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Evaluation of Potato Hybrids Obtained from Tetraploid-Diploid Crosses

I. Parent-Offspring Relationships

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With 5 tables

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Abstract

A total of 45 tetraploid-diploid ($4x-2x$) hybrid progenies were obtained by crossing each of ten diploid parents as males to each of five tetraploid parents. A relatively low degree of determination (R^2) of both $4x$ and $2x$ parents on the performance of their $4x-2x$ hybrid progenies was found for all six traits studied. This implies that test crossing and subsequent progeny analysis is necessary before such parents can be used in a breeding program. Since marketable yield was found to have a higher predictability than total yield, it is the preferred yield trait to be measured. Diploids which produce $2n$ gametes via FDR usually give rise to $4x$ progenies with a greater amount of heterosis than similar progenies derived from diploids which produce $2n$ gametes via SDR, although such heterosis is not necessarily expressed in terms of marketable yield.

Key words: *Solanum tuberosum* — $2n$ gametes — heterosis — yield components — marketable yield

Diploid ($2x$), $2n$ pollen-producing clones now represent a major source of breeding material in the potato, *Solanum tuberosum* L. since they can be used to cross with tetraploid ($4x$) parents to produce $4x$ progenies. Many reports (see reviews by BIRHMAN and GARG 1989, CARROLL and DE MAINE 1989, HERMSEN 1984, HERMUNDSTAD and PELOQUIN 1987, IWANAGA et al. 1989, ROSS 1986) confirm the potential breeding value of this material, but there are still some problems associated with the $4x-2x$ hybridization approach. These include the availability of a sufficiently large number of well-adapted $2n$ pollen-producing diploid parents.

In earlier studies, only a few $2x$ parents were used in producing $4x-2x$ hybrids and although recently more $2n$ pollen-producing diploids have been used in $4x-2x$ hybridization studies (ORTIZ et al. 1988, SCHROEDER 1983), the number still is not large. Another problem is the evaluation of $2x$ parents for their potential to produce superior $4x$ progenies in $4x-2x$ cross combinations. The best way to evaluate a series of $2x$ parents is to hybridize them with a series of $4x$ parents in a factorial mating design. However, fertility levels and other practical problems may prevent the completion of crossing combinations required in the mating design. The loss of symmetry in the mating design would create difficulties in evaluating the combining abilities of $4x$ and $2x$ parents for quantitative traits.

The aim of the present series of reports is: a) to assess the breeding potential of $4x$ and $2x$ parents and their progenies under semi-commercial conditions as practiced in Atlantic Canada, and b) to present a method for evaluating the breeding potential of parents based on data obtained from experiments in an incomplete set of progenies between these parents.

Materials and Methods

Detailed information about the fertility level and genetic background of the ten $2x$ male parents used in this study is presented in Table 1. Each $2x$ male was successfully crossed with three to five $4x$ female parents. Of the possible total 50 cross combinations, 45 were available for analysis. The five missing cross

Table 1. Fertility level and genetic background of 2x male parents

Clone	Pollen				4x—2x cross ²		Genetic background
	Stain %	% Large		2n Mechanism ¹	Total no.	Seeds per fruit	
		Range	Mean		frts.		
W5295.7	70	14—42	25	p.s.	90	74	<i>Phureja</i> × haploid <i>Tuberosum</i>
W5337.3	54	4—10	7	p.s.	67	23	<i>Phureja</i> × haploid <i>Tuberosum</i>
H412-1	55	3—24	8	p.c.	47	11	haploid <i>Tuberosum</i> × haploid <i>Tuberosum</i>
8664-6	62	13—46	31	p.s.	59	158	W5337.3 × H412-1
BPH32-5	75	26—38	32	p.s.	73	234	<i>Phureja</i> × haploid <i>Tuberosum</i>
BPH32-17	62	7—29	14	p.s.	80	60	<i>Phureja</i> × haploid <i>Tuberosum</i>
BPH32-40	82	16—58	37	p.s.	38	151	<i>Phureja</i> × haploid <i>Tuberosum</i>
BPH32-46	56	2—9	6	p.s.	51	28	<i>Phureja</i> × haploid <i>Tuberosum</i>
BPH37-8	86	16—57	37	p.s.	35	102	<i>Phureja</i> × haploid <i>Tuberosum</i>
429	94	12—52	35	p.s.	54	103	<i>Phureja</i>
Weighted mean						95	

¹ p.c. — premature cytokinesis, genetically equivalent to second division restitution.

p.s. — parallel spindle, genetically equivalent to first division restitution.

² Data based on test crosses with the following female parents: Raritan, Superior, Trent, Shepody and Katahdin.

combinations were 'Raritan' × H412-1; 'Raritan' × BPH32-17; 'Superior' × W5337.3; 'Katahdin' × H412-1 and 'Katahdin' × 429. True seed was obtained from the respective crosses in 1983 and 1984. Samples of this seed were planted in the greenhouse and small greenhouse-grown tubers were harvested in 1985. These tubers were planted in the field as "single-hills" in 1986 and from each progeny, one tuber of 50 randomly selected genotypes was saved for subsequent experimentation.

Forty-five medium sized seed-tubers or seed-pieces of each of the 45 progenies were separated into three portions of 15 each and planted in a three-replicate field experiment at the Benton Ridge Potato Breeding Substation in New Brunswick in 1987 and 1988. Four of the five 4x *Tuberosum* parents ('Kennebec', 'Superior', 'Shepody' and 'Katahdin') and eight of the ten 2x parents (BPH32-5, BPH32-17, BPH32-40, BPH32-46, H412-1, W5295.7, W5337.3 and 8664-6) were included in the experiments. Single-row plots, with 45 cm spacing between adjacent plants in a plot, and 91 cm spacing between adjacent plots, were used to plant the trials. In 1987 the plots were planted on May 14 and harvested on October 7 (146 days), and in 1988 planted on May 19 and harvested on October 4 (138 days).

Data of six traits were used in the present study. They were: tuber number (total number of tubers/plot); mean tuber weight (g/tuber derived from total yield/tuber number); total yield (kg/plot of all tubers); marketable yield (kg/plot of tubers larger than

5.1 cm in diameter); chipping score (average reading of color of 15 chips made from 15 medium-sized tubers randomly sampled from a plot). The tubers were stored at 7 °C for three months and reconditioned at 21 °C for 10 days before chipping (scored from 10 [dark] to 100 [light]); and specific gravity (determined by weight-in-water and weight-in-air method).

Analyses of variance (ANOVA) were carried out for each of the six traits according to a randomized block design with three replicates. Separate ANOVA were carried out for the 1987 and 1988 experiments. Combined ANOVA was conducted over the two-year data. Subsequent analyses of data were based on means of progenies and parents over the two-year experiments.

One of the main objectives of the experiment was to evaluate the potential of 2x parents. The mean values of each of the six traits of progenies derived from each of ten 2x parents were calculated based on two-year progeny means.

Data of the four 4x and eight 2x parents and 30 hybrid progenies obtained from them were used for the study of parent-offspring relationships. The means of 4x and 2x parents were compared with those of the progenies for the six traits. A multiple regression analysis of progeny means on means of 4x and 2x parents was carried out to determine whether or not performance of parents can be used to predict merit of their progenies.

Table 2. Analyses of variance of hybrid progenies for six traits

Source	Mean squares						
	Degrees of freedom	Tuber no.	Mean tuber weight	Total yield	Mark. yield	Chip score	Specific gravity
Years	1	2703.2**	4198.9**	295.0**	309.0**	6050.5**	2734.7
Progenies	44	1952.6**	582.6**	6.0**	9.4**	46.4**	43.4**
Years × Progenies	44	427.3	103.7	3.6	4.5*	23.2*	15.4*
Errors	279	373.8	129.6	2.8	2.9	14.0	10.6

* Significant at P = .05

** Significant at P = .01

Results

Analyses of variance revealed highly significant differences ($P < .01$) between hybrid progenies for all traits. Progeny × year interactions were significant ($P < .05$) for marketable yield, specific gravity and chipping score, but not for

total yield, tuber number and mean tuber weight (Table 2).

Table 3 compares the performance of progenies of each of the ten 2x parents. Progenies of 8664-6 and 429 produced a high tuber number and a low mean tuber weight. As a conse-

Table 3. Performance of progenies of each of ten 2x parents based on two-year means of progenies obtained from each parent

2x parent	No. of crosses	Mean ± S.D.					
		Tuber no./ plot	Mean tub. wt. g/tuber	Total yield kg/plot	Mark. yield kg/plot	Specific gravity*	Chip score
W5295.7	5	184.0 ± 22.3	117.6 ± 10.0	21.3 ± 1.2	14.2 ± 1.6	91.6 ± 4.5	47.5 ± 2.9
W5337.3	4	187.2 ± 30.8	109.5 ± 11.3	20.3 ± 2.4	13.7 ± 2.2	86.1 ± 6.8	43.2 ± 5.1
H412-1	3	158.0 ± 5.6	119.0 ± 4.2	18.6 ± 0.8	13.1 ± 1.4	88.2 ± 3.2	47.7 ± 1.5
8664-6	5	232.3 ± 14.4	92.4 ± 8.6	21.2 ± 1.0	11.8 ± 1.9	89.7 ± 2.4	46.2 ± 4.4
BPH32-5	5	196.9 ± 16.4	109.4 ± 7.3	21.0 ± 1.8	13.4 ± 1.3	83.4 ± 3.2	44.2 ± 5.0
BPH32-17	4	158.0 ± 13.0	130.1 ± 4.0	20.0 ± 1.3	14.1 ± 0.7	85.9 ± 4.6	46.4 ± 4.0
BPH32-40	5	166.1 ± 18.3	123.4 ± 8.4	20.2 ± 1.3	14.3 ± 1.7	87.5 ± 4.4	43.3 ± 4.7
BPH37-46	5	205.6 ± 16.1	105.8 ± 6.5	21.4 ± 1.1	13.9 ± 1.2	86.6 ± 3.3	43.9 ± 3.3
BPH37-8	5	159.5 ± 15.0	136.3 ± 14.1	21.3 ± 1.8	15.7 ± 2.1	88.7 ± 4.8	48.2 ± 5.3
429	4	219.4 ± 38.0	89.1 ± 16.2	18.8 ± 2.8	10.0 ± 2.8	93.8 ± 1.6	54.2 ± 2.8

* (specific gravity-1) × 1000

Table 4. Mean performance and standard deviation for six traits of hybrid progenies and their 4x and 2x parents

Trait	Progenies	4x parents	2x parents
Tuber no. per plot	188.7 ± 29.2	103.1 ± 15.6	194.7 ± 57.7
Mean tuber wt. (g/tuber)	113.8 ± 13.2	179.0 ± 39.2	79.6 ± 17.7
Total yield (kg/plot)	20.9 ± 1.5	17.6 ± 2.1	15.0 ± 4.5
Mark. yield (kg/plot)	13.8 ± 1.7	14.8 ± 2.7	6.6 ± 3.2
Chip score	46.4 ± 3.2	52.5 ± 8.0	48.3 ± 6.1
Spec. gr. (s.g. - 1) × 1000	87.0 ± 4.4	89.7 ± 9.3	85.4 ± 6.5
n	30	4	8

Table 5. Relationship between progeny means (y) and $4x$ (x_1) and $2x$ (x_2) parents

Trait	$y = a + bx_1 + cx_2$	R^2
Tuber no.	$125.35 + .14x_1 + .25x_2$	.19
Mean tuber weight	$68.84 + .13x_1 + .33x_2$	.30
Total yield	$15.20 + .21x_1 + .12x_2$	.18
Mark. yield	$7.28 + .34x_1 + .21x_2$	.40
Chip score	$31.21 + .19x_1 + .10x_2$	.22
Specific gravity	$44.90 + .20x_1 + .28x_2$	.25

quence, the progenies of both showed a low marketable yield. Progenies of BPH37-8 gave a high marketable yield because of the high mean tuber weight. Progenies of 429 also gave the highest specific gravity and chipping score. The rest of the progenies showed only small differences in these two traits.

Means of 30 progenies were compared with those of their four $4x$ and eight $2x$ parents tested in the experiments (Table 4). The $4x$ parents on average produced a lower tuber number and a higher mean tuber weight, total and marketable yields than the $2x$ parents. The grand mean of all progenies resulted in a high tuber number which was close to that of $2x$ parents. The mean tuber weight of all progenies was higher than that of $2x$ parents but still lower than the mid-parent value. The total yield of the progenies surpassed both parental groups. The marketable yield of the progenies was high and only slightly lower than that of the $4x$ parents. Progenies and parents were close to one another in chipping score and specific gravity. The $4x$ parental group performed slightly better than the other two groups. The size of standard deviations of all traits indicated the variation between progeny means was much lower than those of the two parental groups with only one exception. The standard deviation of tuber number of progenies was higher than that of $4x$ parents but considerably lower than that of $2x$ parents.

Multiple regression analyses of progeny means of $4x$ and $2x$ parents were performed for all traits (Table 5). The degree of determination (R^2) ranged from .19 to .40. The performance of both $4x$ and $2x$ parents had poor predicting power on their progenies.

Discussion

Results from the present study confirm the high yielding ability of $4x-2x$ hybrids when

grown under semi-commercial conditions. Some previous studies have used transplants in some yield trials. Since it is still not clear whether yields of transplant progenies are correlated with yields of the same progenies grown from tubers (SCHROEDER 1983), the use of transplants was not considered acceptable for this study. Also rejected for a study of this nature was the use of small greenhouse-grown seedling tubers since they do not produce typical growth. This meant that after the seed had been obtained from the various crosses, two years were taken up (one year to produce greenhouse-grown seedling tubers and one year to produce the first generation of field-grown seed tubers) in the raising of a healthy field-grown seed potato crop with which to commence this trial. The results of these experiments should, therefore, not be confounded with the above-mentioned situations which do not occur under commercial conditions. It is conceivable that some of the conflicting results regarding the relative importance of general and specific combining ability of yield in $4x-2x$ crosses (DE JONG and TAI 1977, MENDIBURU and PELOQUIN 1977, McHALE and LAUER 1981a, MOK and PELOQUIN 1975, ORTIZ et al. 1988, SCHROEDER 1983, VEILLEUX and LAUER 1981) may, in part, be explained by the different ways in which the hybrid material was handled (for example, use of transplants and/or greenhouse-grown seed tubers versus field-grown seed tubers). Another reason for the above-mentioned discrepancies might be due, as already pointed out by ORTIZ et al. (1988) to the difference in width of genetic background of the parental material used.

This study indicates a relatively low degree of determination (R^2) performance of $4x-2x$ hybrid progenies from the parental performance for all six traits. It is, nevertheless, of interest that the degree of determination was

.40 for marketable yield but only .18 for total yield (Table 6). In a comparison between progeny means derived from two male parents in 4x—2x crosses DE JONG and TAI (1977) found a significant difference for marketable yield but not for total yield. McHALE and LAUER (1981b) and VEILLEUX and LAUER (1981) also reported a higher predictability of marketable than of total yield.

In this study, the male parents had a greater effect on tuber number, mean tuber weight and specific gravity of their 4x—2x progeny than the tetraploid (female) parents. For total yield, marketable yield and chip score the 4x parents had a greater influence than the 2x parents on the 4x—2x progeny (Table 5). ORTIZ et al. (1988) reported a stronger influence of 2x (male) parents than of 4x (female) parents for all traits studied in their experiment (vigour, earliness, total yield, marketable yield and tuber colour, size, shape and appearance). A strong parental effect between the 2x parent and its 4x—2x progeny for maturity and tuber traits related to appearance was also reported by DE JONG and TAI (1977) and SCHROEDER (1983).

Of the ten diploid parents used in this study, eight were derived from Phureja × haploid Tuberosum hybridizations. All of these eight produced 2n pollen via first division restitution (FDR). Of the remaining two, one, H412-1, was derived from a haploid Tuberosum × haploid Tuberosum hybridization, and produced 2n pollen via second division restitution (SDR). The other clone, 429, was a Phureja selection which produced 2n pollen via FDR. All of the male parents used were selected and, therefore, cannot be considered as representative samples of the populations from which they were derived. It is, nevertheless, of interest to make a comparison between the progenies of H412-1 and 429. H412-1 probably contributed a minimum of heterozygosity to its 4x—2x progeny because: a) it has a strictly Tuberosum background, and b) it produces 2n gametes via SDR. On the other hand, clone 429, probably contributed a great amount of genetic diversity to its 4x—2x progeny since a) it is strictly Phureja, and b) it produces 2n gametes via FDR. H412-1 progenies ranked lowest for total yield but they ranked eighth for marketable yield (Table 3).

Recent analyses of hybrid potato progenies have indicated the importance of the two yield

components tuber number and mean tuber weight in heterosis in both 4x—2x (CARROLL and DE MAINE 1989) and 4x—4x (TARN and TAI 1977) crosses. The increase in ranking for the H412-1 progenies from total yield to marketable yield is probably due to the multiplicative effect of these two yield components. H412-1 progenies were tied for last place for tuber number but they ranked fourth for mean tuber weight. As a result of the multiplicative effect, the H412-1 progenies ranked eighth for marketable yield. The progenies of 429 performed rather differently in ranking second for tuber number but lowest for mean tuber weight. As a result of the multiplicative interaction, there was a greater drop from total yield to marketable yield in the progenies of 429 than any other progenies. Of the 18.8 kg per plot total yield of the progenies of 429, only 10.0 kg per plot (53 %) was in the marketable category (Table 3).

Our findings do not contradict the report by MOK and PELOQUIN (1975) that diploids which produce 2n gametes via FDR generally produce higher yielding 4x progenies in 4x—2x crosses than those diploids which produce 2n gametes via SDR. However, factors related to marketable yield such as those described above, and others such as adaptation and maturity, which are not necessarily strongly related to heterosis, may nevertheless have a strong influence on the performance of the progeny. It is conceivable that previously reported (ERJEFALT 1978 and 1984, VEILLEUX and LAUER 1981) mediocre yields from progenies of some diploid FDR parents in 4x—2x crosses may have been caused by similar factors.

The results reported here, along with the results of previously cited authors, have a number of implications for the use of the 4x—2x breeding method in a practical breeding program. These include: (1) the relatively low predictability of phenotypic yield from both 4x and 2x parents on 4x—2x hybrid progenies requires test crossing and subsequent progeny analysis; (2) marketable yield is the preferred yield trait to be measured since it has a higher predictability than total yield. However, a strong selection pressure for yield at the diploid level is not advisable. Similar conclusions were reached by MASSON and PELOQUIN (1987); (3) although the genetic differences between 2n gametes of diploid parents formed via FDR and SDR play a major role in heterosis and the

performance of $4x-2x$ hybrid progenies, other factors may, on occasion, override the differences between FDR and SDR gametes.

Zusammenfassung

Untersuchungen an Kartoffelhybriden aus Kreuzungen: diploid $\times$ tetraploid

I. Eltern-Nachkommenschaftsbeziehungen

Aus einer Kreuzungsserie von jeweils 10 als männliche Partner verwendeten, diploiden Eltern mit 5 tetraploiden Eltern entstanden insgesamt 45 Hybrid-Nachkommenschaften ($4x-2x$). Die Bestimmtheitsmaße (R^2) der Regressionen zwischen beiden Eltern ($2x$ und $4x$) und ihren $4x-2x$ -Hybrid-Nachkommenschaften waren für alle 6 untersuchten Ertragsmerkmale verhältnismäßig niedrig. Dies bedeutet, daß vor der Verwendung solcher Eltern für die Züchtung Testkreuzungen mit anschließender Prüfung der Nachkommenschaft notwendig sind. Der Ertrag an marktfähigen Knollen läßt sich besser voraussagen als der Gesamtertrag und sollte deshalb für die Beurteilung als Ertragsmaß bevorzugt werden. Diploide Genotypen, die $2n$ -Gameten über die erste Restitutionsteilung ausbilden, erzeugen in der Regel $4x$ -Nachkommen mit höherer Heterosis als ähnliche Nachkommen von Diploiden, die $2n$ -Gameten über die zweite Restitutionsteilung ausbilden, obgleich sich eine solche Heterosis nicht auf die Werte für den Ertrag marktfähiger Ware auswirken muß.

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