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D. S. Douches · D. L. Maas

Comparison of FDR- and SDR-derived tetraploid progeny from $2x \times 4x$ crosses using haploids of *Solanum tuberosum* L. that produce mixed modes of 2n eggs

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Abstract The relationship between heterozygosity and heterosis in tetraploid potato (*Solanum tuberosum* subsp. *tuberosum* L., $2n = 4x = 48$) was examined in a series of first-division restitution (FDR)- and second-division restitution (SDR)-derived tetraploid subpopulations. The subpopulations were constructed using two 2n egg-producing, mixed-mode haploids ($2n = 2x = 24$) crossed to three tetraploid ($2x = 4x = 48$) potato clones. Half-tetrad analysis using a co-dominant electrophoretic marker (*Pgm-2*), which is closely linked to the centromere, discriminated between FDR- and SDR-derived 4*x* progeny. The FDR:SDR ratio of the 4*x* progeny observed was dependent upon the haploid parent used in the $2x \times 4x$ cross. Field studies were conducted between 1992 and 1996 to compare the yield and specific gravity of the two subpopulations and their parents from three crosses. There was no difference in the total tuber yield or specific gravity between the FDR- and SDR-subpopulations based upon family means, despite the expectation that FDR-derived progeny would transmit a greater portion of the genome's heterozygosity intact than SDR-derived progeny. The 4*x* parent in each family had a higher yield than either 4*x* progeny subpopulation. Inbreeding, as a consequence of the haploidization process and a lack of genetic diversity, may have negated any advantage of the FDR-derived progenies over the SDR-derived progenies.

Key words Potato · Unreduced gametes · Megasporogenesis · Heterozygosity

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D. S. Douches (✉) · D. L. Maas
Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824-1325, USA
Tel.: +1 517-355-6887
Fax: +1 517-353-5174
E-mail: douchesd@pilot.msu.edu

Introduction

Bingham (1980) reviewed the relationship between maximum yield and maximum heterozygosity in autopolyploids and has advocated polyploid breeding schemes which maximize the transmission of heterozygosity. Numerous studies have been conducted (reviewed by Bingham et al. 1994) to understand the relationship between heterozygosity and yield in the cultivated potato (*Solanum tuberosum* L., $2n = 4x = 48$) and other polyploid crops.

The discovery that 2*x* potatoes can produce 2n gametes has led to various breeding schemes to synthesize highly heterozygous 4*x* clones through interploidy crosses (i.e. 4*x*-2*x*, and $2x \times 2x$). These breeding methods attempt to capture valuable traits from related species, while concurrently broadening the genetic base of the tetraploid potato. Several meiotic mutants leading to 2n pollen and eggs have been identified in potato (Mok and Peloquin 1975 b; Iwanaga and Peloquin 1979; Stelly and Peloquin 1986; Werner and Peloquin 1987; Douches and Quiros 1988). These 2n gametes are formed by mechanisms genetically equivalent to either first-division restitution (FDR) or second-division restitution (SDR) of meiosis.

The breeding value of both types of 2n gametes have been examined in interploidy crosses (4*x*-2*x* and $2x \times 2x$) in potato (Mok and Peloquin 1975a; Mendiburu and Peloquin 1977 a; Peloquin et al. 1989; Darmo and Peloquin 1990, 1991; Concillo and Peloquin 1991; Ortiz and Peloquin 1991; Ortiz et al. 1991). These studies have concluded that the breeding value of FDR 2n gametes, derived from either haploids of *S. tuberosum* or haploid-species hybrids, is superior to that of SDR 2n gametes when yield performance is measured in the tetraploid progeny of 4*x*-2*x* crosses (Chujoy and Peloquin 1986; Mendiburu and Peloquin 1977a, b; Darmo and Peloquin 1990, 1991; Concillo and Peloquin 1991; Oriz and Peloquin 1991; Oritz et al.

1991; Werner and Peloquin 1991a, b). Heterotic responses from 4*x*-2*x* (FDR) matings have shown progeny yields that surpass mid-parent values and 4*x* cultivars in yield trials. Increased yield production of the 4*x* × 2*x* populations was attributed to the high level of heterozygosity transmitted (80%) through FDR pollen. In contrast, Mendiburu and Peloquin (1977 a), attributed the lower yield of progeny derived from 2*x* × 4*x* crosses to the SDR-type of 2n egg formation which theoretically transmits only 40% of the 2*x* parent's heterozygosity to the 4*x* progeny.

Werner and Peloquin (1990) cytologically identified a number of *S. tuberosum* haploids ($2n = 2x = 24$) which produced both FDR and SDR 2n eggs (mixed-mode haploids). Half-tetrad analysis (HTA) separated the FDR- and SDR-derived 4*x* progeny from the 2*x*-4*x* crosses (Werner et al. 1991). The occurrence of mixed-mode haploids, combined with the use of HTA, created an ideal situation for an unbiased comparison of the breeding value of both FDR and SDR 2n gametes. In the previous 4*x*-2*x* studies described above, estimates of the breeding values of FDR and SDR 2n gametes have been confounded by the genotype of the 2*x* parents used in the 4*x*-2*x* crosses. When mixed-mode diploid parents are used, the 4*x* progeny obtained from 2*x*(FDR) × 4*x* and 2*x*(SDR) × 4*x* crosses are generated from the same genotypes. Therefore, the differences detected between 4*x* progeny from such a cross could be attributed to the differences in the transmission of heterozygosity through 2n gametes.

Our goal is to understand the importance of heterozygosity to the genetic improvement of potato. In the present study, we used mixed-mode haploids producing 2n eggs to generate 4*x* populations through 2*x* × 4*x* crosses; employed HTA to discriminate between FDR- and SDR-derived 4*x* progeny; and compared the breeding value of FDR- and SDR-derived tetraploid progeny.

Materials and methods

Plant materials

Eight haploids ($2n = 2x = 24$), derived from *S. tuberosum*, previously identified as mixed-mode 2n egg-producing and heterozygous for *Pgm-2*, were kindly provided by Drs. J. Werner and S. Peloquin (University of Wisconsin, Madison). The haploids 4182-T and H175 (both white-skinned tubers), derived from WisAg231 and 'Redsen', respectively, were fertile and gave good seed set in 2*x* × 4*x* crosses. Tetraploid clones of 'Yukon Gold', Lemhi Russet, Ranger Russet and breeding lines NDD277-2 and ND860-2, homozygous for *Pgm-2*, were obtained from the Michigan State University potato breeding program.

Isozyme analysis

Crude protein extracts were obtained by crushing 150 mg of fresh juvenile potato leaf tissue from greenhouse-grown plants. Before crushing, 150 μl of 0.1 M tris-HCL buffer, pH 7.8, with 2% glutathione was added to the sample. Each sample was adsorbed into 2 × 10-mm wicks of Whatman 3MM Gel Blot Paper (Schleicher and Schuell, Keene, N.H.) and stored at −20°C overnight. Electrophoretic assays were performed using a tris-citrate, pH 8.3, gel buffer system as described by Quiros (1981). The gel matrix consisted of 10% hydrolyzed potato starch (STARCHart, Corp., Smithville, Tex.). Gel slices were stained for phosphoglucomutase (*PGM*) according to Vallejos (1983).

Half-tetrad analysis (HTA) of 2*x* × 4*x* progeny from mixed-mode haploids

Diploid clones that form mixed-mode 2n gametes provide an opportunity to separate SDR- and FDR-derived 4*x* progeny from the same 2*x* × 2*x* cross (Douches and Quiros 1988). Because no recombination is expected for a marker tightly linked to the centromere, HTA for such a marker can discriminate between SDR- and FDR-derived progeny, provided the diploid 2n gamete-producing parent is heterozygous for the marker and the 4*x* parent is monoallelic or nulliplex (e.g. Aa × aaaa). All 2n gametes produced by FDR will be heterozygous (Aa) and the resulting progeny will be simplex for the marker (Aaaa). However, 2n gametes formed by SDR will be homozygous (either AA or aa) and the resulting progeny will be either duplex (Aaaa) or nulliplex (aaaa) in a 1 : 1 ratio.

The *Pgm-2* locus, which is 2.0 cM from the centromere on chromosome 4 (Douches and Quiros 1987), was used for HTA. Haploids and tetraploids were electrophoretically assayed to determine their isozyme genotype for *Pgm-2*. Only haploids and tetraploids heterozygous and nulliplex for *Pgm-2*, respectively were selected for 2*x* × 4*x* crosses.

2*x* × 4*x* crosses

All 2*x* × 4*x* crosses were made in the greenhouse. Pollen from the tetraploid parents was collected in gelatin capsules with desiccant and stored at 4°C for up to 1 month. Flowers on the haploids were emasculated and pollinated with tetraploid pollen, from March through May. High-pressure sodium lights (400 W) provided supplemental lighting (16 h day length). The greenhouse night-time temperature was maintained at 20°C with day-time temperatures ranging from 20 to 28°C.

Seeds were extracted from mature fruits 2 months after pollination, dried, and treated with 1500 ppm GA_3 for 24 h prior to planting. Seedlings were transplanted into trays (51 seedlings/tray). A newly expanded leaf from each 4-week-old seedling was crushed to obtain a crude protein extract. An electrophoretic assay for *Pgm-2* was done to classify 4*x* individuals as SDR- or FDR-derived progeny (Werner et al. 1991). Seedlings were allowed to mature and a tuber from each seedling was harvested and held at 4°C until the field planting.

Field studies

Six field trials were conducted from 1992 to 1996 at the Montcalm Research Farm (MRF), Montcalm, Mich. Each field trial was planted by hand as 4-hill plots of individual clones of a family, with 30-cm spacing between hills and with 87 cm between rows. Progeny sizes and parents from the three crosses, the number of replications, and the length of growing season are described in Table 1. All experiments were planted in randomized complete block design. Harvested tubers from the current year were used as seed in the following year.

The soil in the experimental plots at MRF is a McBride sandy loam. Additional fertilizer was applied as needed during the growing season as follows: 327 kg/ha 0-0-60 (N : P : K) broadcast pre-plant,

Table 1 Sizes of subpopulations and experimental design for $2x/4x$ crosses planted at Montcalm Research Farm

Year	Cross	Population size		Season	
		FDR	SDR	Length	Replications
1992	4182T × NDD277-2	90	90	118 days	4
1993	4182T × NDD277-2	88	90	124 days	4
1994	4182T × ND860-2	21	31	124 days	4
1995	4182T × ND860-2	21	31	135 days	4
1995	H175 × Yukon gold	43	57	135 days	4
1996	H175 × Yukon gold	43	56	128 days	3

Table 2 An examination of χ^2 values of the ratios of FDR-derived progenies to the SDR-derived progenies in $2x$-$4x$ crosses

Parents		Observed ratios		Expected ratios				χ^2 value		P value	
Haploid	Tetraploid	SDR[a]	FDR[b]	1 : 1		2 : 1		1 : 1	2 : 1	1 : 1	2 : 1
				SDR[c]	FDR[c]	SDR[c]	FDR[c]				
4182-T	Lemhi R.	25	12	18.5	18.5	24.67	12.33	4.57	0.01	0.05	0.9
4182-T	NDD277-2	120	61	90.5	90.5	120.67	60.33	19.23	0.01	0.001	0.9
4182-T	Ranger R.	43	19	31	31	41.33	20.67	9.29	0.20	0.005	0.75
4182-T	ND860-2	31	21	26	26	34.67	17.33	1.92	1.16	0.1	0.6
4182-T	Yukon Gold	42	20	31	31	41.33	20.67	7.81	0.03	0.005	0.9
H175	NDD277-2	13	16	14.5	14.5	19.33	9.67	0.31	6.22	0.65	0.01
H175	Yukon Gold	57	43	50	50	66.67	33.33	1.96	4.21	0.17	0.3

[a] Number of individuals classified as SDR-derived
[b] Number of individuals classified as FDR-derived
[c] Number of individuals based on projected ratios

218 kg/ha 20-10-10 at planting, 109 kg/ha 46-0-0 side-dressed at hilling, and 130 kg/ha 34-0-0 through irrigation. Herbicide treatments (metalochlor 2.2 ai kg/ha with metrabuzin 0.6 ai kg/ha) were applied pre-emergence. Plants were hilled when 25–30 cm in height. Supplemental irrigation was applied as needed. Vines were desiccated with diquat (0.5 ai l/ha) 2 weeks prior to harvest.

A single-row chain harvester was used to lay the tubers on the soil. For all field plots a red-skinned cultivar (Red Norland or Red Pontiac) was planted between plots to facilitate tuber separation at harvest. Tubers were collected and bagged by hand on a per-plot basis.

Total tuber yield was measured from the tubers of each plot and was weighed using a digital scale accurate to ±1 g (Toledo Scale, Worthington, Ohio). Stand counts were taken for the four-hill plots 1 month after emergence. Yield data were adjusted with the stand count data to present yield on a per-plant basis. A 0.5–4.0-kg sample from each plot was taken for specific gravity measurement. Specific gravity was calculated using the weight in air/weight in water method.

Analysis of variance and mean separations of total yield and tuber specific gravity (a measure of tuber dry matter content) and *t*-tests of population means and variances for the progeny classes were performed using MSTAT-C (Michigan State University). Skewness and kurtosis were examined for both subpopulations to characterize the distribution of total yield and specific gravity.

Results

HTA of $2x \times 4x$ progeny

The $4x$ progeny from all successful $2x \times 4x$ crosses were genotyped for *Pgm-2* to discriminate between FDR- and SDR-derived progeny. All $4x$ progeny from the $2x$ parent, 4182-T, fit a 2SDR : 1FDR ratio, whereas those from haploid H175 had ratios that fit a 1SDR : 1FDR (Table 2).

Field experiments

Between 1992 and 1996 three $2x \times 4x$ populations were studied. No difference was seen for total tuber yield or specific gravity between FDR- and SDR-derived tetraploid subpopulations from the crosses 4182-T × NDD277-2, 4182-T × ND860-2, and H175 × Yukon Gold (Table 3). The average yields for the three FDR- and SDR-derived subpopulations approached the mid-parent values in each of the field experiments, while specific gravity was equivalent to, or lower than, the mid-parent value (Table 4). There was no significant mid-parent heterosis exhibited by any of the populations for either trait examined.

The distributions of FDR- and SDR-subpopulations were characterized by their skewness and kurtosis values (Table 5). A positive kurtosis value denotes a peaked curve, whereas a negative value represents a flatter curve. Kurtosis values for yield did not follow any trends in the three crosses (Table 5). If significance was observed in one cross in one year, it was not observed in the other year. Data for specific gravity were similar to that of yield and did not follow any

Table 3 Probability results of two-way ANOVAs by 2n gamete-formation mode (FDR vs SDR) and replication for total tuber yield and specified gravity in FDR- and SDR-derived 2*x*-4*x* populations

Population	Year	Total yield		Specific gravity	
		Replication	Mode	Replication	Mode
H175 × Yukon gold	1996	0.4710[ns]	0.3261[ns]	0.1088[ns]	0.6260[ns]
H175 × Yukon gold	1995	0.0816[ns]	0.5174[ns]	0.4763[ns]	0.6108[ns]
4182t × ND860-2	1995	0·3774[ns]	0.3344[ns]	0.2488[ns]	0.0885[ns]
4182t × ND860-2	1994	0.2766[ns]	0.2766[ns]	0.8516[ns]	0.3705[ns]
4182t × NDD277-2	1993	0.5275[ns]	0.7608[ns]	0.5091[ns]	0.4789[ns]
4182t × NDD277-2	1992	0.5275[ns]	0.7608[ns]	0.4891[ns]	0.5282[ns]

[ns] Denotes non-significance

Table 4 Comparison between FDR and SDR subpopulations means for the average of tuber yield (gm/plant) and specific gravity for three 2*x* × 4*x* crosses grown at Montcalm Research Farm from 1992–1996

Year	Cross	Subpopulation	Yield (gm/plant)	*t*-test[a]	Specific gravity	*t*-test[a]
1992	4182-T × NDD277-2	FDR	482	0.1984[b]	1.076	0.4796[b]
		SDR	542		1.075	
		4182-T	312		1.083	
		NDD277-2	966		1.082	
		Mid-parent	639		1.083	
1993	4182-T × NDD277-2	FDR	551	0.8965	1.055	0.3707
		SDR	554		1.054	
		4182-T	354		1.057	
		NDD277-2	475		1.059	
		Mid-parent	415		1.058	
1994	4182-T × ND860-2	FDR	1085	0.8147	1.065	0.0642
		SDR	1062		1.062	
		4182-T	273		1.079	
		ND860-2	2175		1.074	
		Mid-parent	1224		1.077	
1995	4182-T × ND860-2	FDR	1282	0.8042	1.065	0.6648
		SDR	1179		1.064	
		4182-T	398		1.079	
		ND860-2	1966		1.074	
		Mid-parent	1182		1.077	
1995	H175 × Y. Gold	FDR	1086	0.4390	1.069	0.4998
		SDR	1129		1.068	
		H175	233		1.079	
		Y. Gold	1629		1.063	
		Mid-parent	931		1.071	
1996	H175 × Y. Gold	FDR	412	0.6420	1.077	0.3121
		SDR	391		1.076	
		H175	176		1.089	
		Y. Gold	665		1.071	
		Mid-parent	420		1.080	

[a] Comparison between FDR- and SDR-subpopulations

[b] All *t*-test values are non significant at $P = 0.05$

trends. There was significant skewness observed in the three crosses. In two cases the FDR-subpopulations were skewed and one case the SDR-subpopulation was skewed (Table 5). Figures 1 and 2 show the yield and specific gravity distributions for 4182-T × NDD277-2, respectively.

Discussion

Previous studies, comparing the yield of FDR-derived progeny to SDR-derived progeny from either haploids of *S. tuberosum* or haploid-species hybrids as the 2*x* parent, indicated that the FDR-derived progeny were superior in 4*x* × 2*x* crosses (Mendiburu et al. 1974; Mendiburu and Peloquin 1977 b; Chujoy and Peloquin 1986; Ortiz et al. 1991; Werner and Peloquin 1991 b). In all these cases, the comparisons were based upon FDR- and SDR-derived 4*x* progeny generated from different 2*x* parents, confounding the 2*x* genotype and the mode of 2n gamete formation. Hutten et al. (1994) observed the superior yield performance of FDR over SDR progenies using reciprocal 4*x* × 2*x* crosses. Through the use of mixed-mode haploids of *S. tuberosum*, we were

Table 5 Skewness and kurtosis values for specific gravity and yield data for $2x \times 4x$ crosses at Montcalm Research Farm

Year	Cross	Mode	Specific gravity			Yield		
			Skewness[a]	Kurtosis	*F*-test probability	Skewness[a]	Kurtosis	*F*-test probability
1992	4182-T × NDD277-2	FDR	1.0474***	1.837**	0.2807^{ns}	0.9108**	0.315^{ns}	0.6683^{ns}
	4182-T × NDD277-2	SDR	– 0.1827^{ns}	0.659^{ns}		0.7882**	0.659^{ns}	
1993	4182-T × NDD277-2	FDR	0.4406^{ns}	0.642^{ns}	0.8697^{ns}	1.2710***	1.854***	0.2903^{ns}
	4182-T × NDD277-2	SDR	0.8597***	2.023***		0.3400^{ns}	– 0.729^{ns}	
1994	4182-T × ND860-2	FDR	0.5533^{ns}	0.847^{ns}	0.3066^{ns}	0.3436^{ns}	– 1.048^{ns}	0.4303^{ns}
	4182-T × ND860-2	SDR	0.0619^{ns}	– 0.143^{ns}		1.4057**	2.801***	
1995	4182-T × ND860-2	FDR	0.4406^{ns}	0.642^{ns}	0.1620^{ns}	0.5726^{ns}	– 0.448^{ns}	0.9430^{ns}
	4182-T × ND860-2	SDR	1.0753**	0.532^{ns}		1.1830***	0.928^{ns}	
1995	H175 × Y. Gold	FDR	– 0.0124^{ns}	0.248^{ns}	0.5648^{ns}	0.8095*	0.044^{ns}	0.3805^{ns}
	H175 × Y. Gold	SDR	0.4578^{ns}	0.726^{ns}		0.5571^{ns}	0.725^{ns}	
1996	H175 × Y. Gold	FDR	– 0.1786^{ns}	– 0.146^{ns}	0.3121^{ns}	0.8146**	0.480^{ns}	0.0044***
	H175 × Y. Gold	SDR	0.6361**	0.833**		1.2679***	1.467***	

* Significant at 0.05%
** Significant at 0.01%
*** Significant at 0.001%
[a] ns denotes non significance

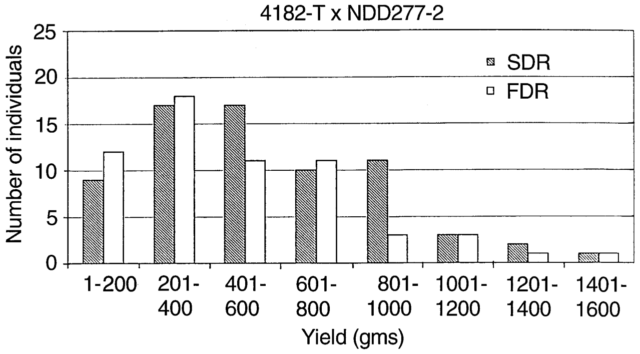

Fig. 1 Distribution of yield for the FDR and SDR subpopulations for the cross 4182-T × NDD277-2 at Montcalm Research Farm in 1992. Yield data are presented on a per-plant basis

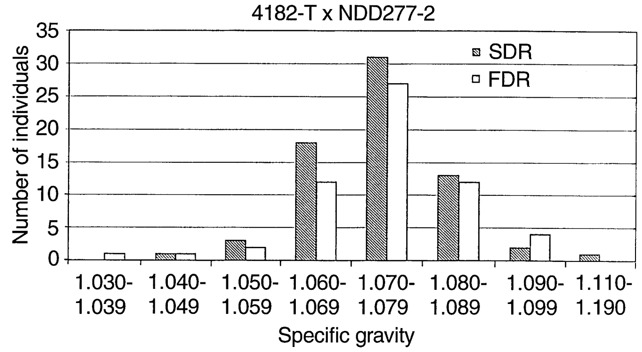

Fig. 2 Distribution of specific gravity for the FDR and SDR subpopulations for the cross 4182-T × NDD277-2 at Montcalm Research Farm in 1992

able to produce both FDR and SDR 2n gametes from the same genotype in the same cross, allowing us to eliminate any genetic bias or cytoplasmic effects of the $2x$ parent.

In this study, no differences between the FDR- and SDR-derived subpopulations were observed for the two quantitatively inherited traits: yield and specific gravity. We observed that the means of both FDR-derived and SDR-derived subpopulations approached the mid-parent value for yield and specific gravity (Table 4). These results support an additive genetic model. Previous studies have identified non-additive effects that contribute to yield in potato (Mendoza and Haynes 1974; Mendiburu and Peloquin 1977 a; Werner and Peloquin 1991 b). Therefore, total yield in potato may be influenced by both additive and non-additive genetic effects. In contrast to yield, inheritance of specific gravity is more strongly influenced by genes with additive effects (Ruttencutter et al. 1979; Haynes and Haynes 1983). Therefore, transmission of heterozygosity should not have as large an influence on specific gravity as yield. Our observations demonstrate no difference in specific gravity between the subpopulations and these means were below the mid-parent value. The difference observed between mid-parent and subpopulation values may be due to the low yield of the plots of the haploid parents. The small sample sizes taken from these plots made it difficult to accurately measure the specific gravity of the haploid parent.

A tighter distribution is expected in FDR-derived tetraploid populations because a higher percentage of the parental genome is transferred intact, resulting in a more uniform gamete production. Therefore, we would expect the FDR-subpopulation to have a narrower distribution than the SDR-subpopulation

(Tai and De Jong 1997). There were no trends in the distribution of values for total yield and specific gravity for either sub-population in the three crosses based upon skewness and kurtosis analyses (Table 5).

If the FDR-subpopulations were higher-yielding than the SDR-subpopulations, we would have additional data to support the importance of heterozygosity to polyploid heterosis. Since there were no differences between the two subpopulations, it follows that: (1) heterozygosity may not be as critical to yield performance as previously reported, (2) the level of inbreeding of the 2*x* parents negated the effect of heterozygosity transmission, or (3) the genetic diversity in this study was similar between the haploids and 4*x* parents. Di-haploids, produced from 4*x* *S. tuberosum* cultivars, are inbred to a level equivalent to three generations of selfing (Yeh et al. 1964; Howard 1970; Ujtewaal et al. 1987). Inbreeding reduces heterozygosity and leads to yield decline, loss of vigor, and reduced fertility (Dewey 1966; Busbice and Wilsie 1966; Levings et al. 1967; Busbice 1968; Dessureaux and Gallais 1969; Rowe 1967; Mendiburu et al. 1974; Mendoza and Haynes 1974; Rice and Dudley 1974; Bingham 1980). In the present study, the haploids lacked vigor and yield (Table 4). Furthermore, if the transmission of heterozygosity was greater with FDR 2n gametes, the FDR subpopulations should have had a narrower progeny distribution. The lack of consistent differences in distribution between FDR- and SDR-derived progeny also supports the idea that inbreeding in the haploid contributed to these results. If the inbreeding level of the haploid parents had an influence on these results, this study can be treated as baseline data on which further studies can be constructed to compare the breeding value of 2n gametes. Therefore, we can interpret these results as a test of the limits of the power of FDR 2n gametes in potato breeding.

To determine whether the level of inbreeding in the haploids was a significant factor in this study, the allelic diversity of mixed-mode parents used in $2x \times 4x$ crosses could be increased. Crossing the haploids to *Solanum* species would increase the allelic diversity of the resulting haploid-species hybrids (Hermundstad and Peloquin 1985; Darmo and Peloquin 1990, 1991; Hawkes 1990; Concillo and Peloquin 1991). These haploid-species hybrids could be used to construct $2x \times 4x$ populations from non-inbred 2*x* parents. A series of mixed-mode-producing *Solanum* species, previously identified by Werner (1989), would be suitable for this purpose.

The ratio of FDR-derived progenies to the SDR-derived progenies observed for the $2x \times 4x$ crosses in the experiment was dependent on the haploid parent used (Table 2). The clone 4182-T always produced a 2:1 (SDR:FDR) ratio; however, H175 had a 1:1 (SDR:FDR) ratio. Despite their unknown genetic basis, these observed ratios may have value if one mode of 2n gamete formation from the haploid is desired over another. The clone 4182-T produces approximately one-third FDR-derived progeny out of the total, compared to one-half with H175 (Table 2). The variability of ratios between these two genotypes suggests that the FDR-SDR gametic ratios are dependent on genotype; however, more crosses are needed to support this observation.

Studies on the importance of heterozygosity in polyploid heterosis are valuable for both basic biology and plant breeding. In the present study we addressed the issue of heterozygosity in a unique and unbiased manner through the use of mixed-mode di-haploids. This study forms a foundation to further examine the relationship between heterozygosity and heterosis in polyploid crop species.

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