

DISTRIBUTION AND SIGNIFICANCE OF DIPLANDROIDS AMONG THE DIPLOID SOLANUMS¹

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ABSTRACT

Clones of several diploid species capable of generating diplandroids (2n pollen) were identified by screening for the occurrence of 2n pollen. Diplandroid production was detected in *Solanum bukasovi*, *S. canasense*, *S. cardiophyllum*, *S. chacoense*, *S. leptostigma*, *S. megistacrolobum*, *S. tarijense*, *S. tuberosum* Group Phureja and Group Stenotomum. Parallel spindles at Ana II was the mechanism producing 2n pollen in *S. chacoense*, Group Phureja, and Group Stenotomum. The widespread distribution both taxonomically and geographically suggests a possible role for diplandroids in evolution. It also encourages exploration of a proposed breeding method in which tetraploids are generated from 2x x 2x matings.

INTRODUCTION

Many high yielding tetraploid families and clones have resulted from matings between 4x cultivars and 2x Group Phureja-haploid Group Tuberosum hybrids (3, 6). Similarly, high yielding tetraploids have been derived from 2x x 2x crosses (6, 7). Tetraploid progeny in both examples were the result of the functioning of either a 2n egg (diplogynoid) or 2n sperm (diplandroid) in the 2x parents. The highest yielding tetraploids were the result of the functioning of 2n sperm generated by a first division restitution mechanism.

Tetraploid-diploid intermatings in potato have been shown to be inefficient, resulting in about two seeds per fruit (2, 4). Exceptions reported by Hanneman (4) were three high seed set pollinators each producing greater than 20 seeds/fruit. Subsequent study showed these to produce diplandroids by first division restitution effected by parallel spindles at Ana II (8, 11). The frequency of parallel spindles was found highly correlated to the percentage of 2n pollen. A high correlation of dyads to 2n pollen was also found for two second division restitution mechanisms (8).

This study was undertaken to ascertain the occurrence and taxonomic distribution of 2n pollen in the diploid tuber-bearing Solanums, to relate such occurrence to efficiency of 4x - 2x hybridization, and ultimately to identify new sources of diplandroids, especially those produced by parallel spindles.

MATERIALS AND METHODS

Diploid populations screened were: (i) 46 of about 100 species-haploid n and 2n pollen grains (Fig. 1). The average size of n pollen grains for

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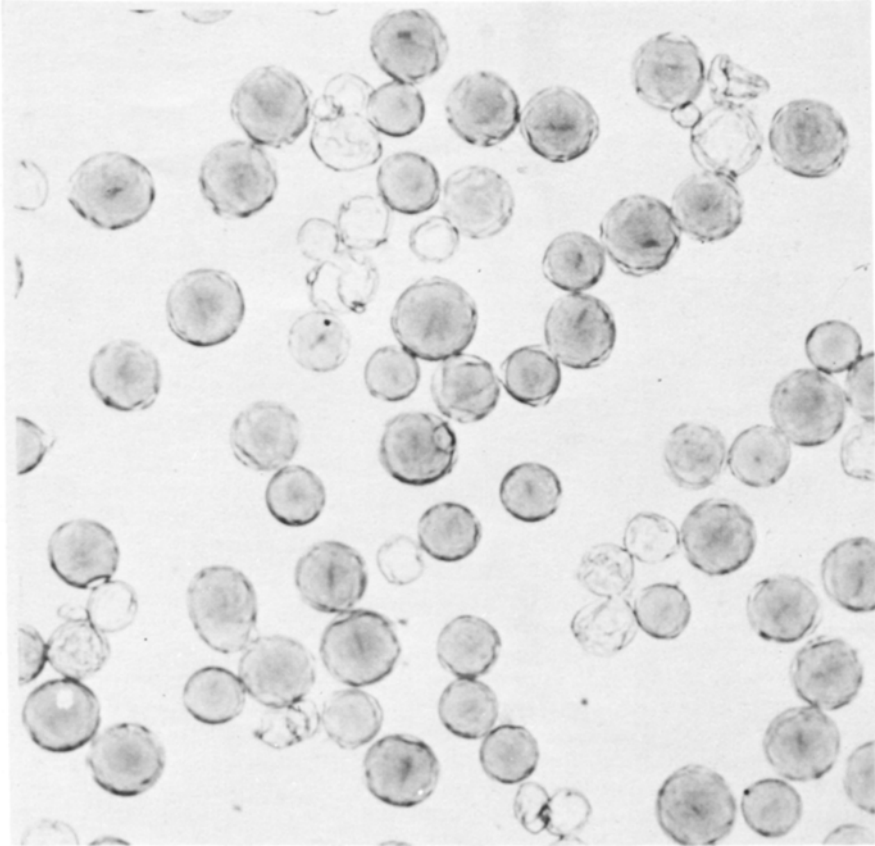


FIG. 1.—Pollen from W5295.7 illustrating the size difference between n and $2n$ pollen grains.

each clone was determined; corresponding values were obtained for $2n$ pollen grains. These averages ranged between 18 and 23 microns and 26 and 33 microns, respectively. The pollen size distribution was bimodal in each clone tested. Open flowers of suspect diploids were field collected into coin envelopes. Following transportation to a laboratory, pollen was vibrated onto glass slides, stained with carmin or iodine, and observed at 100x magnification. The frequency of $2n$ pollen was subjectively estimated using increments of five percent, with a minimum of five percent $2n$ pollen considered significant. Pollen from hundreds of plants could be screened in a day.

Diploid populations screened were: (i) 46 of about 100 species-haploid hybrids utilized by Hanneman (4) in $4x \times 2x$ matings. These were examined to compare the effectiveness of pollen screening versus inter-ploid hybridization for identification of diplandroid producers; (ii) approximately 500 clones representing intercrosses of species-haploid hybrids maintained in 1971 at the University of Wisconsin Potato Research Farm

at Rhinelander, Wisconsin. Most of the hybrids were derived from *S. tuberosum* Group Phureja introductions crossed to Group Tuberosum haploids, although *S. chacoense* and *S. tuberosum* Group Stenotomum and its subspecies *goniocalyx* were in the heritage of some clones; (iii) approximately 500 clones grown at Sturgeon Bay in 1972 which included bulk populations of *S. chacoense* x haploid Group Tuberosum, Group Stenotomum x haploid Group Tuberosum, and bulked Group Stenotomum introductions (9); and (iv) the 1972 seed increase at the IR-1 (Inter-regional Potato Introduction Project) at Sturgeon Bay, Wisconsin, including 1500 clones from 120 introductions involving 34 diploid species within 5 taxonomic series. Thus, the distribution of 2n pollen within diploid species could be assayed.

Plants with 2n pollen were crossed to tetraploids for evaluation of hybridization efficiency as measured in seeds/fruit. In addition, some of the diplandroid producing clones were examined cytologically to determine the mechanism of 2n pollen formation.

RESULTS

A significant level of 2n pollen was found in 1971 for 7 of the 46 diploid clones that were tested in 1967 by Hanneman (4) for the ability to hybridize with tetraploids. Six of these had produced relatively high seed set (5 to 49 seeds/fruit) in 1967. Conversely, for the remaining 39 not showing a significant amount of 2n pollen, only two had given five and seven seeds/fruit in crosses with tetraploids.

The results of 4x x 2x crosses with 22 Group Phureja-haploid hybrids in 1971 and 14 selections from either Group Stenotomum-haploid hybrids, *S. chacoense*-haploid hybrids or bulked Group Stenotomum in 1972 are presented in Table 1. All 36 had demonstrated at least 5% 2n pollen. Twenty-three also produced greater than five seeds/fruit, with seeds per fruit highly correlated to 2n pollen both in 1971 ($r = .61^{**}$) and 1972 ($r = .62^*$). However, 13 clones shown in Table 1 did not hybridize well with tetraploids (less than five seeds/fruit), indicating blocks to hybridization not circumvented by the production of 2n pollen. Regardless, all evidence indicates that pollen screening can identify diplandroid producers as effectively as interplod crossing, but with far less labor and expense.

The taxonomic distribution and frequency of diplandroid producing clones among the diploid species screened in 1972 is presented in Table 2. Diplandroid producers were found in 19 of 90 total introductions, but in only 1.3% of all clones. This is not surprising as all known mechanisms of 2n gamete formation seem to be determined by recessive genes (8). The origin and geographic distribution of diplandroid producers is shown in Table 3. Four series are represented with introductions from Mexico to Argentina. The occurrence of diplandroids seems to be wide-spread and fairly frequent.

S. tuberosum Group Phureja appears to be a prolific diplandroid source, as 5 introductions and 8 of 44 clones screened yielded greater than 5% 2n pollen (Table 2). Group Stenotomum must also be a productive diplandroid source, since screening results from 54 bulked Group Stenotomum clones showed three with at least 5% 2n pollen (BP 7.12, 7.28 and 7.51), as well as four more (BP 25.2, 25.44, 25.66 and 140.90) found within 85 F₁ hybrids from crosses of Group Stenotomum x haploid Group Tuberosum (Table 1).

TABLE 1.—*Comparison of estimated 2n pollen and seeds/fruit in 4x x 2x matings.*

1971			1972			
Ident. No.	Estimated % 2n pollen	Seeds/fruit	Ident. No.	Source population	Estimated % 2n pollen	Seeds/fruit
W5337.3	15	10.8	BP141.42*	stn x tbr	30	4.8
W5295.7	40	20.4	BP141.71	stn x tbr	20	0.0
W1570.1	10	2.0	BP141.165	stn x tbr	15	2.7
W1587.1	35	37.4	BP 25.2	stn x tbr	25	45.2
W1589.3	30	11.0	BP 25.44	stn x tbr	15	78.7
W1607.2	5	1.0	BP 25.66	stn x tbr	5	2.8
W1627.1	5	.5	BP140.90	tbr x stn	5	4.3
W1693.1	20	.4	BP 7.12	stn	10	18.2
W1731.8	5	2.0	BP 7.28	stn	5	6.2
W1754.3	20	1.5	BP 7.51	stn	5	7.1
W1755.4	10	2.0	BP136.3	tbr x chc	20	18.5
W1777.1	60	55.7	BP136.20	tbr x chc	10	17.0
W1777.2	5	2.0	BP136.87	tbr x chc	30	37.2
W1777.4	40	62.0	BP136.104	tbr x chc	50	82.4
W1780.4	25	55.0				
W1780.5	40	12.4		Average	17.5	23.2
W1781.3	60	8.3				
W1783.4	15	5.5				
W1788.1	20	9.1				
W1798.1	40	20.6				
W1806.3	10	7.6				
W9013.1	5	8.0				
Average	23.4	15.2				

*BP numbers refer to bulk populations maintained at the Interregional Potato Introduction Project, Sturgeon Bay.

Cytological examination of some of the 2n pollen sources revealed that clone .9 of Phureja P.I. 243465 exhibited parallel spindles at Ana II, as did both clones of *S. chacoense*, P.I. 230580. Prior investigation has shown that four Phureja-haploid Tuberosum F₁ hybrids, W5288.2, W5293.3, W5295.7 and W5337.3 also demonstrated parallel spindles (8). As homozygous recessive genotype ps/ps determines this condition, their Phureja parents from P.I.'s 225683, 225696, 243462 and 225710 must have been at least heterozygous for this gene. Two selections involving Group Stenotomum, BP 7.12 and F₁ hybrid BP 25.44 (Table 1), also displayed parallel spindles.

DISCUSSION

The widespread occurrence of diploids capable of producing 2n pollen and concurrent demonstration that such 2n pollen producers usually hybridize well with tetraploid cultivars offers new breeding approaches and implies new revolutionary pathways.

Many 2n gamete producing diploids have proved to be good parents when crossed to 4x cultivars. Diploids that form diplandroids via parallel

TABLE 2.—*Taxonomic distribution and frequency of diplandroid producing clones among diploid species screened.*

Species	Number of introductions	Number of clones	Number of introductions having clones with 5% 2n pollen	Number of clones with 5% 2n pollen	Percent of clones with 5% 2n pollen
<i>Series Commersoniana</i>					
chacoense	6	100	1	2	2.0%
tarijense	10	176	3	3	1.7%
<i>Series Cuncoalata</i>					
infundibuliforme	14	232	0	0	0.0%
<i>Series Megistacroloba</i>					
megistacrolobum	11	205	1	3	1.5%
raphanifolium	4	45	0	0	0.0%
<i>Series Pinnatisecta</i>					
cardiophyllum	4	55	1	1	1.8%
<i>Series Tuberosa</i>					
bukasovii	4	76	1	1	1.3%
canasense	8	142	1	2	1.4%
kurtzianum	4	80	0	0	0.0%
microdontum	4	63	0	0	0.0%
Group Phureja	5	44	5	8	18.2%
sparsipilum	3	39	0	0	0.0%
spgazzinii	11	193	0	0	0.0%
vernei	2	39	0	0	0.0%
Totals	90	1489	13	19
Average	1.3%

*Data from species with at least two introductions and at least 30 clones.

TABLE 3.—*Origin of diplandroid producing introductions of diploid species.*

Species	Source	No. diplandroid forming clones	Series	Origin
<i>S. bukasovi</i>	Haw 5233	1	Tuberosa	Argentina
<i>S. canasense</i>	Haw 5074	2	Tuberosa	Argentina
<i>S. cardiophyllum</i>	283062*	1	Pinnatisecta	Mexico
<i>S. chacoense</i>	230580	2	Commersoniana	Argentina
<i>S. leptostigma</i>	Haw 5027	1	Tuberosa	Argentina
<i>S. megistacrolobum</i>	Oka 4024	3	Megistacroloba	Argentina
Group Phureja	225683	2	Tuberosa	Columbia
Group Phureja	225705	2	Tuberosa	Columbia
Group Phureja	225710	1	Tuberosa	Columbia
Group Phureja	243465	1	Tuberosa	Columbia
Group Phureja	283113	2	Tuberosa	Columbia
Group Stenotomum	BP 7.12	3	Tuberosa	Peru
<i>S. tarijense</i>	Hof 1713	1	Commersoniana	Argentina
<i>S. tarijense</i>	Hof 1717	1	Commersoniana	Argentina
<i>S. tarijense</i>	Hof 1892	1	Commersoniana	Argentina

*P.I. numbers.

spindles, a genetic first division restitution mechanism, create especially high yielding progeny (3, 6). Often whole families outyield their highest parent. In addition, diplandroids and diplogynoids are valuable for transfer of disease resistance into tetraploid cultivars (1, 10). It seems logical to seek and create diploid parents that are capable of efficient hybridization to tetraploids and that possess desirable yield and other characteristics.

It is also feasible to generate tetraploids from matings between 2n gamete producing diploids. Tetraploids from interdiploid matings of Phureja-haploid hybrids have been shown to outyield their diploid "full-sibs" by 50% (6). The broad distribution and simple identification of diplandroid producing clones should facilitate a breeding method proposed by Peloquin and Mendiburu (7) to take maximum advantage of the genetic diversity within the *Solanums*. Tetraploids would be produced from matings of (hybrid Group Tuberosum haploids x *S. chacoense*) with (hybrid Group Phureja x Group Tuberosum haploids). Desirable clones of Group Stenotomum and haploids of Group Tuberosum ssp. *andigena* could also be utilized.

The widespread occurrence and high frequency of diplandroids in *S. tuberosum* Groups Phureja and Stenotomum, as well as evidence of diplogynoids in Phureja-haploid hybrids (4) suggests a role for 2n gametes in the evolution of cultivated tetraploid *Solanums*. Furthermore, the diplandroids identified in *S. chacoense* and *S. cardiophyllum* can explain the existence of naturally occurring triploids found within these species.

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