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Breeding Value of 2n Pollen (Diplandroids) in Tetraploid × Diploid Crosses in Potatoes

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Summary. The relative breeding value of first division restitution (FDR) and second division restitution (SDR) 2n male gametes from diploids, and n (2x) gametes from tetraploids were compared. This was done by measuring tuber yield of 105 4x families obtained from 4x × 2x (FDR), 4x × 2x (SDR), and 4x × 4x crosses at two locations. All tetraploid families obtained from 4x × 2x (FDR) matings exhibited heterosis (the mean of the F_1 exceeded that of the higher yielding parent), and outyielded other tetraploid families and 4x cultivars at both locations. The tuber yield of 4x × 2x (SDR) families was higher than that of the families derived from 4x × 4x matings, although the 2x parents had significantly lower yield than tetraploid parents. Specific combining ability (S.C.A.) was found to be significant when families obtained from each category (4x × FDR, 4x × SDR and 4x × 4x) were analyzed individually. Both general combining ability (G.C.A.) (2x) and S.C.A. were significant when families obtained from: 1) 4x × FDR plus 4x × SDR; 2) 4x × FDR plus 4x × 4x; and 3) all categories, were analyzed. Only S.C.A. was found to be significant when 4x × SDR and 4x × 4x families were analyzed together. Consistent results were obtained at each of, and over, the two locations. These results strongly demonstrated that FDR gametes were superior in breeding value to either SDR or n (2x) gametes, and were more homogeneous. Gametes formed by SDR might be superior to n (2x) gametes although they were as heterogeneous. Distinct yield differences between 4x × FDR and 4x × SDR families plus the significant G.C.A. (2x) detected when these two categories were compared, substantiated the cytological interpretation of genetically distinct modes of diplandroid formation.

Introduction

Three mechanisms of diplandroid (2n pollen) formation in diploid potatoes have been discovered (Mok and Peloquin 1972). One mechanism, termed parallel spindles (ps), is characterized by parallel Ana II spindles instead of the spindles having an angle of approximately 60 degrees to each other as in normal microsporogenesis. A single cleavage-furrow at the end of the 2nd meiotic division forms a dyad which gives rise to two 2n microspores. Diplandroids formed by ps are genetically equivalent to first division restitution (FDR) gametes (Mok and Peloquin 1974). The genetic significance of FDR gametes is that all heterozygous loci from the centromere to the first crossover and one-half of the heterozygous loci between the first and the second crossover in the parent will be heterozygous in the gamete. The other two mechanisms of 2n pollen formation, premature cytokinesis 1 (pc 1) and premature cytokinesis 2 (pc 2), form diplandroids by omission of the 2nd meiotic division. Diplandroids formed by pc 1 and pc 2 are genetically equivalent to second division restitution (SDR) gametes. All heterozygous loci from the centromere to the first crossover in the parent will be homozygous, and those between the first and the second crossover will be heterozygous, in the SDR gametes.

The significance of diplandroids formed by FDR in potato breeding is that they provide a unique method of transferring a large proportion of the non-additive genetic effects (intra- and interlocus interactions) from parent to offspring. In contrast, normal meiotic products of diploids are only capable of transmitting largely additive effects. Meiotic products of a tetraploid conserve a certain amount of intralocus interactions (heterozygosity), because there are two alleles per locus in the gametes. But the amount of heterozygosity transmitted depends mainly on the genetic constitution of the tetraploid at each locus (whether it is tetrallelic, triallelic or diallelic, etc.), chromosome pairing and the nature of the tetraploid. The other portion of the non-additive effect, namely interlocus interactions (epistasis) will still be disrupted through meiosis. Mendiburu (1971) studied the relative importance of different genetic effects on tuber yield, and he found that non-additive effects were the major component. This finding together with the unique nature of FDR gametes, transferring nonadditive genetic effects, illuminated the importance of FDR gametes in potato breeding. The hypothesis of the superiority of FDR gametes in breeding provided the explanation for the high tuber yield of tetraploid families obtained from 4x × 2x (FDR) matings (Mendiburu and Peloquin 1971, Kidane-Mariam and Peloquin 1972).

Interpretation of the results obtained by Mendiburu also provided a possible explanation for the superiority of tetraploids over diploids in tuber yield. Since the number of alleles per locus is limited to two in a diploid, the number of possible intra- and inter-locus interactions are far smaller than that of a tetraploid (Mendiburu, Peloquin and Mok 1974). And since non-additive genetic effects are the essential component of tuber yield, the relatively higher number of genetic interactions possible in a tetraploid makes it more desirable than a diploid. The effectiveness of 2n gametes in synthesizing superior tetraploids, with regard to maximizing heterozygosity and epistasis, is obviously higher than obtaining tetraploids by colchicine doubling. For with the latter, the subsequently formed tetraploid is limited to two alleles per locus, so the number of intra- and inter-locus interactions will be fewer. The basis of the desirability of FDR 2n gametes in breeding was partly substantiated by Mendiburu's studies (1971). However, the relative advantage of FDR gametes in contrast to SDR gametes in breeding is not known.

Although SDR gametes are less desirable than FDR gametes in conserving non-additive genetic interactions, they may still be more advantageous in potato improvement than the normal meiotic products of tetraploids because they theoretically transfer more intra- and inter-locus interactions from parent to offspring than normal n (2x) gametes of tetraploids (Mendiburu, Peloquin and Mok 1974).

The relative breeding values of 1) FDR and SDR, and 2) SDR and n (2x) gametes can now be experimentally approached, since clones that produce FDR and SDR diplandroids exclusively have been identified (Mok and Peloquin 1973). This paper deals with these problems by comparing tuber yield of tetraploid families obtained from 4x × 2x (FDR), 4x × 2x (SDR) and 4x × 4x matings.

Materials and Methods

Formation of 4x families

Nine tetraploid cultivars (2n = 4x = 48) as female parents (W231, W623, W629, W639, W643, Merrimack, Norland, Platte and Superior) were crossed to four FDR (JI-9, IJ-12, IF-8, and IF-10) and four SDR (IF-1, IJ-25, IJ-31 and LI-12) diploids (2n = 2x = 24) in 4x × 2x matings. The nine cultivars were also intermated in all possible combinations to produce 36 tetraploid families. The tetraploid cultivars represent *S. tuberosum* materials and the eight diploids are Phureja-haploid Tuberosum hybrids.

These crosses were made in 1972 and seeds were germinated and seedlings transplanted into the field to obtain tubers in Rhinelander in 1973. Twenty clones with four uniform size tubers were selected from each family. Five families (W231 × IJ-12, Platte × Superior, Platte × Norland, Superior × Norland and Norland × Merrimack) had less than 20 clones that satisfied this requirement, and they were not included in the yield trial.

Field design

Each family consisted of 20 randomly picked clones (with regard to yield). These clones were planted in two replications in each of the two locations (Hancock Experimental Farm and Rhinelander Experimental Farm).

There were 71 4x families obtained from 4x × 2x crosses, and 32 4x families generated from 4x - 4x crosses. In addition, all of the 17 parental clones (both 4x and 2x) were included. Each family was considered as one entry, and clones within each entry and entries were planted according to a randomized complete block design. The spacing between rows was 36 inches and between plants in a row was 18 inches at Hancock and 32 inches at Rhinelander. Tubers were harvested at Hancock after 134 days and at Rhinelander after 119 days.

Statistical analysis

The tuber yield of each clone in each replication was measured and weighted to the closest 1/4 lb. The family mean in each replication was used for statistical analysis. The yield of the five missing families was estimated using methods described by Steel and Torrie (1960) for missing plots. These estimates do not add further information to the experiment but facilitate the statistical analysis.

Two-way analysis of variance was performed on values obtained from each location. A three-way analysis of variance model was used to analyze the values obtained over two locations. Seven analyses of variance for data obtained at each location were made: (1) one analysis for the 108 families; (2) three analyses for each category of 36 4x families (4x × FDR, 4x × SDR, and 4x × 4x); and (3) three analyses for comparing the three categories pair-wise (4x × FDR with 4x × SDR, 4x × FDR with 4x × 4x, and 4x × SDR with 4x × 4x), 72 families in each analysis. For the sake of convenience, 4x × FDR families will be designated as category 1 and those from 4x × SDR and 4x × 4x are designated as categories 2 and 3, respectively. Combining abilities in each analysis of variance were partitioned. Data obtained from both locations were combined and analyzed in the same subclasses.

Results

Results of the yield trial at Hancock are presented as averages of family means from two reps, in Table 1. The mean yields of the parental clones are also included in this table. Tuber yield of tetraploid families obtained from 4x × FDR, 4x × SDR and 4x × 4x matings are presented in Table 2. It is obvious that families derived from 4x × FDR matings yielded (7.7 lbs./hill) significantly higher than that of the families obtained from 4x × SDR (5.1 lbs./hill) and 4x × 4x (4.6 lbs./hill) matings at Hancock. Tuber yield of 4x × SDR families was higher than, but not significantly, that of the 4x × 4x families. Heterosis (mean yield of the family higher than the highest parent) in tuber yield was observed in every 4x × FDR family, but in none of the 4x × SDR or 4x × 4x families.

Partitioning of the genotypic differences (differences due to families) into general and specific combining

Table 1. Tuber yields (lbs./hill), as averages of family mean for two reps, of 4x families obtained from 4x × 2x (FDR), 4x × 2x (SDR) and 4x × 4x matings, and parents at Hancock

Parent	2x (FDR)				2x (SDR)				4x								
	JI-9	IJ-12	IF-8	IF-10	IF-1	IJ-25	IJ-31	LI-12	W231	W623	W629	W639	W643	Merr.	Nor.	Plat.	Sup.
	3.7	2.1	1.5	2.4	1.4	2.1	2.2	3.2	6.0	5.7	4.7	5.0	6.1	4.6	4.8	4.6	5.1
W231 6.0	7.5	(7.6)	7.2	7.9	5.1	4.5	5.1	5.0		5.4	4.8	5.1	5.1	4.4	4.0	4.6	4.9
W623 5.7	6.7	8.3	8.5	8.3	5.1	5.0	5.1	5.1	5.4		4.0	5.2	5.2	4.2	4.6	4.9	4.7
W629 4.7	7.5	7.2	7.1	6.9	5.2	5.5	5.0	4.9	4.8	4.0		4.7	5.3	4.3	4.3	4.4	5.2
W639 5.0	7.6	7.9	8.0	8.0	5.3	4.7	5.5	5.0	5.1	5.2	4.7		5.0	5.0	4.6	5.7	3.8
W643 6.1	7.4	7.9	8.3	7.9	5.3	5.3	4.5	4.7	5.1	5.2	5.3	5.0		4.7	4.4	5.0	3.5
Merr. 4.6	7.3	7.1	7.1	7.3	5.0	5.2	4.4	5.3	4.4	4.2	4.3	5.0	4.7		(4.3)	4.8	4.3
Nor. 4.8	7.6	7.9	7.8	6.2	5.7	4.5	5.1	5.0	4.0	4.6	4.3	4.6	4.4	(4.3)		(4.1)	(4.2)
Plat. 4.6	7.1	8.3	7.8	8.2	5.7	4.9	5.3	5.5	4.6	4.9	4.4	5.7	5.0	4.8	4.1		(3.9)
Sup. 5.1	8.3	8.5	8.1	7.6	5.1	5.0	5.0	4.9	4.9	4.7	5.2	3.8	3.5	4.3	(4.2)	(3.9)	
Mean	7.4	7.8	7.8	7.6	5.3	5.0	5.0	5.0	4.8	4.8	4.7	4.6	4.8	4.4	4.4	4.7	4.2

Average tuber yield of parents at Hancock

Parent	JI-9	IJ-12	IF-8	IF-10	IF-1	IJ-25	IJ-31	LI-12	W231	W623	W629	W639	W643	Merr.	Nor.	Plat.	Sup.
Yield	3.7	2.1	1.5	2.4	1.4	2.7	2.2	3.2	6.0	5.7	4.7	5.0	6.1	4.6	4.8	4.6	5.1

Mean	FDR parents	SDR parents	Tetraploid parents
	2.7	2.4	5.2

Table 2. Tuber yield (lbs./hill), as averages of family means, of tetraploid families by category of male parents, from 4x × 2x (FDR), 4x × 2x (SDR) and 4x × 4x matings

Parent	Location	W231	W623	W629	W639	W643	Merr.	Nor.	Plat.	Sup.	Mean
FDR (2x)	Han.	7.6	8.0	7.2	7.9	7.9	7.2	7.4	7.9	8.1	7.7
	Rhi.	4.5	4.6	4.2	4.3	4.0	4.2	3.8	4.6	4.6	4.3
	Tot.	6.1	6.3	5.7	6.1	6.0	5.7	5.6	6.2	6.4	6.0
SDR (2x)	Han.	4.9	5.0	5.2	5.1	5.0	5.0	5.1	5.4	5.0	5.1
	Rhi.	3.0	3.4	3.1	3.1	3.0	3.0	3.0	3.7	3.6	3.2
	Tot.	3.9	3.9	4.2	4.1	4.0	4.0	4.0	4.6	4.3	4.1
Cult. (4x)	Han.	4.8	4.8	4.6	4.9	4.8	4.5	4.6	4.7	4.3	4.6
	Rhi.	3.8	3.4	3.0	3.0	3.2	2.9	3.1	2.9	2.7	3.2
	Tot.	4.3	4.1	3.8	4.0	4.0	3.7	3.7	3.8	3.5	3.9

Han. (Hancock), Rhi. (Rhinelander), Tot. (both locations).

abilities is meaningful, since significant differences between families were observed in all seven analyses (Tables 3-5). When each category of 36 families was analyzed (Table 3), no significant general combining ability (G.C.A.) was observed. Genotypic differences within each category were due to specific combining ability (S.C.A.). However, when categories 1 and 2 were analyzed together (Table 4), both G.C.A. (2x) and S.C.A. were highly significant. Similarly, significant G.C.A. (2x) and S.C.A. were observed when families of categories 1 and 3 were analyzed together (Table 4). However, significant contributions of S.C.A. only, were detected when families from categories 2 and 3 were analyzed (Table 4). The G.C.A. was not responsible for the significant differences between families. When families of all three categories were analyzed together, not unexpectedly, both G.C.A. of diploid parents and S.C.A. were significant (Table 5).

Table 3. Summarized results of analysis of variance (mean squares, means and L.S.D.) of 36 families from: (1) 4x × FDR, (2) 4x × SDR, and (3) 4x × 4x matings for tuber yield

	4x×FDR families (category 1)				4x×SDR families (category 2)				4x×4x families (category 3)			
Source	DF	Han.	Rhine.	two locations	DF	Han.	Rhine.	two locations	DF	Han.	Rhine.	two locations
Family	35	0.59**	0.38**	0.60**	35	0.2	0.3**	0.32**	35	0.49**	0.56**	0.83**
G.C.A.(2x)	3	0.06	0.07	0.07	3	0.02	0.007	0.03				
G.C.A.(4x)	8	0.24	0.14	0.05	8	0.03	0.15	0.003	8	0.08	0.07	0.11
S.C.A.	24	0.78**	0.50**	0.86**	24	0.28	0.39**	0.46**	27	0.61**	0.7**	1.04**
Error	35	0.24	0.08	0.18	35	0.14	0.11	0.09	35	0.17	0.21	0.18
Mean^{a}		7.65	4.26	5.96		5.07	3.21	4.14		4.59	3.02	3.82
L.S.D.$^{a}_{5\%}$		0.99	0.59	0.86		0.76	0.68	0.62		0.82	0.94	0.87
L.S.D.$^{a}_{1\%}$		1.33	0.79	1.15		1.02	0.91	0.84		1.10	1.26	1.18

[a] lbs/hill

Table 4. Summarized results of analysis of variance (mean squares, means and L.S.D.) of 72 families obtained from: (1) 4x × FDR and 4x × SDR, (2) 4x × FDR and 4x × 4x, and (3) 4x × SDR and 4x × 4x families

	(1) 4x × FDR and 4x × SDR				(2) 4x × FDR and 4x × 4x				(3) 4x × SDR and 4x × 4x			
Source	DF	Han.	Rhine.	two locations	DF	Han.	Rhine.	two locations	DF	Han.	Rhine.	two locations
Family	71	3.86**	0.89**	3.82**	71	5.19**	1.26**	5.35**	71	0.44**	0.45**	0.67**
G.C.A.(2x)	7	3.89**	0.65**	4.38**	3	7.44**	2.36**	5.36**	3	0.24	0.17	0.3
G.C.A.(4x)	8	0.067	0.14	0.20	8	0.09	0.25	0.24	8	0.03	0.02	0.16
S.C.A.	56	4.4**	1.032	4.35**	60	5.76**	1.33**	6.03**	60	0.52**	0.51**	0.76**
Error	71	0.28	0.18	0.14	71	0.35	0.2	0.19	71	0.15	0.17	0.15
Mean^{a}		6.36	3.72	5.05		6.12	3.64	4.89		4.83	3.12	3.98
L.S.D.$^{a}_{5\%}$		1.06	0.84	0.74		1.19	0.9	0.89		0.78	0.82	0.78
L.S.D.$^{a}_{1\%}$		1.41	1.13	0.98		1.58	1.2	1.18		1.04	1.09	1.03

[a] lbs/hill

Table 5. Summarized results of analysis of variance (mean squares, means and L.S.D.) of 108 families obtained from 4x × FDR, 4x × SDR and 4x × 4x matings for tuber yield

Sources	DF	Hancock	Rhinelander	2 locations
Family	107	4.0**	1.01**	4.17**
G.C.A.(2x)	7	7.61**	1.09**	7.39**
G.C.A.(4x)	8	0.16	0.21	0.30
S.C.A.	92	4.17**	1.07**	4.26**
Error	107	0.29	0.19	0.16
Mean^{a}		5.77	3.49	4.64
L.S.D.$^{a}_{5\%}$		1.08	0.87	0.80
L.S.D.$^{a}_{1\%}$		1.45	1.14	1.06

[a] lbs/hill

Table 6. Tuber yield (lbs./hill), as averages of family mean for two reps, of 4x families obtained from 4x × 2x (FDR), 4x × 2x (SDR) and 4x × 4x matings, and parents at Rhinelander

Parent	2x (FDR)				2x (SDR)				4x								
	JI-9 1.4	IJ-12 1.4	IF-8 1.3	IF-10 1.4	IF-1 1.0	IJ-25 1.4	IJ-31 1.4	LI-12 1.6	W231 3.2	W623 3.3	W629 3.4	W639 4.1	W643 5.2	Merr. 2.9	Nor. 3.5	Plat. 3.7	Sup. 2.9
W231 3.2	4.2	(4.5)	3.9	5.5	3.0	3.3	3.0	2.7		3.4	2.7	4.4	3.5	3.8	3.4	3.5	2.7
W623 3.3	4.6	4.6	4.4	4.5	3.3	3.4	3.5	3.2	3.4		2.8	3.0	4.2	2.8	4.0	3.3	3.1
W629 3.4	4.0	3.9	4.7	4.3	3.5	3.3	2.9	2.8	2.7	2.8		2.8	2.1	2.9	2.4	2.0	4.0
W639 4.1	4.5	4.5	3.9	4.2	3.6	2.3	3.5	3.2	4.4	3.0	2.8		3.3	3.0	2.9	3.2	2.7
W643 5.2	4.2	3.9	3.8	4.2	3.0	3.5	2.4	3.1	3.5	4.2	3.1	3.3		2.7	3.2	3.0	2.4
Merr. 2.9	4.5	4.2	4.0	4.2	2.7	2.8	3.4	3.1	3.8	2.8	2.9	3.0	2.7		(2.3)	3.0	2.0
Nor. 3.5	4.6	4.3	2.8	3.6	3.1	2.9	2.4	3.2	3.4	4.0	2.4	2.9	3.2	(2.3)		(2.9)	(2.7)
Plat. 3.7	4.2	5.0	4.6	4.4	3.4	3.8	4.1	3.5	3.5	3.3	2.0	3.2	3.9	3.0	(2.9)		(2.6)
Sup. 2.9	4.4	5.1	4.3	4.6	3.4	3.8	3.1	3.9	2.7	3.1	4.0	2.7	2.4	2.0	(2.7)	(2.6)	
Mean	4.4	4.5	4.0	4.2	3.2	3.3	3.1	3.2	3.4	3.2	3.2	3.0	2.7	2.8	2.9	2.9	2.8

Average tuber yield of parents at Rhinelander

Parent	JI-9	IJ-12	IF-8	IF-10	IF-1	IJ-25	IJ-31	LI-12	W231	W623	W629	W639	W643	Merr.	Nor.	Plat.	Sup.
Yield	1.4	1.4	1.3	1.4	1.0	1.4	1.4	1.6	3.2	3.3	3.4	4.1	5.2	2.9	3.5	3.7	2.9
Mean	FDR parents				SDR parents				Tetraploid parents								
	1.4				1.3				3.6								

Results obtained at Rhinelander were consistent with those obtained at Hancock. Category 1 had significantly higher yield (4.3 lbs./hill) than category 2 (3.2 lbs./hill) and category 3 (3.0 lbs./hill) (Table 2). Tuber yield of the tetraploid parents was higher than that of the diploid parents (Table 6). These results can be summarized as follows: (1) tuber yield of tetraploid families of category 1 was significantly higher than that of categories 2 and 3 (Table 6); (2) average tuber yield of families of category 2 was higher than that of category 3, but the difference was not significant; (3) significant differences in tuber yield between families of the same category were observed (Table 3); (4) general combining abilities of parental clones within each category were not significant; only S.C.A. contributed to the differences between families; (5) both S.C.A. and G.C.A. (2x) were significant when families of categories 1 and 2, and 1 and 3 were analyzed together; (6) only S.C.A. was significant when categories 2 and 3 were analyzed (Table 4); both S.C.A. and G.C.A. (2x) were significant when all three categories were analyzed together (Table 5).

Analyses of data over two locations did not reveal any inconsistencies with regard to results obtained from analyses at each location (Tables 2 and 7). The results are summarized as follows: (1) tuber yield of 4x × FDR (6.0 lbs./hill) families was significantly higher than that of 4x × SDR families (4.1 lbs./hill) and 4x × 4x families (3.9 lbs./hill) (Table 2); (2) heterosis was observed in all 4x × FDR families (Table 7); (3) significant differences between families within each category were due to specific combining ability of the parents (Table 3); (4) both G.C.A. (2x) and S.C.A. were significant when families of categories 1 and 2, and 1 and 3 were analyzed in two separate analyses (Table 4); (5) no significant G.C.A. was detected when families from categories 2 and 3 were analyzed (Table 4), only S.C.A. of the parents was significant (Table 4); (6) both S.C.A. and G.C.A. (2x) were found to be significant when families of all three categories were analyzed (Table 5); (7) significant genotype x environment interaction was observed.

Discussion

The superiority of FDR gametes in breeding as compared to either SDR gametes or n (2x) gametes of tetraploids is apparent from the results presented. The average tu-

Table 7. Tuber yield (lbs./hill), as averages of family mean for two reps, of 4x families obtained from 4x × 2x (FDR), 4x × 2x (SDR) and 4x × 4x matings and parents at both locations

Parent	2x (FDR)				2x (SDR)				4x								
	JI-9 2.5	IJ-12 1.7	IF-8 1.4	IF-10 1.7	IF-1 1.2	IJ-25 2.0	IJ-31 1.8	LI-12 2.4	W231 4.6	W623 4.5	W629 4.4	W639 4.6	W643 5.7	Merr. 3.8	Nor. 4.2	Plat. 4.2	Sup. 4.0
W231 4.6	5.9	(6.0)	5.6	6.7	4.0	3.9	4.0	3.8		4.4	3.4	4.8	4.3	4.8	4.0	3.9	3.3
W623 4.5	5.6	6.5	6.3	6.4	4.2	4.2	4.3	2.8	4.4		3.8	4.1	4.7	3.4	4.3	4.1	3.9
W629 4.1	5.7	5.5	5.9	5.6	4.3	4.4	4.0	3.9	3.4	3.8		3.8	4.2	3.6	3.4	3.2	4.6
W639 4.6	6.0	6.2	5.9	6.1	4.5	3.4	4.5	4.1	4.8	4.1	3.8		4.1	3.8	3.7	4.5	3.2
W643 5.7	5.8	5.9	6.1	6.1	4.2	4.4	3.5	3.9	4.3	4.7	4.2	4.1		3.7	3.8	4.4	3.0
Merr. 3.8	5.9	5.6	5.5	5.8	3.9	4.0	3.9	4.2	4.8	3.4	3.6	3.8	3.7		(3.3)	3.9	3.2
Nor. 4.2	6.1	6.1	5.3	4.9	4.4	3.7	3.7	4.1	4.0	4.3	3.4	3.7	3.8	(3.3)		(3.5)	(3.5)
Plat. 4.2	5.7	6.7	6.2	6.3	4.6	4.4	4.7	4.5	3.9	4.1	3.2	4.5	4.4	3.9	(3.5)		(3.2)
Sup. 4.0	6.3	6.8	6.2	6.1	4.3	4.4	4.0	4.4	3.3	3.9	4.6	3.2	3.0	3.2	(3.5)	(3.2)	
Mean	5.9	6.2	5.9	5.9	4.3	4.1	4.0	4.1	4.0	4.0	4.0	3.8	3.8	3.6	3.7	3.8	3.5
Average tuber yield of parents at both locations																	
Parent	JI-9	IJ-12	IF-8	IF-10	IF-1	IJ-25	IJ-31	LI-12	W231	W623	W629	W639	W643	Merr.	Nor.	Plat.	Sup.
Yield	2.5	1.7	1.4	1.7	1.2	2.0	1.8	2.4	4.6	4.5	4.1	4.6	5.7	3.8	4.2	4.2	4.0
Mean	FDR parents				SDR parents				Tetraploid parents								
	1.8				1.9				4.4								

ber yield of 4x × FDR families over two locations was 6.0 lbs./hill as compared with 4.1lbs./hill of 4x×SDR families and 3.9 lbs./hill of 4x × 4x families. These results are even more revealing when the tuber yield of the parents is considered (Table 7). The average yield of the four FDR parents was 1.8 lbs./hill, which is not significantly different from that of the four SDR parents (1.9 lbs./hill), and far lower than that of the nine cultivars (4.4 lbs./hill). The fact that FDR gametes provide such an improvement is quite surprising because FDR gametes are not as advantageous if they are not generated by superior genotypes. However, the present experiment indicated that FDR gametes, or the amount of heterozygosity and epistasis they transmitted, have a definite advantage, even though these FDR parents are not selected for tuber yield. These eight parental clones generating FDR and SDR gametes are closely related (some of them are full sibs), so the genotypic differences among parents should not account for the tremendous differences observed in the progeny. The differences observed between 4x × FDR and 4x × SDR families established the fact that if two kinds of 2n gametes (FDR and SDR) are generated by genotypically similar parents, FDR gametes are very superior in terms of increased yield.

The superiority of FDR gametes is not limited however to this advantage alone. If we compare the progeny yield of 4x × FDR with that of 4x × 4x families, the average yield of the tetraploid parents was 4.4 lbs./hill which is significantly higher than that of the FDR parents (1.8 lbs./hill). Further, these tetraploids are highly selected clones and represent superior genotypes. The fact that progeny obtained from intermating these superior genotypes had lower yields (3.9lbs./hill) than progeny obtained from 4x × FDR matings (6.0lbs./hill) suggested that: 1) FDR gametes from unselected genotypes are superior to normal meiotic products from a superior tetraploid; and 2) tetraploid meiosis is possibly the most obstructive factor in improving tuber yield by 4x × 4x matings.

It is unreasonable, however, to make the above statement without some further considerations. These diploid materials (Phureja-Tuberosum haploid hybrids) contain different germplasm sources than tetraploid Tuberosum cultivars. Thus the increase in genetic diversity in progeny obtained from intermating them could have a favorable effect, since unlike alleles will be incorporated and different kinds of interactions made possible. This consideration, however, becomes quite unnecessary when the performance of 4x × SDR and 4x × 4x families are compared. If the significantly higher tuber yield observed in 4x × FDR families was caused by increased genetic diversity alone, we would expect the amount of increase to be similar to that observed in 4x × SDR families, since all diploid parental clones were of similar genetic background.

These observations are encouraging, for they provide further evidence for the practicality of maximizing diversity and heterozygosity at the tetraploid level by FDR sexual polyploidization. It is understood that these conclusions are limited to the materials used in this experiment, but considering the amount of materials and number of parental clones involved, these conclusions may well be applicable in a much wider range of materials. The observed genotype × environment interaction may present a problem in selection, but these significant interactions may be due to the extremely different growing conditions of Hancock and Rhinelander.

The tuber yield of category 2 families (4.1 lbs./hill) was higher than that of category 3 families (3.9 lbs./hill), but the difference was not significant. This observation may be taken to indicate that SDR gametes are as good as, or better than meiotic products from tetraploids. If we consider the tuber yield of the four SDR parents (1.9 lbs./hill), the increase in tuber yield of their progeny obtained from 4x × SDR matings is quite significant. On the other hand, tuber yield of families from 4x × 4x matings (3.9 lbs./hill) was lower than their 4x parents (4.4 lbs./hill). This comparison alone, appears to favor SDR gametes in breeding over the n (2x) gametes. However, this increase may be explained by the increase in genetic diversity instead of the superiority of SDR gametes. If this explanation is valid, it somehow strengthens the advantage of FDR gametes, because, as mentioned above, if genetic diversity accounts for the increase in tuber yield up to the level of 4x × 4x families, as in the case of 4x × SDR families, then the increase observed in 4x × FDR families which was above this point must be attributed to the advantage of FDR gametes.

An alternative explanation for the increase in yield of 4x × SDR families is that SDR gametes do have an advantage over n(2x) gametes, but the amount of advantage is only large enough to compensate for the parental genotypic inferiority of the diploid parents as compared to the superior tetraploid parents used in this experiment. A third possible explanation is that SDR gametes have only a limited amount of advantage over the n (2x) gametes regardless of the 2x parental genotype due to the amount of homozygosity contained in SDR gametes. A superior diploid genotype forming SDR gametes will not produce better progeny, when mated to a tetraploid, than those obtained from 4x × 4x matings. These possible explanations can be differentiated by crossing diploid clones with significantly different tuber yield, of diverse genetic background, and forming SDR gametes, to a number of 4x parents. If the first explanation is correct, the increase in tuber yield of the progeny should be disproportional to the genetic relationships between the 4x and 2x parents. If the second explanation is correct, then the increase in tuber yield of the progeny should be proportional to the tuber yield of the diploid parents. If there is no significant differences between progeny obtained, then the third possible explanation is correct. Unfortunately, in the present experiment the diploid parental clones were not significantly different in either tuber yield or genetic makeup, and we were not able to differentiate these possible explanations.

The partitioning of genotypic differences into general and specific combining abilities facilitated our interpretations in regard to the comparative values of FDR, SDR and n (2x) gametes, provided further evidence for the cytological interpretation of distinct mechanisms of diplandrogenesis and lent support to Mendiburu's previous interpretation concerning the essential components of yield. When families from one category were analyzed, only S.C.A. was significant. This finding supports Mendiburu's interpretations that non-additive genetic effects are the important components for tuber yield. Thus, the superiority of FDR gametes in breeding is due to their ability to transfer a large amount of the intra- and interlocus interactions from parent to offspring. It also indicates that although FDR in general is superior, there are differences between progeny obtained from crosses involving different FDR diplandrous clones. Some combinations between parents may be superior than others even if FDR gametes participated in all matings.

When families from category 1 and 2 or 1 and 3 were analyzed, both S.C.A. and G.C.A. (2x) were significant although no significant G.C.A. was observed when each category was analyzed separately. The increased contribution of G.C.A. (2x) observed can only be attributed to the difference between FDR and SDR (or FDR and n (2x)) gametes. This observation not only indicates the general superiority of FDR gametes over SDR and n (2x) gametes, but also the uniformity of FDR gametes because no significant G.C.A. was detected when category 2 and 3 were analyzed together. The differences between FDR and SDR gametes in combining ability further substantiated our cytological interpretations that mechanisms of diplandroid formation we have discovered, namely ps, and pc 1 and pc 2 are distinctly different.

The increase of G.C.A. (2x) also suggests that FDR gametes were more homogeneous than SDR or n (2x) gametes. This observation should not be taken to indicate the importance of additive genetic effects as the main cause of general combining ability, since the differences observed between families within each category were due to S.C.A. (non-additive genetic effects). The significant G.C.A. of FDR gametes was by virtue of their ability in conserving parental genotypes and especially the non-additive portion of the genetic effects.

The homogeneity of FDR gametes provides an interesting prospect of using FDR diplandroid clones as testers for evaluating the performance of tetraploid parents. In general, two main variables contribute to the differences between progeny obtained from matings between testers and the genotype being tested; the variability of gametes from the tester, and the variability of gametes from the genotype being tested. Since FDR gametes from a diplandrous clone will be "significantly" more homogeneous than n (2x) gametes from a tetraploid tester, the variability of gametes from a tester can be minimized and a more critical evaluation can be made of the gametes from the tetraploid being tested. Furthermore, the highly heterozygous nature of FDR gamates may provide tester stocks that form homogeneous, but heterozygous, gametes which are not available in conventional breeding methods. If a number of FDR testers are available which differ significantly in performance, the difference between tetraploids may be detected by studying progeny obtained from 4x × FDR matings. Gametes produced by SDR have little advantage as testers over n (2x) gametes, since they may be as heterogeneous.

The results obtained from this experiment clearly demonstrated the advantage of FDR gametes in breeding over SDR and n (2x) gametes. Tuber yields of 4x × FDR families were significantly improved despite the unselected diploid parents from which FDR gametes were generated. It is possible that even greater improvement can be achieved by using selected (higher yielding) diploid clones that form FDR gametes. The feasibility and advantage of improving tuber yield of potato by sexual polyploidization with FDR gametes are evident.

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