Theor. Appl. Genet. 59, 95-100 (1981)

Variation for 2n Pollen Production in Clones of *Solanum phureja* Juz. and Buk.*

R.E. Veilleux and F.I. Lauer
Department of Horticultural Science and Landscape Architecture, University of Minnesota, St. Paul, Minnesota (USA)

Summary. Frequency of unreduced pollen grains was estimated for five genotypes of *Solanum phureja* (2n = 24) growing in three environments; (E1) cool (7.2-13.3°C) and (E2) warm (12.2-17.2°C) growth chambers and (E3) field conditions. Highly variable frequencies were found, with genotype, environment, and genotype × environment interaction as significant components of variance. The frequency of unreduced gametes for two additional genotypes was studied over time in two growth chamber environments (cool and warm). One genotype, characterized by mostly fused spindles at the second meiotic division, expressed a high frequency of big pollen (BP) in both environments, whereas the second, characterized by fused, parallel and tripolar second division spindless was found to increase in BP frequency over time in the cool chamber, but remained consistently low in the warm chamber. The identification of specific environmental components with general effect on the expression of unreduced gametes is not possible because of the large genotype × environment interaction component of variance. A genetic hypothesis based on incomplete penetrance and variable expressivity of a dominant gene is presented as an alternative to the currently accepted theory of control of parallel spindles by a single recessive gene.

Key words: *Solanum phureja* – Unreduced gametes – Diploid pollen – Fused spindles – Meiotic abnormalities

Introduction

The occurrence of unreduced male gametes, which are widespread in the plant kingdom (Skiebe 1969; Harlan and de Wet 1975), has been attributed to three influences which affect meiotic processes: 1) hybridization between sufficiently unrelated species so that normal meiosis, particularly pairing of homologous chromosomes, cannot proceed properly in the F1 (Karpechenko 1927; Woodworth 1929; Darlington 1930; Wagenaar 1968a, b); 2) gene mutations which alter the course of microsporogenesis (Bergner et al. 1934; Satina and Blakeslee 1935; Dowrick 1953; Mok and Peloquin 1975a, b); and 3) extremes of environment (reviewed by Sax 1937; Okuno 1951, 1952). Infestation with virus (Chavez and de Sosa 1971) or gall mites (Kostoff and Kendall 1929), either natural (Longley and Clark 1930) or artificial (Giles 1939) dehydration, age of the plant (Ramanna 1974) and treatment with chloroform (Lutkov 1937) have all been identified as environmental agents which promote the formation of unreduced gametes. Allele differences influence the occurrence of unreduced gametes (Skiebe 1972). Extremes of temperature, cold [Belling 1925 (*Uvularia*); de Mol 1929 (*Tulipa, Hyacinthus*); Lutkov 1937 (*Raphanobrassica*); Okuno 1951, 1952 (*Solanum*)], heat [Stow 1926 (*Solanum*); Lebedeff 1940 (*Zea*); Lewis 1943 (*Prunus*); Jain 1962 (*Lolium*)], and cold followed by heat [Matsuda 1936 (*Petunia*); Sax 1936, 1937 (*Rhoeo, Tradescantia*)] are the environmental influences most commonly thought to affect meiosis.

Regardless of the causal agent, frequency of unreduced gametes has usually been found to be highly variable among locules within an anther [Fukushima 1930 (*Brassica*); Vorsa and Bingham 1979 (*Medicago*)], among anthers within a bud [Sakamura and Stow 1926 (*Gagea*); de Mol 1929 (*Tulipa*); Darlington 1930 (*Prunus*); Matsuda 1936 (*Petunia*); Giles 1939 (*Tradescantia*)], among flowers on a plant [Matsuda 1936; Lebedeff 1940 (*Zea*)] and among plants of the same clone [Jacobsen 1976 (*Solanum*)] or cultivar [Eenink 1975 (*Brassica*)]. Only Dowrick (1953) reported a consistent 63% 'precentric' cells, i.e. cells which showed precocious splitting of centromeres, in

* Manuscript no. 11,311 of the scientific journal series of the Agricultural Experiment Station, University of Minnesota, St. Paul, MN 55108

0040/5752/81/0059/0095/$ 1.20

all five anthers per floret on four plants, presumably of the same clone of *Chrysanthemum*. Mok and Peloquin (1975a) found a high correlation between the frequencies of dyads and unreduced pollen grains in diploid *Solanum* hybrids. Vorsa and Bingham (1979) observed a much weaker correlation between these same frequencies in diploid *Medicago* selections, in which parallel second division spindles were identified, and they attributed the imperfect correlation to sampling error due to variation among anthers and locules. Mok and Peloquin (1975b) later reported that the frequency of unreduced pollen varies from 3 to 99% among their *Solanum* genotypes.

Significant levels (> 5%) of unreduced pollen were determined in flower buds of several genotypes of *Solanum phureja* Juz. & Buk. which had been grown in the field. When some of these same genotypes were subsequently grown in the greenhouse the following winter, big pollen frequency was found to be insignificant (< 5%). Mok and Peloquin (1975b) have presented evidence that expression of unreduced gametes in diploid *Solanum* genotypes is due to the presence of one of several recessive mutations which alter the course of microsporogenesis. The variability in frequency of unreduced gametes in genetically identical clones grown simultaneously in three environments is the subject of this report.

Materials and Methods

Twenty-five seedling families (about 1000 plants) of *S. phureja*, which had previously undergone several cycles of recurrent selection for photoperiod adaptation by F.I. Haynes at the University of North Carolina, were grown under irrigation at the Sandplains Research Station in 1977 at Becker, MN. Buds were collected from each plant and pollen samples were screened at a magnification of 400X for the presence of greater than 5% big pollen (BP) (Quinn et al. 1974), or if pollen size was ambiguous, for a significant frequency of dyads. Sixty-two BP selections representing ten families were made. Seven of these BP genotypes representing six different families were chosen for the frequency study. Cytological determination of the type of restitution present in each genotype was made with aceto-carmine anther squashes. Two randomized complete blocks consisting of one plant/genotype of the five genotypes were placed in each of three environments: E1) cool growth chamber (7.2-13.3°C, 19 hr photoperiod), E2) warm growth chamber (12.2-17.2°C, 19 hr photoperiod) and E3) field (St. Paul, planted 5/9/78). Tubers for each genotype for planting in all three environments were derived from the same parent plant. Plants were maintained in their respective environments from planting through flowering. Separate pollen samples were taken from the first three flowers to bloom on each plant and again on three flowers in bloom 10-20 days later. Frequency of unreduced gametes was determined by examination of a minimum of 200 pollen grains/sample using the size classification of Quinn et al. (1974). A Zeiss standard RA routine and research microscope equipped with a focusing eyepiece and 10 X 10 NET eyepiece micrometer was employed to facilitate classification and scoring. In a second study, plants of two genotypes (148-17 and 154-1) were grown in warm (8.3-18.3°C) and cool (8.3-12.8°C) growth chambers under a 19 hr photoperiod. A cool night temperature was employed in both chambers because it was thought to promote flowering. Pollen was collected from three different flowers twice weekly during a 4-week flowering period and frequency of BP was estimated as in the first study.

Results

Meiotic restitution in all seven genotypes was found to occur by spindle abnormalities during the second meiotic division (Table 1). Most genotypes expressed some combination of fused, tripolar and parallel spindle arrangements as well as the normal tetrahedral orientation of second division poles. The absence of one or more of these abnormal configurations was notable and genotype specific. Parallel but unfused spindles could be readily identified in microsporocytes of 148-17 and 127-14; in 154-1, however, parallel spindles were indistinct from fused spindles.

All genotypes were highly variable with respect to expression of BP (Table 2), with 115-1 showing the least and 126-1 showing the most variability. Significant (> 5%) as well as nonsignificant (< 5%) frequencies of unreduced gametes were found for each genotype over the range of environments tested. Both plants of the same genotype generally responded to each environment with a similar expression of BP, e.g. in E2, both plants of genotype 127-14 expressed a low percentage of BP at the initial flowering period and a higher percentage at the second flowering period (Table 2). Bud-to-bud variability was high for a given genotype, flowering time, and environment, particularly when the mean frequency of BP was greater than 10%.

Table 1. Pedigree and cytological observations of the seven clones of *Solanum phureja* used in the study

Clone no.	Pedigree	Meiotic configurations[a]	Functional 2n pollen?[b]
115–1	147–6 X 153–4	ps, fs, ts, nm	?
126–1	154–1 X 155–12	ps, fs, ts, nm	no
127–14	154–1 X 160–6	ps, fs, nm	yes
128–26	154–1 X 165–15	ps, fs, ts, nm	?
136–1	162–1 X 160–7	ps, fs, nm	?
148–17	PI 225669 OP[c]	ps, fs, ts, nm	yes
154–1	PI 225682 OP	fs, nm	yes

[a] ps = parallel spindles at the second meiotic division; fs = fused spindles at the second meiotic division; ts = tripolar spindles at the second meiotic division; nm = normal meiosis

[b] Determined by seed set and the generation of 4x hybrids in crosses with 4x potato cultivars; ? = insufficient pollinations for unambiguous interpretation

[c] Open pollinated by *S. phureja* and *S. stenotomum* plant introductions

Table 2. Mean big pollen percentages (3 buds/mean), standard errors and ranges for individual buds of five clones of *S. phureja* growing in three environments at two flowering times. The original BP estimates made from 3 buds/plant grown in Becker, MN in 1977 are also given

Genotype	Environment[a]	Early flowering[b] Plant 1 $\bar{x}$ ± S.E.	Early flowering[b] Plant 2 $\bar{x}$ ± S.E.	Late flowering[b] Plant 1 $\bar{x}$ ± S.E.	Late flowering[b] Plant 2 $\bar{x}$ ± S.E.	Range	Original estimates, Becker 1977
	E_1	1.2 ± 1.1	5.0 ± 6.0	3.7 ± 3.2	6.0 ± 4.1		
115–1	E_2	1.3 ± 0.8	3.3 ± 2.8	3.8 ± 0.9	2.8 ± 0.7	0–12.1	26.3 ± 5.1
	E_3	2.0 ± 1.4	3.3 ± 1.3	7.0 ± 1.5	2.7 ± 4.1		
	E_1	60.1 ± 18.4	37.9 ± 9.4	51.9 ± 10.2	22.5 ± 18.4		
126–1	E_2	2.4 ± 2.4	1.9 ± 2.8	M[c]	31.5 ± 4.6	0–76.1	27.4 ± 15.2
	E_3	2.3 ± 1.6	1.2 ± 1.7	1.0 ± 0.6	0.2 ± 0.3		
	E_1	1.7 ± 1.9	0.0 ± 0.0	1.5 ± 1.5	2.2 ± 3.1		
127–14	E_2	1.6 ± 0.5	3.9 ± 3.1	10.1 ± 6.8	36.2 ± 1.3	0–37.7	12.8 ± 13.9
	E_3	3.7 ± 3.0	12.2 ± 10.8	11.2 ± 3.7	7.5 ± 6.8		
	E_1	2.3 ± 1.2	4.1 ± 0.9	12.2 ± 7.7	17.0 ± 3.1		
128–26	E_2	23.6 ± 17.9	12.4 ± 11.1	8.2 ± 4.8	20.3 ± 5.0	0.9–43.3	20.0 ± 14.0
	E_3	4.3 ± 1.3	1.9 ± 1.7	4.2 ± 2.2	6.8 ± 3.6		
	E_1	0.8 ± 1.0	1.6 ± 1.6	1.1 ± 1.2	1.7 ± 0.9		
136–1	E_2	1.5 ± 0.7	0.3 ± 0.6	0.5 ± 0.5	2.6 ± 0.9	0–13.2	15.7 ± 13.7
	E_3	2.0 ± 1.1	0.6 ± 1.0	7.0 ± 2.8	9.3 ± 2.8		

[a] E_1 = cool growth chamber, 7.2–13.3°C; E_2 = warm growth chamber, 12.2–17.2°C; E_3 = field, St. Paul, 1978
[b] Early = first flowers on each plant; late = flowers in bloom 10–20 days later
[c] Missing plot

Table 3. Analysis of variance for percent unreduced gametes of five clones of *S. phureja*, growing in three environments, with pollen collections made at two flowering times

Source	d.f.	SS	MS	F
Environment (E)	2	1554.5	777.2	4.9*
Blocks/E	3	757.7	252.6	
Genotype (G)	4	5505.3	1376.3	8.7**
E × G	8	12039.0	1504.8	9.5**
Flowering time (F)	1	448.4	448.4	2.8
F × E	2	290.5	145.2	0.9
F × G	4	258.0	64.5	0.4
F × G × E	8	1948.7	243.6	1.5
Experimental error	27	4283.8	158.7	
Sampling error	120	3691.8	30.8	

* Significant at 5%
**Significant at 1%

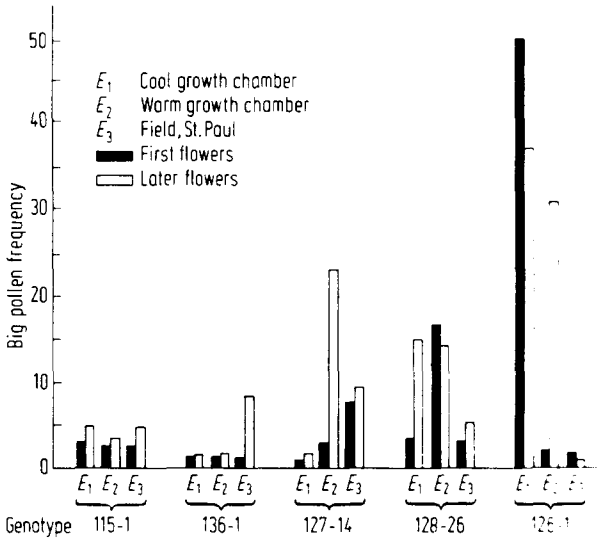

Fig. 1. Mean frequency of big pollen for five genotypes of *Solanum phureja* in three environments at two flowering periods

Analysis of variance revealed significant main effects for genotype (G) and environment (E) as well as a highly significant G × E interaction (Table 3). Frequency of unreduced gametes was lowest (mean = 4.5% over all genotypes) under field conditions and highest (mean = 11.7% over all genotypes) in the cool growth chamber; however, the G × E interaction prevents generalization about the effect of these environments across genotypes.

Although analysis of variance did not reveal flowering time as a significant effect, a trend toward higher BP frequency later in the flowering period was apparent for several combinations of genotype and environment (126-1, E2; 127-14, E2; 128-26, E1; 136-1, E3) (Table 2, Fig. 1). Mean percentage of BP over all genotypes and environments was 6.6% for the first flowers and 10.5% for the later flowers. Specific plants which did not exhibit this

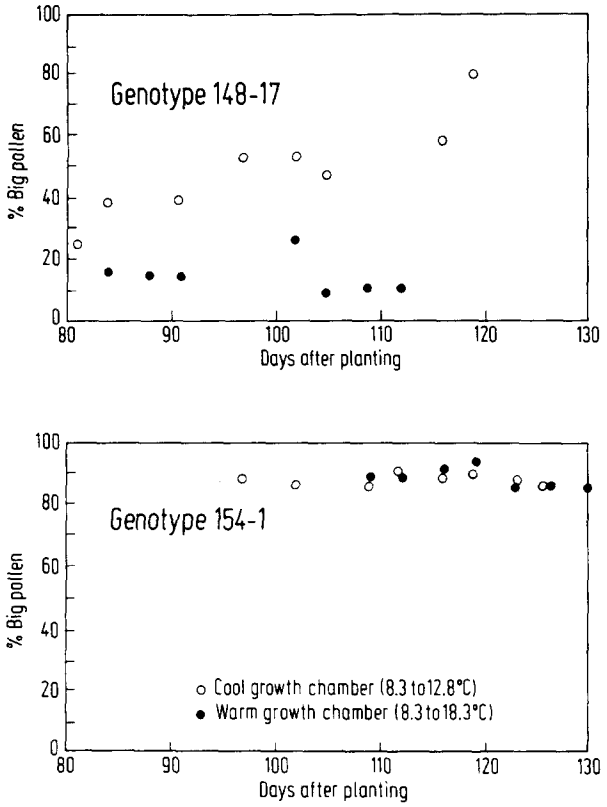

Fig. 2. Frequency of big pollen over time in cool (8.3-12.8°C) and warm (8.3-18.3°C) growth chambers for genotypes 148-17 and 154-1 (*Solanum phureja*)

trend (126-1, E1) were observed to have sufficiently large standard errors such that discrimination between the two flowering periods was not possible. BP estimates for buds of the parent clones grown at Becker in 1977 were typically higher than those for any of the environments studied in 1978.

The second study again revealed genotype-specific patterns of expression of unreduced gametes over time in different environments. Genotype 154-1 was found to have a high constant expression (approximately 90%) of BP in both environments throughout the flowering period (Fig. 2). However, genotype 148-17 was found to gradually increase in expression of BP over time in the cool chamber, but to maintain a considerably lower constant expression of BP throughout the flowering period in the warm chamber (Fig. 2).

Discussion

No one set of environmental conditions, apart from the 1977 field conditions at Becker, induced a high frequency of unreduced gametes in all five genotypes in the first study, despite the occurrence of similar cytogenetic abnormalities in these genotypes. Many tetraploid potato cultivars express some level of dyads or BP, resulting from the same mechanisms found in diploid *Solanum* species, i.e. formation of restitution nuclei after the first meiotic division or fused spindles at the second meiotic division (Ellison 1936; Fukuda 1927; Stow 1926, 1927). Longley and Clark (1930) reported that the frequency of dyads in the same potato cultivars differed over two years of observation. They suggested that the higher frequencies in one year may have been caused by soil moisture deficit, the most apparent climatic difference between the two growing seasons. Our experience with *S. phureja* would not confirm this because the plants in which the highest frequencies were found were grown under irrigation and would have been expected to encounter little soil moisture deficit.

Our observation that plants of the same genotype respond similarly to each environment, with respect to expression of BP at a given flowering time, leads us to conclude that selection for individuals which express a high level of unreduced gametes within the same clone, as suggested by Jacobsen (1976), would be futile. The observed increase in expression of unreduced gametes as plants mature is in agreement with Ramanna (1974). The process appears to be a function of physiological rather than environmental factors, because of the stable environmental conditions provided by the growth chambers throughout the flowering period.

The identification of specific environmental components which influence BP expression is not possible, both because of the large G x E interaction and because of several uncontrolled environmental factors among our treatments. The temperature regimes employed were not as extreme as those of others working with the effects of temperature on meiotic processes; attempts to induce flowering on plants of *S. phureja* in a growth chamber with mean temperature greater than 22°C were unsuccessful.

Mok and Peloquin (1975b) have provided genetic evidence in the form of segregation ratios from test crosses among genotypes with various mechanisms leading to the formation of unreduced gametes to demonstrate that these cytological phenomena in diploid potatoes are governed by several distinct recessive genes. The observation of such segregation patterns depends upon the selection of some 'significant' level of BP expression around which gene presence or absence is decided. Neither the 3% level of Mok and Peloquin (1975b) and den Nijs and Peloquin (1977) nor the 5% level of Quinn et al. (1974) would have provided the same phenotypic classification of our five genotypes over all three environments.

During our initial screening for unreduced gametes in hundreds of genotypes of the diploid species, *S. phureja*, it was observed that occasional unreduced pollen grains could be found in most genotypes, the majority of which have never been observed to express a frequency greater

than 5%. The present study clearly indicates that even those genotypes which do express a significant frequency of unreduced gametes, do so only in some environments. Alternative genetic explanations to the single recessive mutation hypothesis appear to be viable.

A genetic hypothesis that we favor is that parallel or fused spindles at the homotypic division of meiosis are due to an incompletely penetrant dominant gene with variable expressivity. The gene product is possibly essential to the normal progress of microsporogenesis and cytokinesis. Certain microenvironmental influences on developing pollen mother cells, perhaps by causing premature or delayed induction of a key enzyme, result in the abnormal phenotype. The environment of the whole plant may generally affect microsporogenesis, but the intralocular microenvironment determines the fate of individual microsporocytes. This hypothesis can accomodate the occurrence of occasional unreduced gametes in genotypes which have mostly reduced gametes as well as the variable nature of genotypes with significant but inconsistent expression of unreduced gametes. We hope to provide anatomical and cytogenetic evidence for this hypothesis in a future publication.

Parallel, tripolar, and fused homotypic spindles can be regarded as various phenotypic manifestations of the same gene. Alternatively, these various configurations may be similar but genetically distinct cytogenetic events, each dependent on a separate locus. Genotype 154-1, the most consistent with respect to expression of BP, was also found to have the least variable cytogenetic mechanism underlying this trait, i.e. only fused second division spindles. This could be interpreted to mean that fs is the most intense expression of the same gene that induces parallel and tripolar homotypic spindles.

That three progeny of 154-1 (Table 1) were found to be more variable with respect to both spindle arrangements and BP frequencies, lends some credence to this hypothesis. On the other hand, genetic contribution from the male parents may have been responsible for the appearance of tripolar and parallel spindles. Further elucidation of the relationship, if any, between spindle arrangements and intensity of expression of unreduced gametes must await progeny testing of hybrids between known genotypes.

Acknowledgement

This project was partially supported by a research grant from the Red River Valley Potato Growers Association and the University of Minnesota Computer Center. The authors wish to thank Drs. Peter D. Ascher, Iris D. Charvat and Ronald L. Phillips for critical review of the manuscript.

Literature

Belling, J. (1925): The origin of chromosomal mutations in *Uvularia*. J. Genet. 15, 245-266

Bergner, A.D.; Cartledge, J.L.; Blakeslee, A.F. (1934): Chromosome behavior due to a gene which prevents metaphase pairing in *Datura*. Cytologia 6, 19-37

Chavez, R.S.; de Sosa, M.H. (1971): Use of dihaploids in the breeding of *Solanum tuberosum* L. I. Cytological considerations. Hereditas 69, 83-100

Darlington, C.D. (1930): Studies in *Prunus*, III. J. Genet. 22, 65-93

de Mol, W.E. (1929): The originating of diploid and tetraploid pollen grains in Duc van Thol tulips (*Tulipa suaveolens*) dependent on the method of culture applied. Genetica 11, 119-212

den Nijs, T.P.; Peloquin, S.J. (1977): 2N gametes in potato species and their function in sexual polyploidization. Euphytica 26, 585-600

Dowrick, G.J. (1953): The chromosomes of *Chrysanthemum*, III: meiosis in *C. atratum*. Heredity 7, 219-226

Eenink, A.H. (1975): Matromorphy in *Brassica oleracea* L. VII. research on products of microsporogenesis and gametogenesis from prickle pollinated plants. Euphytica 24, 45-52

Ellison, W. (1936): Meiosis and fertility in certain British varieties of the cultivated potato (*Solanum tuberosum* L.). Genetica 18, 217-254

Fukuda, Y. (1927): Cytological studies on the development of the pollen grain in different races of *Solanum tuberosum* L., with special reference to sterility. Bot. Mag. 41, 459-474

Fukushima, E. (1930): Formation of diploid and tetraploid gametes in *Brassica*. Jpn. J. Bot. 5, 273-284

Giles, N. (1939): The effect of dehydration on microsporogenesis in *Tradescantia*. Amer. J. Bot. 26, 334-338

Harlan, J.R.; deWet, J.M.J. (1975): On Ö Winge and a prayer: the origins of polyploidy. Bot. Rev. 41, 361-390

Jacobsen, E. (1976): Cytological studies on diplandroid production in a dihaploid potato clone and its correlation with seed set in 4x × 2x crosses. Z. pflanzenzücht. 77, 10-15

Jain, H.K. (1962): Breakdown of division cycle and organisation of atypical spindles in fused pollen mother cells of *Lolium*. Chromosoma 12, 812-818

Karpechenko, G.D. (1927): The production of polyploid gametes in hybrids. Hereditas 9, 348-368

Kostoff, D.; Kendall, J. (1929): Irregular meiosis in *Lycium halimifolium* Mill. produced by gall mites (*Eriophyes*). J. Genet. 21, 113-115

Lebedeff, G.A. (1940): Failure of cytokinesis during microsporogenesis in *Zea mays* following heat treatment. Cytologia 10, 434-442

Lewis, D. (1943): The incompatibility sieve for producing polyploids. J. Genet. 45, 261-264

Longley, A.E.; Clark, C.F. (1930): Chromosome behavior and pollen production in the potato. J. Agric. Res. 41, 867-888

Lutkov, A.N. (1937): On the artificial induction of polyploid gametes by treatment with low temperature and chloroform. Trudy po prikladnoi botanike genetike i selektsii 7, 127-150

Matsuda, H. (1936): The effect of abnormal temperature upon the pollen formation of *Petunia*. Tokyo Daigaku Nogakabu. J. Coll. Agric. 14, 71-92

Mok, D.W.S.; Peloquin, S.J. (1975a): Three mechanisms of 2n pollen formation in diploid potatoes. Can. J. Genet. Cytol. 17, 217-225

Mok, D.W.S.; Peloquin, S.J. (1975b): The inheritance of three

mechanisims of diplandroid (2n pollen) formation in diploid potatoes. Heredity 35, 295-302

Okuno, S. (1951): Cytological studies on potatoes, with some remarks on genetical experiments. Part. 1. Jpn. J. Genet. 26, 79-103

Okuno, S. (1952): Cytological studies on potatoes, with some remarks on genetical experiments. Part II. Jpn. J. Genet. 27, 3-21

Quinn, A.A.; Mok, D.W.S.; Peloquin, S.J. (1974): Distribution and significance of diplandroids among the diploid *Solanums*. Amer. Potato J. 51, 16-21

Ramanna, M.S. (1974): The origin of unreduced microspores due to aberrant cytokinesis in the meiocytes of potato and its genetic significance. Euphytica 23, 20-30

Sakamura, T.; Stow, I. (1926): Über die experimentelle veranlasste Entstehung vom keimfähigen Pollenkörnern mit abweichenden Chromosomenzahlen. Jpn. J. Bot. 3, 111-139

Satina, S.; Blakeslee, A.F. (1935): Cytological effects of a gene in *Datura* which causes dyad formation in sporogenesis. Bot. Gaz. 96, 521-532

Sax, K. (1936): The experimental production of polyploidy. J. Arnold Arboretum. Harvard Univ. 17, 153-159

Sax, K. (1937): Effect of variations in temperature on nuclear and cell division in *Tradescantia*. Amer. J. Bot. 24, 218-225

Skiebe, K. (1969): Untersuchungen über das Auftreten von unreduzierten Gameten. Biol. Zbl. 88, 47-60

Skiebe, K. (1972): Der Einfluss eines Allelunterschiedes auf das Auftreten unreduzierter Gameten. Biol. Zbl. 91, 111-119

Stow, I. (1926-27): A cytological study on pollen sterility in *Solanum tuberosum* L. Jpn. J. Bot. 3, 217-238

Vorsa, N.; Bingham, E.T. (1979): Cytology of 2n pollen formation in diploid alfalfa, *Medicago sativa*. Can. J. Genet. Cytol. 21, 525-530

Wagenaar, E.B. (1968a): Meiotic restitution and the origin of polyploidy. I. Influence of genotype on polyploid seedset in a *Triticum crassum* × *T. turgidum* hybrid. Can. J. Genet. Cytol. 9, 836-843

Wagenaar, E.B. (1968b): Meiotic restitution and the origin of polyploidy. II. Prolonged duration of metaphase I as causal factor of restitution induction. Can. J. Genet. Cytol. 10, 844-852

Woodworth, R.H. (1929): Cytological studies in the Betulaceae. I. *Betula*. Bot. Gaz. 87, 331-363

Received July 25, 1980
Accepted September 4, 1980
Communicated by R. Hagemann

Richard E. Veilleux
Prof. Florian I. Lauer
Department of Horticultural Science
and Landscape Architecture
University of Minnesota
St. Paul, Minn. 55108 (USA)