between the hybrids and natural tetraploids.

In spite of our efforts, it was not possible to distinguish lagging chromosomes from other faintly stained cytoplasmic granules at both anaphase I and II. Meiotic aberrations, occasionally observed in the hybrids A48 and A101, included delayed separation of chromatids to the poles at anaphase II (Fig. 2c–f) and subsequent formation of restitution nuclei at telophase II (Fig. 2g, h). These were probably due to partial suppression of the spindle activity.

The frequency of micronuclei was markedly different among the hybrids and natural tetraploids (Table 4). Relatively high frequencies (more than 20%) of the tetrads containing micronuclei were seen in six hybrids (A48, A65, A100, A101, A106, and A115), and more than one micronucleus per tetrad were observed in four hybrids, A48, A100, A106, and A115. As shown in Table 3, the hybrids A100, A101, and A106 had univalents fewer than one per PMC. Therefore, a high frequency of micronuclei in these hybrids suggests that univalents at MI are not the sole source of micronuclei. The frequencies of micronuclei were quite low in two hybrids (A111 and A112) and two natural tetraploids.

Sporads with an abnormal number of microspores (monad, dyad, triad, and polyad) were found in all hybrids except A111 and A112 (Table 4, Fig. 3a–c). The total frequencies of these abnormal sporads were high in A48, A65, and A101 at 17.5, 28.3, and 21.6% respectively. Monads contained one to four nuclei and were sometimes irregularly clefted by incomplete cytokinesis. Polyads consisting of more than six microspores seemed to be the products of syncytes or the result of multipolar division. Since microspores in these monads and polyads are hardly expected to be functional, these sporads were excluded in estimating the frequency of unreduced (2n) pollen. Then the frequency of unreduced (2n) pollen from the dyads and triads was estimated to be 0.2–6.4%. In two hybrids (A111 and A112) and two natural tetraploids, sporads formed were mostly normal.

Fertility reduction

All hybrids and two natural tetraploid strains were determined to be self-incompatible. Among a total of 40 crosses between the hybrids and natural tetraploid strains, the two crosses (2232-34♀ × A48♂ and 2232-34♀ × A115♂) were incompatible, but their reciprocal crosses (A48♀ × 2232-34♂ and A115♀ × 2232-34♂) were compatible (Table 5). Similarly, l.c. reciprocal differences existed between the two tetraploid strains. 2232-33♀ × 2232-34♂ was incompatible, while its reciprocal cross was compatible.

The hybrids showed less than 63% stainable pollen, whereas the natural tetraploids produced more than 90% normal pollen (Fig. 3e, f). The cross 2232-34♀ × 2232-33♂ yielded a 79% seed set. The crossing of each hybrid to these natural tetraploids revealed various degrees of fertility reduction. Based on the higher value of seed set percentage, the fertility of each hybrid and natu-

Table 5. Pollen fertility (% stainable pollen), and male and female fertilities (% seed set) of sweet potato × diploid *I. trifida* F_1 hybrids

Hybrid	Pollen fertility	Male fertility			Female fertility		
		2232-33x	2232-34x	Class[a]	x2232-33	x2232-34	Class
2x *I. trifida* × sweet potato F_1							
A48	40.0	2.1	CI[b]	S	1.5	1.7	S
A65	30.7	0.7	0.6	S	1.2	1.6	S
Sweet potato × 2x *I. trifida* F_1							
A100	39.3	19.8	9.2	PF	12.9	9.0	PF
A101	41.9	ND	ND	S	4.3	1.2	S
A106	58.6	23.9	9.3	PF	32.9	28.4	F
A110	47.5	38.5	18.4	F	30.4	17.1	F
A111	63.0	40.5	38.7	F	12.3	8.9	PF
A112	57.4	37.7	48.0	F	15.6	26.9	PF
A113	48.5	44.1	41.7	F	34.4	31.8	F
A115	56.0	2.3	CI	S	37.9	36.8	F

[a] Assigned fertility class, see the text
[b] Cross-incompatible
[c] Anthers of A101 did not dehisce

ral strain was arbitrarily classified into one of the following fertility classes: S (sterile, seed set less than 10%); PF (partially fertile, 10–30%); F (fertile, 30–50%); and HF (highly fertile, more than 50%). The fertility of each hybrid is then expressed, e.g., as S/F when it is male sterile (S) and female fertile (F).

Hybrids A48 (S/S) and A65 (S/S) showed meiotic aberrations with relatively high frequencies of univalents, micronuclei, and abnormal sporads. Hybrid A101 (S/S) also exhibited irregular meiosis with frequent micronuclei and abnormal sporads. A high frequency of micronuclei was the only conspicuous aberration in A100 (PF/PF) and 4106 (PF/F). In the four hybrids, A110 (F/F), A111 (F/PF), A112 (F/PF), and A113 (F/F), micronuclei and abnormal sporads were observed infrequently. Hybrid A115 (S/F) showed a remarkable reciprocal difference and seemed to be male sterile. The two natural tetraploids 2232-33 (HF/-) and 2232-34 (-/HF) showed very low frequencies of micronuclei.

Discussion

Cytogenetic structure of sweet potato

The hybridization of the sweet potato with diploid *I. trifida* has been attempted in order (1) to clarify the cytogenetic structure of the hexaploid sweet potato, and (2) to incorporate useful traits of wild diploid materials into the sweet potato.

With regard to the cytogenetic structure of the sweet potato, the allopolyploid theory has been proposed (Ting et al. 1957; Jones 1965). The conclusion of Magoon et al. (1970) can be interpreted as a segmental allopolyploid or segmental autoallopolyploid theory. On the other hand, Shiotani (1988) and Shiotani and Kawase (1987, 1989) favored the view of autopolyploidy, based on the cytological analyses of interspecific hybrids of sweet potato × polyploid *I. trifida* and of intraspecific hybrids in the *I. trifida* complex. They proposed the genomes BB for diploid, BBBB for tetraploid, and BBBBBB for both hexaploid *I. trifida* and sweet potato. The genomic duplication at the hexaploid level is characterized by predominant multivalent formation at meiosis, as confirmed in the present investigation (Table 2, Fig. 1a–c).

Jones (1970) suggested an autoploid origin of the wild *Ipomoea* tetraploid accessions (named *I. gracilis* R. Br.) based on the quadrivalent formation at MI. Jones' material is almost identical to the tetraploid *I. trifida* strain, designated K233 in Japan. The results of meiotic analyses on K233 (Shiotani and Kawase 1987) are in close agreement with those of Jones (1970). Further, Martin et al. (1974) reported considerable homolgy between the two genomes in two wild tetraploids collected in Colombia and Ecuador. These tetraploids undoubtedly belong to tetraploid *I. trifida* because of their high crossability with other tetraploid *I. trifida* strains (I. Shiotani, unpublished results). These results indicate that autoploidy is a prevailing feature in wild tetraploid *I. trifida*.

From these findings, the tetraploid hybrids between sweet potato and diploid *I. trifida* are expected to be autotetraploid with four B genomes, being genomically identical to the tetraploid *I. trifida* strains. The present meiotic analysis of ten hybrids and two natural tetraploids revealed the formation of 3–5 quadrivalents per PMC, indicating the presence of four duplicated chromosome sets (Table 3, Fig. 2a, b). This result supports the autopolyploid nature of sweet potato. At the

same time, the frequent formation of quadrivalents indicates possible genetic recombination between the chromosomes of sweet potato and diploid *I. trifida*.

Causes of fertility reduction in the tetraploid hybrids

The marked meiotic aberrations detected in these hybrids between sweet potato and diploid *I. trifida* include the following: (1) relatively frequent univalent formation; (2) frequent occurrence of micronuclei with almost complete meiotic pairing, probably formed by lagging chromosomes due to disturbed segregation of multivalent chromosomes at anaphase I; and (3) abnormal sporads, such as monads with a single (one to four nucleate) microspore, dyads containing two, or triads containing one unreduced (2n) microspore, and polyads (Table 3).

These aberrations may be attributable to the autotetraploid nature of the hybrids and/or some defect in the spindle apparatus. The univalent formation due to structural heterozygosity of the chromosome complements and the multivalent formation due to the duplicated chromosome complements and the multivalent formation due to the duplicated chromosome sets may be ascribed to the autoploid hybridity. On the other hand, the disturbed chromosome segregation at anaphase I, the formation of a restitution nucleus at telophase II, and the production of polynucleate microspores may be the results of partial suppression of the spindle function.

Cross-fertility in more than 100 single crosses between natural tetraploid *I. trifida* strains was low, with a mean seed set of about 40% (KNAES 1981). The present tetraploid hybrids were classified into four fertility classes. Their cross-fertilities varied from less than 10% seed set (class S) to about 50% (class F)) on both male and female sides. Three hybrids (A48, A65, and A101) which showed striking meiotic aberrations, were sterile in both sexes. Comparing the hybrids to the natural tetraploids, both pollen stainability and seed set were low even in the two hybrids, A111 (F/PF) and A112 (F/PF), which did not show noticeable meiotic aberrations (Table 5). These facts suggest that an aberration other than the formation of univalents, micronuclei, and abnormal sporads is also involved in the fertility reduction.

Significance of interploidy hybridization in the breeding and evolution of sweet potatoes

Since the first tetraploid hybrids between sweet potato and diploid *I. trifida* were obtained by using natural hexaploid *I. trifida* as a bridge species (KNAES 1972–1973), the breeding program with these hybrid strains has been undertaken to produce new-type cultivars at the Kyushu National Agricultural Experiment Station, Japan (KNAES 1985). Further, such a program can be extended to the analytic breeding scheme, as proposed for polyploid crops by Chase (1963), wherein the hexaploid is resynthesized with the lines selected at the tetraploid level.

The function of unreduced (2n) gametes in producing hexaploid hybrids from the cross involving natural triploid *I. trifida* strains has been studied (Shiotani and Kawase 1989). The present results provide another possibility of synthesizing hexaploids from the union of a 2n gamete with a normal n gamete in the $4x \times 4x$ cross.

As to the origin of the natural tetraploids, Austin (1977) proposed that they originated from a cross between sweet potato and a diploid species, probably *I. trifida*. The present results demonstrate that the reproductive barriers between the two ploidy levels are not very strong, and suggest that similar hybridization may have occurred under natural conditions. We have held the view that the tetraploid *I. trifida* originated by natural polyploidization of a diploid *I. trifida* form (Shiotani 1988). The natural interploidy ($6x \times 2x$) hybridization, as suggested by Austin (1977), can allow the gene flow from the cultivated sweet potato to the natural tetraploid *I. trifida* gene pool. Moreover, recovery of the hexaploidy by nonreduction mechanisms at the tetraploid level may cause the reverse gene flow from the natural diploid *I. trifida* gene pool to the cultivated sweet potato. This reciprocal gene flow between sweet potato and its wild relatives might have played an important role in the evolution of the sweet potato.

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