GENOMIC STRUCTURE AND THE GENE FLOW IN SWEET POTATO AND RELATED SPECIES

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This presentation consists of three points. The first point is that the cytogenetical study provides evidence of autoploidy of sweet potato and the wild polyploids in the Ipomoea trifida complex. The second point concerns the feasibility of the gene flow in a circulating system among sweet potato and its wild relatives. The third point relates to the degrees of heterozygosity of the resynthesized hexaploids by unreduced gametes of triploids.

Preface

The use of gene sources from wild plants in sweetpotato improvement was reviewed by Sakamoto (27) and Kobayashi (11). To efficiently utilize the gene sources from these wild plants, exact knowledge of the genomic structure of hexaploid sweet potato and of the genomic relationship between sweet potato and the wild species are essential.

Many wild plants ranging from diploid to hexaploid were successfully hybridized directly with sweet potato (24 25, 26, 32), and they were grouped into the Ipomoea trifida complex by Kobayashi (12).

1. Genomic structure in sweet potato and the polyploids in the Ipomoea trifida complex

In order to define the genomic structure of sweet potato, the cytogenetical studies (28, 29) were carried out in the following two steps: the first step was to synthesize hexaploid plants with the diploid and tetraploid forms of I. trifida. The next step was to determine the degree of homology between the two basic genomes in sweet potato with the two kinds of hybrids at the tetraploid level. The hybridization process to the tetraploid hybrids is illustrated in Fig. 1.

Meiotic data on the metaphase I of sweet potato showed a complicated pattern with a wide range of univalent to hexavalent, and the frequent multivalents suggested a high degree of genomic duplication (Table 1). The meiotic data

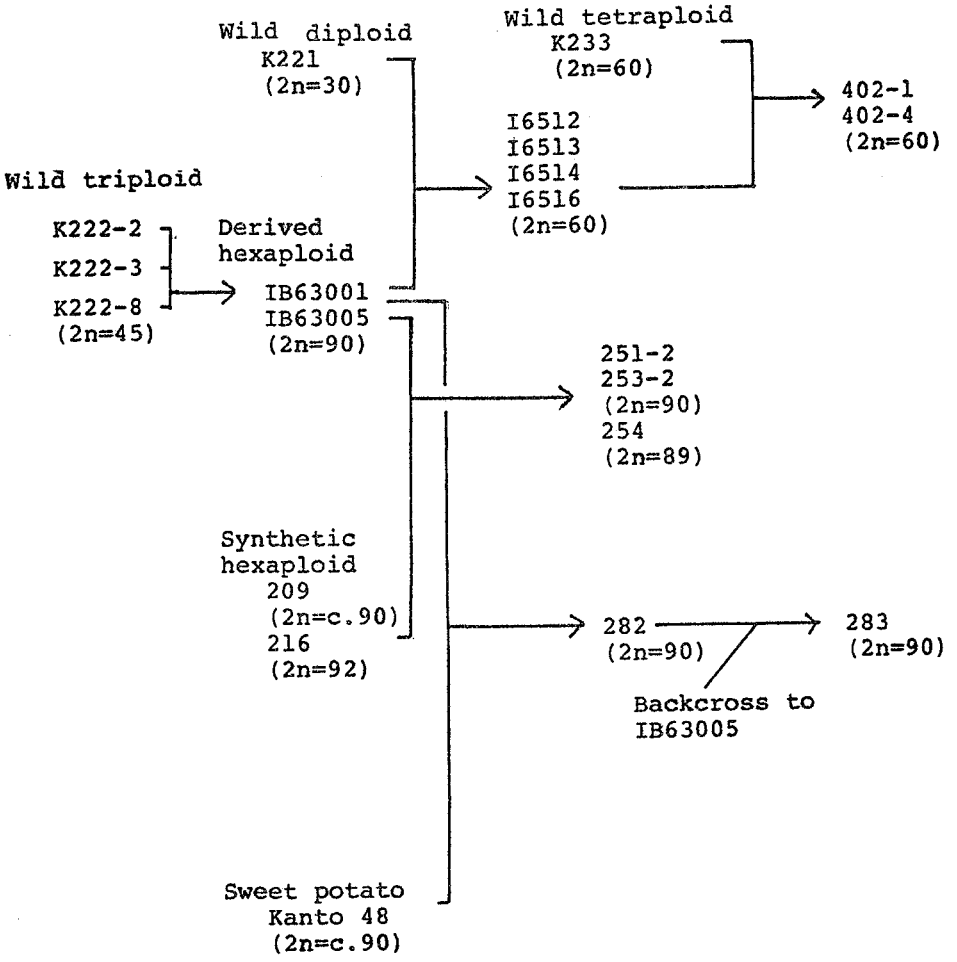

Fig. 1. A schematic representation of the hybrids for identifing the genomes in sweet potato.

Table 1. Chromosome pairing at MI in sweet potato(Kyushu 58)

	I	II	III	IV	V	VI	
	1.3	26.8	0.9	5.7	0.1	2.2	
2n=94		II-EQ 45.9		IV-EQ 8.0			CPM (%) 39.1(42)

II-EQ, bivalent-equivalents; IV-equivalents, tetravalent-equivalents; CPM, chromosomes participating in multivalents.

was rearranged with the bivalent-equivalent (II-EQ) as an indication of the overall amount of chromosome pairing, the trivalent- and tetravalent-equivalent (III-EQ, IV-EQ) and hexavalent each of which represents the degree of genomic repetition, and the number of chromosomes participating in multivalents (CPM).

As shown in Table 2, meiosis of the diploid parent K221 was regular with 15 bivalents. The tetravalent parent K233 was assumed to be an autotetraploid because of almost complete chromosome pairing with the frequent tetravalents. Therefore, the bivalent-equivalents accounting for a genomic pair in the 3x-F_1 hybrids of K221 x K233 were ascribed to an autosyndetic pair of the two genomes from K233. The synthetic hexaploids (SH) exhibited, as expected, chromosome pairing characterized by the frequent tetravalents and some hexavalents. The bivalent-equivalents, about half of the 2n chromosome number, indicated mostly complete chromosome pairing. The hybrid of SH x sweet potato showed a similar meiotic pattern to those of SH. As to seed fertil-

Table 2. Chromosome pairing at MI and the genomic formula of the synthetic hexaploids(SH) induced by chromosome doubling of 3x-F_1 hybrids of K221 x K233.

Parent or hybrid	2n	Mean per cell of					Genomic formula
		II-EQ	III-EQ	IV-EQ	VI	CPM (%)	
Parent							
K221	30	15				0	B_1B_1
K233-1	60	30.0		4.1		16.4(27)	$B_2B_2B_2B_2$
K233-2	60	30.0		4.8		19.3(32)	
3x-F_1 hybrids							
202-1	45	16.0	3.0			9.0(20)	
202-2	45	16.3	3.0			9.1(20)	$B_1B_2B_2$
202-3	45	16.8	2.5			7.5(17)	
Synthetic hexaploids(SH)							
216	92	44.6		9.0	2.6	42.7(46)	$B_1B_1B_2B_2B_2B_2$
220	90	43.8		7.7	2.5	40.0(44)	
SH x Sweet potato(Kanto 48)							
K6843	93	45.3		8.7	3.4	42.6(46)	$B_1B_1B_2B_2B_2B_2$
Sweet potato							
Cultivars	88 90 94	45.9		8.0	3.0	39.1(43)	$B_1B_1B_2B_2B_2B_2$

ity, the synthetic hexaploids and their F_1 hybrids with sweet potato cultivars were fertile in intercrosses and backcrosses with sweet potato. As a result, the synthesis of the hexaploids from K221 x K233 is considered to be resynthesis of sweet potato in regard to the genomic frame. The genomic formula for sweet potato was labelled as $B_1B_1B_2B_2B_2B_2$, in which B_1B_1 was given to K221 and $B_2B_2B_2B_2$ to K233. For a more conclusive genomic structure, however, it was necessary to ascertain the degree of homology between the two basic genomes B_1 and B_2.

The second step started with the natural triploid K222. The derived hexaploids (DH) were the progenies from intercrosses of K222. As shown in Table 3, the derived hexaploids, and their hybrids with SH and sweet potato demonstrated the similar pairing patterns having the frequent tetravalents and some hexavalents. These results suggested that the derived hexaploids have the same genomic structure as those of the synthetic hexaploids and sweet potato. The tetraploid hybrids of DH x K221 may have a genomic struc-

Table 3. Chromosome pairing and the genomic formula of the derived hexaploids(DH) from K222, and of the tetraploid hybrids involving DH.

Parent or hybrid	2n	Mean per cell of					Genomic formula
		II-EQ	III-EQ	IV-EQ	VI	CPM(%)	
K222, the natural triploid							
K222-3	45	16.3	1.6			4.8(11)	$B_1B_2B_2$
K222-8	45	16.6	3.0			9.1(20)	
Derived hexaploids(DH)							
IB63001	90	28.0		6.1	1.5	28.0(31)	$B_1B_1B_2B_2B_2B_2$
IB63005	90	30.3		6.4		30.3(34)	
DH x SH							
251-2	90	42.7		6.7	0.9	29.4(33)	$B_1B_1B_2B_2B_2B_2$
253-2	90	43.1		4.3	1.1	19.9(22)	
DH x Sweet potato(Kanto 48)							
282	90	43.7		9.4	4.1	46.0(51)	$B_1B_1B_2B_2B_2B_2$
DH x K221							
I6513	60	28.5		4.0		18.4(31)	$B_1B_1B_2B_2$
I6516	60	29.8		3.3		13.3(22)	$(B_1=B_2)$
(DH x K221) x K233							
402-1	60	30.0		3.3		13.3(22)	$B_1B_2B_2B_2$
402-2	60	29.8		4.0		16.0(27)	$(B_1=B_2)$

ture of $B_1B_1B_2B_2$, that is of amphidiploid if B_1 is nonhomologous to B_2. Further, subsequent hybridization of the above tetraploid hybrids with the natural tetraploid K233 may produce the hybrids of the genomic structure $B_1B_2B_2B_2$, that are expected to be sterile due to considerably irregular meiosis if B_1 is nonhomologous to B_2. The meiotic data on the above two kinds of tetraploid hybrids were mostly regular in having about 30 bivalent-equivalents, and both showed tetravalents as frequent as K233.

Consequently, these observations led to the conclusion that B_1 is homologous to B_2, and that the autotetraploidy for K233 was a proper assumption. In addition, the relatively high fertility in both of the hybrids in intercrosses or in crosses with sweet potato confirmed the functional homology between the two genomes. In conclusion, sweet potato has a genomic structure of autohexaploidy with the B genome, that also exists in the autotetraploid K233 and in the diploid K221 of the I. trifida complex.

The conclusion drawn here is in disagreement with the view of allopolyploid origin in previous cytological studies (7, 33, 34). Based on the analyses of the chromosomes at the pachytene and metaphase stages, Magoon et al. (19) reached the conclusion that three genomes of sweet potato are partly homologous and two of the genomes show closer homology to one another than to the third. However, the results of the present study ruled out such a genomic differentiation with respect to the degree of genomic homology.

2. The gene flow between sweet potato and the I. trifida complex

As indicated in Fig. 2, autoploidy enables the recurring gene flow between sweet potato and a polyploid complex of I. trifida (29). If any hybrid polyploids have at least 2 nonhomologous genomes, it will result in sterility which will limit the gene flow. There are two pathways through which genes can flow: that of the process of ordinary hybridization between the diploid and the polyploid, and that of the process of exceptional hybridization through the sterile triploid. The percentage of seed fertility shown in the literature (13, 14, 15, 16, 17, 21, 25), although it varied according to the parental lines involved, is proof of the relative value of the efficiency of the flow.

Salient features in the circulating system of the gene flow are summarized as follows:

1) The diploid acts only as a donor of gene sources due to the one-way flow from the diploid gene pool to other polyploids.

2) The sterile triploid plays an important role as a bridge from the diploid to tetraploid gene pool, and as a bridge for the conflux to the hexaploid gene pool.
3) Influx of the gene flow to the tetraploid gene pool undertaken by hybridization diploid x hexaploid is restricted to the cross with the hexaploids as female parent.
4) Frequent gene flow or gene exchange can be expected at a consistent ploidy level, such as that of the flow between sweet potato cultivars and the hexaploid gene pool of I. trifida.

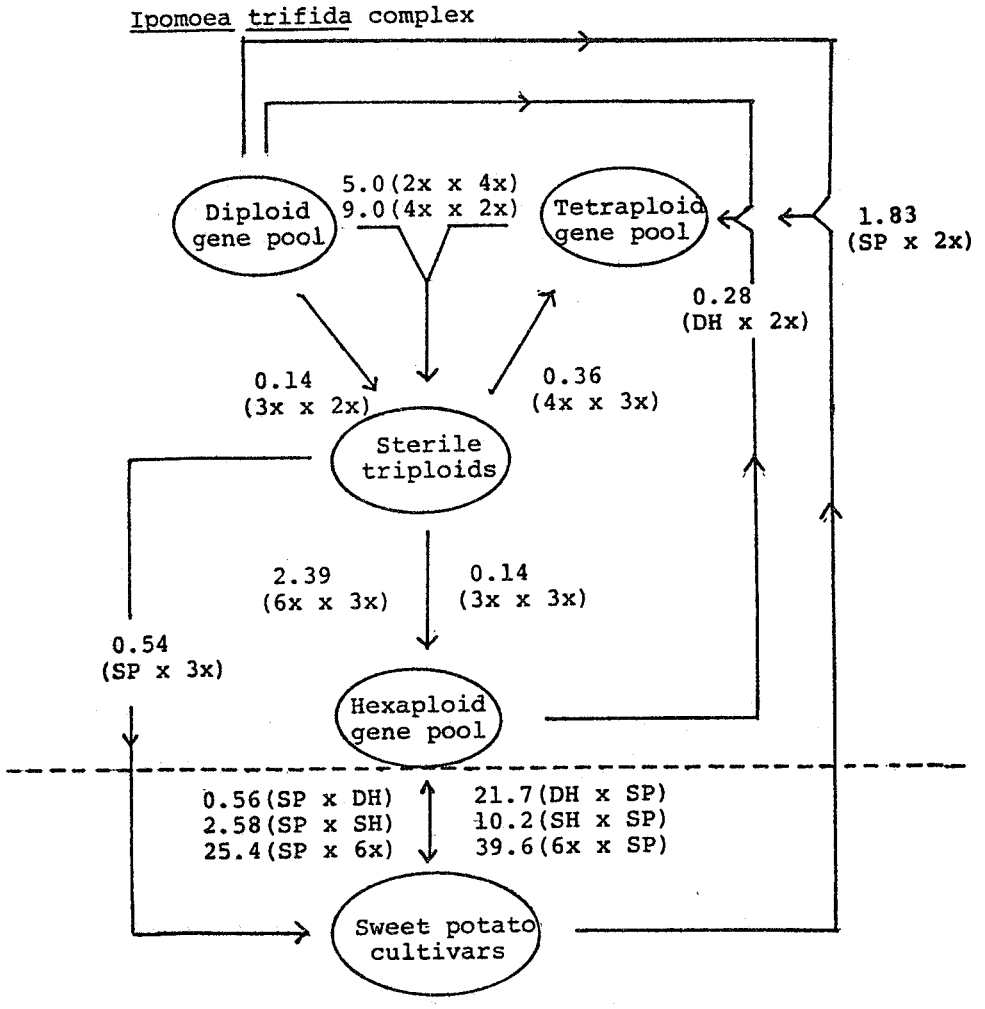

Fig. 2. A circulating system of the gene flow among the diploid and autopolyploids of I. trifida complex and sweet potato. Values along the pathways indicate percentage of seed set of the hybridization. 2x, K221; 3x, K222; 4x, K233; 6x, K123; DH, derived hexaploids; SH, synthetic hexaploids; SP, sweet potato cultivars (13, 14, 15, 16, 17, 21, 25).

In Fig. 2, the gene flow through the sterile triploid is caused by the functional diploid or unreduced triploid gametes. There may be other pathways which have not been demonstrated experimentally, for example, genes could flow from diploidy to tetraploidy, and also through pentaploidy.

Austin in his taxonomical studies (1, 2, 3) was the first to suggest the possible gene flow among sweet potato and its relatives. According to his hypothesis, K233 (24) and other tetraploids (9, 20) are of hybrid origin from the cultivated sweet potato and a diploid species, presumably I. trifida. We, however, believe that most of the plants making up the tetraploid gene pool are spontaneous plants (23, 29, 30), and there is some possibility that the wild gene pool at the tetraploid level contains the gene(s) from the cultivated sweet potato as shown in Fig. 2.

A similar case of interploidy gene flow is seen in the allogamous orchard grass, Dactylis glomerata, that forms an autoploidy series from diploid to hexaploid. Zohary and Nur (35) suggested that the natural triploid hybrids acted as a bridge for the efficient gene flow from the diploid to tetraploid level. Jones and Borrill (10) further discussed the significant role of artificial triploid hybrids through which the genes flow and their value to the breeding of orchard grass.

The gene flow system discussed above is being utilized as a scheme for sweet-potato breeding. The hypothetical scheme of analytic breeding proposed by Chase (5, 6) can be applicable if some modifications are made. Nowadays, reduction of hexaploid sweet potato to the plants of the diploid level is difficult for lack of the influx of gene flow to the diploids.

Regarding the process of resynthesis from the triploid lines, the desirable diploid parents are those selected for a specific trait such as resistance to a pathogen. On the other hand, tetraploid derivatives from cultivars x diploids would be used as parents after selection for root weight, starch content and starch yield.

Recent research of the tetraploid lines (called tetraploid sweet potato), being conducted since 1971 at Kyushu Agricultural Experiment Station, indicates the feasibility of attaining as high root yield at the tetraploid level as sweet potato (18).

3. Resynthesis of the autohexaploids

Last, a problem concerning the resynthesis process of autohexaploids will be discussed. There have been two attempts to induce autohexaploid plants from the diploid material. A single autohexaploid plant from the diploid hy-

brids of I. ramoni - I. lacunosa - I. triloba was so highly sterile that no progeny was obtained in controlled pollination (8). Similarly, "raw" autohexaploids from the diploid K221 were highly sterile, neither intercrosses nor crosses with sweet potato were successful (22).

Raw autoploid plants after colchicine treatment will be homozygous for loci in each genome. Such a homozygous condition seems to have a deleterious effect, just as an inbreeding effect, on fertility and vegetative vigor. To resynthesis, there are two methods for chromosome doubling; by colchicine treatment of the somatic cells, or somatic doubling (S), and by syngamy of the unreduced gametes, or gametic doubling (G). A comparison of the two methods was made in the genic system of the resynthesized hexaploids.

A model with four multiple alleles for a locus in random assortment of chromosomes was used for detecting possible genic systems and their frequencies. The genic system described in this paper is a group of genotypes that have N_1 alleles of the first kind, and N_2 alleles of the second kind, ..., and N_4 alleles of the fourth kind, and then total alleles $N = N_1 + N_2 + N_3 + N_4$. The degree of heterozygosity in a genic system can be expressed as follows: Entropy (En) = $\log ({}^{N!}/_{N_1!N_2!N_3!N_4!})$ as defined by Brillouin (4). Entropy may increase as the degree of heterozygosity becomes larger.

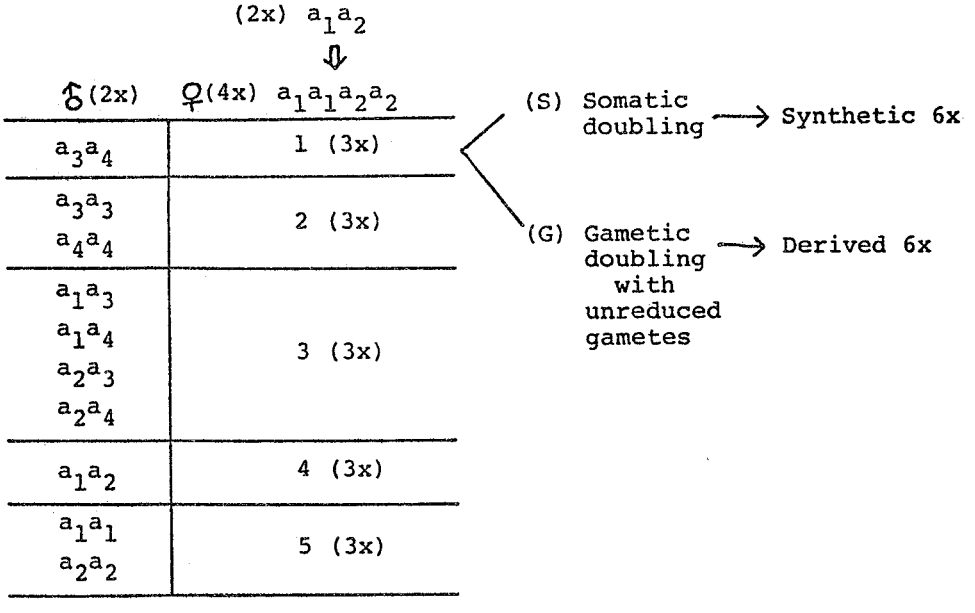

Fig. 3. Types of hybridization between 4x x 2x, and the two ways of inducing 6x. A model with four alleles for a locus.

Table 4. Possible genic systems and the entropy of a genic system in autohexaploids induced by somatic(S) or gametic doubling(G).

No.	Genic system* $N_1N_2N_3N_4$	Entropy of a genic system	Type of hybidization 1 S	1 G	2 S	2 G	3 S	3 G	4 S	4 G	5 S	5 G
1	6 0 0 0	0					1/12	1/144	2/12	2/144	1/6	1/36
2	5 1 0 0	0.778						10/144		20/144		8/36
3	4 2 0 0	1.176	4/12	4/144	2/6	2/36	7/12	42/144	10/12	70/144	5/6	19/36
4	3 3 0 0	1.301						8/144		52/144		8/36
5	4 1 1 0	1.477		4/144				18/144				
6	3 2 1 0	1.778		32/144		16/36		56/144				
7	2 2 2 0	1.954	8/12	36/144	4/6	18/36	4/12	9/144				
8	3 1 1 1	2.079		32/144								
9	2 2 1 1	2.255		36/144								
		Average	1.69	1.98	1.69	1.83	1.34	1.47	0.98	1.15	o.98	1.08

* Genotypes consisting of N_1 alleles of the first kind, N_2 alleles of the second kind, ... , N_4 alleles of the fourth kind. Entropy = $\log(N!/ N_1!N_2!N_3!N_4!)$, where $N = N_1+N_2+N_3+N_4$.

As represented in Fig. 3, an induced autotetraploid from a heterozygous diploid is crossed with a diploid different in genotype. All possible crosses can be classified into 5 types of hybridization. In each of the hybridization types, the genic systems of resulting hexaploids either by somatic or gametic doubling are shown in tabular form (Table 4). Every hybridization type, an array of hexaploids derived by gametic doubling represents the higher mean value of entropy than that by somatic doubling. As a result, the resynthesis by means of gametic doubling is an advantageous way to secure the genic system of higher heterozygosity.

Resynthesis of common wheat by gametic doubling, for example, was suggested to be genotypically controlled because of the extreme range of 0 to 73 percent in seed fertility shown by the different Emmer wheat-Aegilops triploid hybrids (31). In allogamous Ipomoea plants, chromosome doubling by syngamy of unreduced gametes would be a less frequent event. There may be, however, a possibility that the functioning of unreduced gametes is enhanced by a proper triploid hybrid. The genetic control of unreduced gamete formation, that has of yet to be studied, is of general importance not only to understand a prime cause of polyploidization in Nature, but also to find an effective means to utilize heterozygosis and heterotic effects of the genes in the homologous genomes.

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