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Origin and Evolution of Cultivated Tetraploid Potatoes via 2n Gametes

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Summary. A high gene frequency for *ps* (parallel spindles) is expected in cultivated tetraploid potatoes, *S. tuberosum* Group Tuberosum, if 2n pollen produced by ancestral diploid plants which were *psps* was involved in the origin and evolution of the potato. Fifty-six North American cultivars (varieties and advanced selections) were pollinated by diploid clones, either W 5295.7 or W 5337.3 which are homozygous recessive for *ps*. The segregation ratios in regard to 2n pollen production in derived tetraploid progenies, from 4x×2x crosses, reveal the genotype of *ps* in the cultivars. Microsporogenesis of 2n pollen producing 4x progeny was observed to avoid an overestimation of the frequency of 2n pollen producing plants due to mechanisms other than parallel spindles. More than 50% of the 56 cultivars are simplex (*Pspspsps*), since in each of these cultivars about 50% of their progeny produced 2n pollen. The *ps* gene frequency in the 56 cultivars was estimated as high as 0.69. The high frequency of *ps* in the tetraploid cultivars clearly supports the hypothesis that 2n pollen produced by plants homozygous recessive for *ps* have been involved in the origin of cultivated tetraploid potatoes, since a higher frequency of *ps* in the tetraploid than in the ancestral diploid population can be expected from sexual polyploidization but not from somatic doubling. The importance of meiotic mutants such as *ps* for the successful evolution of polysomic polyploids is emphasized.

Key words: Cultivated potato – Evolution – Parallel spindles – 2n gametes

Introduction

Polyploidization can be achieved mainly in two ways: either by somatic doubling of the chromosomes (asexual polyploidization) or by functioning of 2n gametes, gametes or gametophytes with the sporophytic chromosome number, produced by aberrations in the meiotic process (sexual polyploidization). Although both achieve doubling of the chromosome number, the genetic consequences of the two modes of polyploidization which determine the fitness and genetic flexibility of newly arisen polyploids are clearly different and favor sexual polyploidization (Mendiburu and Peloquin 1977; den Nijs and Peloquin 1977a; Camadro and Peloquin 1980). A recent review of the mode of origin of polyploids by Harlan and De Wet (1975) indicates the wide occurrence of 2n gametes, and suggests that proven examples of somatic doubling are indeed difficult to document.

Polyploidization has been of considerable importance in speciation in the tuber-bearing Solanums which include the white or Irish potato, *Solanum tuberosum* Group Tuberosum, that is a typical polysomic tetraploid (autotetraploid). Information on the occurrence of 2n gametes, their cytological basis, genetic determination, and genetic consequences has been used to demonstrate that sexual polyploidization must be regarded as a most potent evolutionary mechanism, as opposed to somatic doubling.

Mok and Peloquin (1975) found three cytological mechanisms of 2n pollen formation in diploid potatoes, parallel spindles (*ps*), premature cytokinesis-1 (*pc-1*) and premature cytokinesis-2 (*pc-2*); they are inherited as recessives. Parallel spindles results in 2n pollen genetically equivalent to first division restitution (FDR) gametes, whereas premature cytokinesis-1 and -2 produce meiotic products genetically equivalent to second division restitution (SDR) gametes. A possible mechanism for FDR 2n egg formation due to poor pairing and subsequent formation of restitution nuclei in megasporogenesis was found in some diploid potatoes: it is also simply inherited (Iwanaga and Peloquin 1979). SDR 2n eggs appear to be formed due to the omission of the second meiotic division in one clone (Iwanaga

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and Peloquin 1980). FDR 2n gametes, formed via parallel spindles, provide a powerful way for transferring fitness to polyploid offspring because more than 80% of the heterozygosity of the parent as well as the majority of the epistasis can be transmitted to their offspring (Mendiburu 1971).

2n gametes occur abundantly in almost every species examined at the diploid, triploid and tetraploid levels in series Tuberosa to which the cultivated tetraploids and their ancestral species belong (Quinn et al. 1974; den Nijs and Peloquin 1977a, b). According to the current evolutionary hypothesis (Hawkes 1979), the primitive cultivated tetraploid, Group Andigena, originated as a hybrid between the diploid cultivated Group Stenotomum and the weed diploid *S. sparsipilum*. The widespread occurrence of 2n gametes in species which are candidates for being ancestors of the cultivated tetraploid, the genetic determination of 2n gametes, and the consequences of sexual polyploidization led den Nijs and Peloquin (1977a) to emphasize that 2n gametes have been involved in the origin of the cultivated tetraploid.

An important consideration is obvious. If 2n gametes, produced by individuals homozygous for alleles governing their formation, were involved in the origin and evolution of the cultivated tetraploid potato, one should expect to find that allele in the tetraploid potato cultivars. Den Nijs and Peloquin (1977a) cited the existence of the *ps* allele in two cultivars, 'Katahdin' and 'Sebago', as evidence for the presence of alleles responsible for sexual polyploidization in cultivated tetraploids. However, it is not convincing evidence for sexual polyploidization, since we can expect to find *ps* alleles in cultivated tetraploids regardless of the mode of polyploidization. For example, if a tetraploid originates from a diploid with the genotype *Psps* by somatic doubling, the tetraploid is duplex (*PsPspsps*). Therefore, quantitative estimates of the *ps* gene frequency in cultivated tetraploids are essential as evidence for or against sexual polyploidization.

The objectives of this investigation are to determine the genotypes of 63 Tuberosum cultivars at the *ps* locus and to estimate the gene frequency of *ps*. It is a test of the hypothesis that 2n pollen produced by *ps* has been involved in the origin and evolution of cultivated tetraploid potatoes.

Materials and Methods

Sixty three cultivars (varieties and advanced selections) which belong to *S. tuberosum* Group Tuberosum were pollinated by either W5295.7 (I) or 5337.3 (J). I and J are 'Phureja'-haploid Tuberosum hybrids (2n=2x=24) and produce 2n pollen by parallel spindles (Mok 1975). The hybrid seed of the RD selections was kindly provided by Dr. M. S. Cipar of Frito-Lay Inc. Among 63 hybrid families, three had very low seed germination, and consequently they were eliminated from the experiment. Twenty-eight plants and thirty-four plants from each of 60 families were grown at Hancock and Rhinelander, Wisconsin, respectively. – Genotypes of the tetraploid cultivars as to *ps* were estimated in the following way. If a cultivar is nulliplex, all hybrid progeny will produce 2n pollen. If a cultivar is simplex (*Pspspsps*), we can expect about 50% of the progeny to produce 2n pollen based on a random chromosome assortment hypothesis, assuming no production of 2n pollen by mechanisms other than *ps*. In a similar way, duplex (*PsPspsps*) cultivars would result in 17% of progeny with 2n pollen. Triplex (*PsPsPsps*) and quadraplex (*PsPsPsPs*) cultivars would not produce any progeny with 2n pollen. Therefore, it is not possible to distinguish between triplex and quadriplex cultivars with the populations used. Both a random chromosome assortment hypothesis and a random chromatid assortment hypothesis were used to test the fitness of segregation ratios, because the location of the *ps* locus in relation to the centromere was not known. Expected segregation ratios for the hypotheses are presented in Table 1. – It is possible that some plants produce 2n pollen by premature cytokinesis because I and J are heterozygous for *pc-1* and *pc-2*. If so, the result will be an overestimation of 2n pollen producers and *ps* frequency. To minimize this overestimation meiosis was analyzed in 117 plants representing 43 families. – The determination of 2n pollen frequency was done according to Quinn et al. (1974), using acetocarmine-glycerol jelly (Marks 1954). Plants with more than 1% large size pollen were regarded as 2n pollen producers, plants with less than 5% pollen stainability were considered male sterile. Meiosis was studied by squashing anthers in acetocarmine followed by very gentle pressure to avoid modifying the spindle orientation at anaphase II. Telophase I was critically observed to detect premature cytokinesis. The distinction between *pc-1* and *pc-2* was done according to Mok (1975). The existence of tripolar and/or parallel spindles at anaphase II and telophase II were used as key observations for identifying parallel spindles. Later stages were also observed to check for other abnormalities which might produce 2n size pollen.

Results

All individuals in three families were found to be male sterile. Male sterility was a serious problem and reduced the number of progeny examined for 2n pollen formation in most of the families (Table 2). Meiosis was studied in 117 2n pollen producing plants; 85% of them had parallel spindles. Although premature cytokinesis was found in some plants, it was assumed that 2n pollen was

Table 1. Expected segregation ratios for 2n pollen production in progeny of cultivar × *ps/ps* cross on the basis of two hypotheses concerning gamete formation in tetraploid potatoes

Genotype of cultivar	Random chromosome assortment	Random chromatid assortment
	Normal:2n pollen producer	Normal:2n pollen producer
pspspsps	0 : 1	0 : 1
Pspspsps	1 : 1	0.87 : 1
PsPspsps	5 : 1	3.7 : 1
PsPsPsps	1 : 0	27 : 1
PsPsPsPs	1 : 0	1 : 0

Table 2. The number of plants per family, and the number of plants with male sterility, male fertility, n pollen, 2n pollen, *ps*, and *pc*, plus the proposed genotypes of 57 cultivars for *ps*

Family	Parents Location	Number of plants: No. of plants	Male sterile	Male fertile	n pollen	2n pollen	cytology	*ps*	*pc*	Proposed genotype: Chromosome assortment	Chromatid assortment
1)	'WisBaker' × I										
	Rhinelander	22	14	8	5	3	1	1	0		
	Hancock	19	11	8	2	6					
	Combined	41	25	16	7	9				*Pspspsps*	*Pspspsps*
2)	'Lenape' × I										
	Rhinelander	27	17	10	5	5	3	2	1		
	Hancock	24	18	6	2	4					
	Combined	51	35	16	7	9				*Pspspsps*	*Pspspsps*
3)	'Monona' × I										
	Rhinelander	17	7	10	4	6	2	1	1		
	Hancock	26	15	11	5	6					
	Combined	43	22	21	9	12				*Pspspsps*	*Pspspsps*
4)	'Seminole' × I										
	Rhinelander	17	16	1	0	1	1	1	0		
	Hancock	10	7	3	2	1					
	Combined	27	23	4	2	2				*Pspspsps* or *PsPspsps*	*Pspspsps* or *PsPspsps*
5)	'Superior' × I										
	Rhinelander	16	13	3	2	1	0	0	0		
	Hancock	11	8	3	2	1					
	Combined	27	21	6	4	2				*Pspspsps* or *PsPspsps*	*Pspspsps* or *PsPspsps*
6)	'F 5,850' × I										
	Rhinelander	21	7	14	8	6	3	3	0		
	Hancock	17	9	8	2	6					
	Combined	38	16	22	10	12				*Pspspsps*	*Pspspsps*
7)	'Red La Soda' × I										
	Rhinelander	26	18	8	3	5	4	2	2		
	Hancock	18	16	2	0	2					
	Combined	44	34	10	3	7				*Pspspsps*	*Pspspsps*
8)	'Wischip' × I										
	Rhinelander	31	13	18	4	14	5	5	0		
	Hancock	17	8	9	5	4					
	Combined	48	21	27	9	18				*Pspspsps*	*Pspspsps*
9)	'Sebago' × I										
	Rhinelander	13	10	3	0	3	2	2	1		
	Hancock	21	19	2	0	2					
	Combined	34	29	5	0	5				*pspspsps*	*pspssps*
10)	'Early Gem' × I										
	Rhinelander	8	8	0	0	0	0	0	0		
	Hancock	12	8	4	2	2					
	Combined	20	16	4	2	2				*Pspspsps* or *PsPspsps*	*Pspspsps* or *PsPspsps*
11)	'W 231' × I										
	Rhinelander	27	13	14	10	4	3	3	0		
	Hancock	27	11	16	14	2					
	Combined	54	24	30	24	6				*PsPspsps*	*PsPspsps*
12)	'Raritan' × I										
	Rhinelander	32	0	32	27	5	2	2	0		does not fit
	Hancock	22	0	22	22	0					to any ex-
	Combined	54	0	54	49	5				*PsPspsps*	pected ratio

Table 2 (continued)

Family	Parents Location	Number of plants: No. of plants	Male sterile	Male fertile	n pollen	2 n pollen	cytology	*ps*	*pc*	Proposed genotype: Chromosome assortment	Chromatid assortment
13)	'La-01-20' × I										
	Hancock	18	8	10	8	2	0	0	0	*Pspspsps* or *PsPspsps*	*PsPspsps*
14)	'W 707' × I										
	Rhinelander	23	10	13	11	2	0	0	0		
	Hancock	19	5	14	7	7					
	Combined	42	15	27	18	9				*Pspspsps*	*PsPspsps*
15)	'Chieftan' × I										
	Rhinelander	8	6	2	2	0	0	0	0		
	Hancock	14	9	5	4	1					
	Combined	22	15	7	6	1				*Pspspsps* or *PsPspsps*	*PsPspsps*
16)	'La-11-118' × I										
	Rhinelander	28	18	10	6	4	2	2	0		
	Hancock	22	11	11	7	4					*Pspspsps*
	Combined	50	29	21	13	8				*Pspspsps*	or *PsPspsps*
17)	'W 726' × I										
	Rhinelander	23	15	8	3	5	2	2	0		
	Hancock	17	7	10	4	6					
	Combined	40	22	18	7	11				*Pspspsps*	*Pspspsps*
18)	'Kennebec' × I										
	Rhinelander	9	9	0	0	0	0	0			
	Hancock	11	8	3	2	1					
	Combined	20	17	3	2	1				*Pspspsps* or *PsPspsps*	*Pspspsps* or *PsPspsps*
19)	'Norland' × I										
	Rhinelander	16	6	10	3	7	2	1	1		
	Hancock	10	1	9	4	5					
	Combined	26	7	19	7	12				*Pspspsps*	*Pspspsps*
20)	'W 639' × J										
	Rhinelander	32	12	20	12	8	6	5	1	does not fit	
	Hancock	24	13	11	9	2				to any ex-	
	Combined	56	25	31	21	10				pected ratio	*PsPspsps*
22)	'Red Pontiac' × I										
	Rhinelander	18	12	6	1	5	3	3	0		
	Hancock	22	18	4	3	1					
	Combined	40	30	10	4	6				*Pspspsps*	*Pspspsps*
23)	'Targhee' × I										
	Rhinelander	23	16	10	5	5	0	0	0		
	Hancock	15	10	5	4	1					*Pspspsps*
	Combined	38	26	15	9	6				*Pspspsps*	or *PsPspsps*
24)	'Platte' × I										
	Rhinelander	32	9	23	2	21	8	5	3		
	Hancock	23	14	9	1	8					
	Combined	55	23	32	3	29				*Pspspsps*	*Pspspsps*
25)	'Atlantic' × I										
	Rhinelander	26	16	10	4	6	2	1	1		
	Hancock	14	6	8	5	3					
	Combined	40	22	18	9	9				*Pspspsps*	*Pspspsps*

Table 2 (continued)

Family	Parents Location	Number of plants: No. of plants	Male sterile	Male fertile	n pollen	2n pollen	cytology	*ps*	*pc*	Proposed genotype: Chromosome assortment	Chromatid assortment
26)	'Neb42-1' × I										
	Rhinelander	28	23	5	2	3	1	1	0		
	Hancock	19	14	5	2	3					
	Combined	47	37	10	4	6				*Pspspsps*	*Pspspsps*
27)	'HS-17'										
	Rhinelander	18	12	6	2	4	2	1	1		
	Hancock	17	11	6	5	1					*Pspspsps*
	Combined	35	23	12	7	5				*Pspspsps*	or *PsPspsps*
28)	'Norgold R.' × I										
	Rhinelander	21	11	10	5	5	1	1	0		
	Hancock	13	6	7	7	0				*Pspspsps*	
	Combined	34	17	17	12	5				or *PsPspsps*	*PsPspsps*
29)	'W738' × I										
	Rhinelander	22	16	6	0	6	1	0	1		
	Hancock	22	13	9	4	5					
	Combined	44	29	15	4	11				*Pspspsps*	*Pspspsps*
32)	A 6,867-8' × I										
	Hancock	14	6	8	5	3	0	0	0	*Pspspsps* or *PsPspsps*	*Pspspsps* or *PsPspsps*
33)	'W710' × I										
	Rhinelander	26	3	23	19	4	0	0	0		
	Hancock	15	3	12	8	4					
	Combined	41	6	35	27	8				*PsPspsps*	*PsPspsps*
34)	'RD-1-9-32' × I										
	Rhinelander	18	11	7	6	1	0	0	0		
	Hancock	19	15	4	2	2				*Pspspsps*	
	Combined	37	26	11	8	3				or *PsPspsps*	*Pspspsps*
35)	'Rd-2-9-19' × I										
	Rhinelander	30	9	21	7	14	3	2	2		
	Hancock	23	9	14	6	8					
	Combined	53	18	35	13	22				*Pspspsps*	*Pspspsps*
36)	'RD-5-4-14' × I										
	Rhinelander	24	0	24	22	2	0	0	0		
	Hancock	17	0	17	14	3					
	Combined	41	0	41	36	5				*PsPspsps*	*PsPspsps*
37)	'Rd-7-9-127' × I										
	Rhinelander	26	16	10	0	10	3	3	0		
	Hancock	9	8	1	0	1					
	Combined	35	24	11	0	11				*pspspsps*	*pspspsps*
38)	'RD-8-9-7' × I										
	Rhinelander	21	13	8	4	4	0	0	0		
	Hancock	11	6	5	2	3					
	Combined	32	19	13	6	7				*Pspspsps*	*Pspspsps*
39)	'RD-12-8-1' × I										
	Rhinelander	21	0	21	19	2	0	0	0		
	Hancock	18	4	14	14	0					*PsPspsps*
	Combined	39	4	35	33	2				*PsPspsps*	or *PsPsPsps*

Table 2 (continued)

Family	Parents Location	Number of plants: No. of plants	Male sterile	Male fertile	n pollen	2 n pollen	cytology	*ps*	*pc*	Proposed genotype: Chromosome assortment	Chromatid assortment
40)	'RD-13-9-2' × I										
	Rhinelander	32	9	23	10	13	3	3	0		
	Hancock	26	11	15	9	6					
	Combined	58	20	38	19	19				*Pspspsps*	*Pspspsps*
41)	'RD-41-6-2' × I										
	Rhinelander	18	11	7	0	7	3	3	0		
	Hancock	12	8	4	4	0					
	Combined	30	19	11	4	7				*Pspspsps*	*Pspspsps*
42)	'RD-51-5-74' × I										
	Rhinelander	29	12	17	12	5	1	1	0		
	Hancock	20	4	16	7	9					
	Combined	49	16	33	19	14				*Pspspsps*	*Pspspsps*
43)	'RD-72-9-2' × I										
	Rhinelander	27	12	15	6	9	4	4	0		
	Hancock	19	8	11	6	5					
	Combined	46	20	26	12	14				*Pspspsps*	*Pspspsps*
44)	'RD-94-15' × I										
	Rhinelander	22	12	10	0	10	4	4	0		
	Hancock	16	9	7	6	1					
	Combined	38	21	17	6	11				*Pspspsps*	*Pspspsps*
45)	'RD-96-7-2' × I										
	Rhinelander	26	12	14	1	13	4	4	0		
	Hancock	17	5	12	3	9					
	Combined	43	17	26	4	22				*Pspspsps*	*Pspspsps*
46)	'RD-135-8-2' × I										
	Rhinelander	22	20	2	1	1	0	0	0		
	Hancock	21	11	10	1	9					
	Combined	43	31	12	2	10				*Pspspsps*	*Pspspsps*
48)	'RD-142-7-2' × I										
	Rhinelander	31	6	25	10	15	3	3	0		
	Hancock	25	3	22	5	17					
	Combined	56	9	47	15	32				*Pspspsps*	*Pspspsps*
49)	'RD-148-8-5' × I										
	Rhinelander	26	13	13	5	8	3	2	1		
	Hancock	21	5	16	10	6					
	Combined	47	18	29	15	14				*Pspspsps*	*Pspspsps*
50)	'RD-193-9-1' × I										
	Rhinelander	26	0	26	23	3	1	1	0		
	Hancock	23	1	22	19	3					
	Combined	49	1	48	42	6				*PsPspsps*	*PsPspsps*
51)	'RD-211-9-1' × I										
	Rhinelander	26	22	4	2	2	1	0	1		
	Hancock	20	12	8	4	4					
	Combined	46	34	12	6	6				*Pspspsps*	*Pspspsps*
52)	'RD-222-15' × I										
	Rhinelander	23	4	19	3	16	10	10	0		
	Hancock	20	7	13	8	5					
	Combined	43	11	32	11	21				*Pspspsps*	*Pspspsps*

Table 2 (continued)

Family	Parents Location	Number of plants: No. of plants	Male sterile	Male fertile	n pollen	2n pollen	cytology	*ps*	*pc*	Proposed genotype: Chromosome assortment	Chromatid assortment
53)	'RD-280-0-12' × I										
	Rhinelander	34	13	21	9	12	3	3	2		
	Hancock	18	10	8	6	2					
	Combined	52	23	29	15	14				*Pspspsps*	*Pspspsps*
54)	'RD-318-12' × I										
	Rhinelander	23	12	11	8	3	1	1	0		
	Hancock	18	4	14	8	6					*Pspspsps*
	Combined	41	16	25	16	9				*Pspspsps*	or *PsPspsps*
55)	'RD-329-8' × I										
	Rhinelander	29	10	19	9	10	2	2	0		
	Hancock	13	6	7	4	3					
	Combined	42	16	26	13	13				*Pspspsps*	*Pspspsps*
56)	'RD-333-30' × I										
	Rhinelander	23	15	8	4	4	1	1	0		
	Hancock	18	12	6	6	0				*Pspspsps*	*Pspspsps*
	Combined	41	27	14	10	4				or *PsPspsps*	or *PsPspsps*
57)	'RD-335-8-1' × I										
	Rhinelander	29	14	15	7	8	5	3	2		
	Hancock	22	8	14	7	7					
	Combined	51	22	29	14	15				*Pspspsps*	*Pspspsps*
58)	'F 5,356' × I										
	Rhinelander	16	12	4	1	3	1	0	1		
	Hancock	12	12	1	0	1					
	Combined	28	23	5	1	4				*Pspspsps*	*Pspspsps*
61)	'Neb 63-71-1' × I										
	Rhinelander	17	10	7	1	6	1	1	0		
	Hancock	19	13	6	1	5					
	Combined	36	23	13	2	11				*Pspspsps*	*Pspspsps*
62)	'Norchip' × I										
	Rhinelander	12	5	7	0	7	1	1	0		
	Hancock	16	10	6	0	6					
	Combined	28	15	13	0	13				*pspspsps*	*pspspsps*
63)	'La 42-38' × J										
	Rhinelander	33	29	4	1	3	3	3	0		
	Hancock	17	15	2	2	0					*Pspspsps*
	Combined	50	44	6	3	3				*Pspspsps*	or *PsPspsps*

produced by parallel spindles in all 2n pollen producing plants to test the fitness of segregation ratios. This assumption probably results in some overestimation of the *ps* frequency, but it is not serious as is discussed later. No other meiotic abnormality which might result in 2n size pollen production was observed in male fertile plants.

The number of plants analyzed in each family, and the number of plants with male sterility, male fertility, n pollen, 2n pollen, *ps*, and *pc* are presented in Table 2. Proposed genotypes based on random chromosome assortment and random chromatid assortment hypotheses are also indicated in Table 2. The proposed genotypes were obtained by testing segregation in the progeny for 2n pollen producing plants vs. non-2n pollen producing plants for the expected ratios by chi-square test at the 5% probability level. Family 12 had a segregation ratio which did not fit any expected segregation ratio based on the random chromatid assortment hypothesis. Similarily, family 20 had a segregation ratio which did not fit any expected ratio of the random chromosome assortment hypothesis. Based on the random chromatid

Table 3. Frequency of assigned genotypes at the *ps* locus for the fifty six cultivars based on two hypotheses

Genotype	Random chromosome assortment	Random chromatid assortment
1) *pspspsps*	3	3
2) *Pspspsps*	37	32
3) *Pspspsps* or *PsPspsps*	10	11
4) *PsPspsps*	6	9
5) *PsPspsps* or *PsPsPsps*	0	1

assortment hypothesis, 3, 32, 11, 9, and 1 cultivars were determined as nulliplex, simplex, simplex or duplex, duplex, and duplex or triplex, respectively. On the other hand, 3, 37, 10 and 6 cultivars were found to be nulliplex, simplex, simplex or duplex, and duplex, respectively, based on the random chromosome assortment hypothesis (Table 3).

Calculation of the gene frequency of *ps* in 56 cultivars was done as follows. Nulliplex, simplex, and duplex were regarded as having 4, 3, and 2 *ps* alleles, respectively. Cultivars that could be either simplex or duplex were arbitrarily regarded as having 2.5 alleles. In the same way, 1.5 alleles were given to cultivars which were either duplex or triplex. The frequency of the *ps* allele was obtained by dividing the total *ps* allele number by the total allele number (56×4) at this locus. Thus, 0.69 and 0.71 were obtained as the *ps* gene frequencies for the random chromatid assortment hypothesis and random chromosome assortment hypothesis, respectively; with both hypotheses, the *ps* frequency was very high.

Discussion

The high gene frequency of *ps* clearly supports the hypothesis that 2n pollen produced by individuals recessive homozygous for *ps* has been involved in the origin of cultivated tetraploid potatoes. If somatic doubling (asexual polyploidization) rather than sexual polyploidization via 2n pollen has been involved in their origin, we can expect the same *ps* gene frequency in the tetraploids as in their ancestral diploid population. On the other hand, if sexual polyploidization via 2n pollen by *ps* has been involved, higher *ps* gene frequencies in the tetraploids than in the diploids can be expected, because 2n pollen produced by male diploid parents recessive homozygous for *ps* carry only *ps*, but not *Ps*, and subsequently increase the *ps* gene frequency in newly arisen tetraploids. For example, if the diploid female and male progenitor populations have *ps* at a frequency of 0.4, the new tetraploid population produced by sexual polyploidization has a 0.7 *ps* gene frequency, whereas only a 0.4 gene frequency is expected through asexual polyploidization. Since preliminary results (Quinn et al. 1974; den Nijs and Peloquin 1977a, Iwanaga unpublished data) indicated that *ps* frequency in the ancestral diploid group and species, such as *S. tuberosum* Group Stenotonum and *S. sparsipilum* is lower than 0.4, sexual polyploidization is the most reasonable way to explain the very high frequency of *ps* in cultivated tetraploids.

The high frequency of *ps* also supports the possibility of continuous introgression from diploid species to cultivars via 2n pollen. It is likely that gene flow from diploid species or groups to cultivated tetraploids has been achieved through 4x–2x crosses in nature where FDR 2n pollen of the diploid has a comparative advantage over normal n pollen in growing in the style of the tetraploid, as indicated by Simon and Peloquin (1976). The FDR 2n pollen is recessive homozygous for *ps* and contributes two *ps* alleles to the tetraploid population. Thus, introgression from a diploid to a tetraploid population through 2n pollen can increase the *ps* frequency in the tetraploid population.

A small overestimation of the number of plants producing 2n pollen by parallel spindles occurs because a few produce 2n pollen by premature cytokinesis, but this will not signifcantly affect the estimate of the *ps* frequency. For example, we might assume that 10 cultivars were assigned the wrong genotypes because of the involvement of premature cytokinesis and a subsequent overestimation of number of plants producing 2n pollen by parallel spindles resulted. Further, if 5 cultivars should be assigned (*Pspspsps* or *PsPspsps*) rather than *Pspspsps* and 5 assigned *PsPspsps* rather than (*Pspspsps* or *PsPspsps*) the *ps* frequency would be 0.67. Even if we reassign new genotypes for twenty cultivars in the same way, we will get a 0.64 *ps* gene frequency. It is not likely that so many cultivars were assigned wrong genotypes due to the overestimation, because most (85%) of the plants in which meiosis was studied had parallel spindles.

Only a small difference was found between the random chromosome and random chromatid assortment hypotheses in estimating the *ps* frequency. Although disagreement in assigned genotypes by these hypotheses was found in nine cultivars, the difference in total *ps* frequency was only 0.02.

The possible existence of triploid progeny was not a problem. A low frequency of triploid progeny are expected from $4x \times 2x$ crosses, as reported by Hanneman and Peloquin (1968). Since *pspsps* triploids have parallel spindles (Mok et al. 1975), the frequency of 2n pollen producers is not affected whether normal eggs are fertilized by normal n pollen (*ps*) or 2n pollen (*psps*).

It appears that the 56 cultivars used are a good representation of Group Tuberosum. However, it may not be a good sample of *S. tuberosum* which includes Group Andigena and Group Tuberosum. It has been said that Group Tuberosum has a relatively narrow genetic background. Thus, there is a possibility that the high frequency of *ps* is due to the fact that Group Tuberosum in the United States originated from a relatively small ancestral population which had a high *ps* frequency. To check this, studies of the frequency of *ps* in a large number of Group Andigena selections will be necessary.

The importance of *ps* for the evolution of potatoes is comparable to that of the *Ph* gene or 5B effect (Riley and Chapman 1958; Sears and Okamoto 1958) for the evolution of bread wheat: *Ph* is essential for diploidization of wheat (Riley 1960), a disomic polyploid (allopolyploid), and *ps* is crucial to enhance heterozygosity in potatoes, a polysomic polyploid (autopolyploid). For both disomic and polysomic polyploids, a high degree of genetic diversity is very important to compete with their diploid parents and colonize ecological niches unavailable to both diploid parents. Genetic diversity of bread wheat has been obtained by 1) combining the specific adapted genetic complexes of three parents, and 2) disomic inheritance via the *Ph* locus and subsequent further diploidization to develop "built-in" heterozygosity even under self-pollination. The high degree of genetic diversity of the potato has been accomplished by 1) sexual polyploidization which offers transmission of heterozygosity of the diploid parents to the polyploids and the recurrent occurrence of new polyploid hybrids with some genetic diversity, 2) polysomic (tetrasomic) inheritance which enhances intra- and inter-locus interactions, and 3) continuous introgression from the diploid parents via 2n gametes.

The degree of genomic differentiation of diploid parents and the mode of propagation might have contributed to the difference in the pattern of evolution between polysomic polyploids and disomic polyploids. Multivalent formation in polysomic polyploids may result in low fertility, but it is not a problem for a vegetatively propagated species such as potatoes. On the other hand, reduced fertility due to multivalent formation is a crucial problem for the success of newly arisen polyploids which have no way of vegetative propagation. In an example like bread wheat, development of genetic control of pairing specificity is essential. If there is no geonomic differentiation in diploid parents, bivalent pairing control and subsequent diploidization by a meiotic mutant is difficult, and an alternative is to keep polysomic inheritance and to maximize heterozygosity by 2n gametes. In summary, we emphasize the importance of meiotic mutants such as *ps* for the successful evolution of polysomic polyploids.

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