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Evaluation of Potato Hybrids Obtained from Tetraploid-Diploid Crosses

II. Progeny Analysis

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With 4 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. Means of six traits of the 45 progenies obtained from a two-year experiment were used in progeny analysis. A new mathematical model is developed for analyzing the incomplete two-way table. It is modified from the conventional model for factorial mating design. The aim of the model is to evaluate the potential of 2x parents in terms of their mean effects (μ_i) and sensitivity measures (B_i) to the 4x parents. The 4x parents were treated as testers in the model. They were compared by the estimates of the magnitude of tester effects (g_j). The mean effects of 2x parents showed a dominant influence on variation of tuber number and mean tuber weight of the hybrid progenies. They also demonstrated a substantial influence on the variation of total and marketable yield, chipping score and specific gravity. The linear response of 2x parents to 4x parents, however, also showed a substantial influence on the variation of the latter traits. The information on μ_i and B_i are useful in terms of choosing superior 2x parents and, together with g_j of 4x parents, 4x—2x progenies for specific traits. The μ_i and B_i estimates of the six traits showed a complicated interrelationship to each other.

Key words: *Solanum tuberosum* — progeny analysis — incomplete mating design — 4x—2x hybrids

There are two ways to evaluate the potential of hybrid progenies obtained from mating between many parents: (a) parent-offspring relationships and (b) progeny analysis. Parent-offspring relationships compare the performance of progenies to that of their parents. It is particularly suitable to study heterosis. High parent-offspring association also implies high heritability and general combining ability of parents of a concerned trait. Genetical interpretation of results of parent-offspring relationships may be difficult when the parents have different genomic structures. Such is the case of progenies of tetraploid-diploid (4x—2x) crosses in potatoes.

Progeny analysis uses data obtained from hybrid progenies in progeny test experiments. It does not require the involvement of parents in the experiments. The analytic results are aimed to evaluate parents and their progenies in terms of general and specific combining abilities. The progenies are generated by mating between parents according to a specific mating design. The purpose of the diallel design is to test progenies obtained between all possible combinations of a group of parents. It is not applicable to test progenies from 4x—2x crosses because the parents of a progeny are from two distinct groups (i.e. 4x and 2x) of parents. The factorial design uses all possible crossing combinations between a group of male parents to another group of female parents. This is the design used in many studies on progenies of 4x—2x of potatoes (MOK and PELOQUIN 1975, DE JONG and TAI 1977, TAI and DE JONG 1980, MASSON 1985, SCHROEDER 1983, VEILLEUX and LAUER 1981, ORTIZ et al. 1988). The aim of the present report is to evaluate the

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breeding potential of parents and hybrid progenies based on data obtained from experiments in an incomplete set of progenies between 4x and 2x parents.

Mathematical Model

The conventional mathematical model for a m*n factorial mating design is as follows:

$$y_{ij} = \mu + g_i + g_j + s_{ij} + e_{ij} \quad (1)$$

where y_{ij} is the observed value of the progeny obtained from crossing the parent of the first group of m parents with the parent of the second group of n parents, g_i and g_j are their respective general combining ability (GCA) effects, s_{ij} is the specific combining ability (SCA) effect between the parents, and e_{ij} is the error deviate. All GCA and SCA effects can be readily estimated with a complete m*n two-way table. This is carried out by the routine statistical analysis of factorial experiments. It is not so, however, when some of the cells in the table are empty or 'missing'. For evaluating parents and their hybrid progenies tested in an incomplete m*n factorial experiment, the following modified model is proposed:

$$y_{ij} = \mu + g_i + g_i + b_i g_j + \sigma_{ij} + e_{ij} \quad (2)$$

in which $b_i g_j + \sigma_{ij} = s_{ij}$. This model treats the two groups of parents in an asymetrical fashion. It is assumed that the first group of parents are the ones desired to be evaluated for their merit in a breeding program. They may represent newly developed breeding materials or selections from exotic germplasm resources. The second group of parents are treated as "testers". They are mostly likely samples of the parental stocks employed in a breeding program. Another important assumption is that the s_{ij} effects in (1) can be largely accounted for by the linear component $b_i g_j$ in (2). In other words, SCA is mainly induced by the differential linear response of the parents in the first group to the testers. Model (2) can be further simplified as follows:

$$y_{ij} = \mu_i + B_i g_j + \varepsilon_{ij} \quad (3)$$

where $\mu_i = \mu + g_i$, $B_i = b_i + 1$ and $\varepsilon_{ij} = \sigma_{ij} + e_{ij}$. The μ_i and B_i are referred to as the mean effect and sensitivity measure of the ith parent and g_j the tester effect of the jth tester. DIGBY (1979), in analyzing genotype-environment interactions, proposed an iteration procedure for estimating the mean and sensitivity of each of a group of genotypes tested over a series of environments based on data obtained from incomplete two-way tables. The procedure is equally applicable to the modified model in (3).

Materials and Methods

Detailed information about the fertility level and genetic background of the ten 2x male parents used in this study was presented by DE JONG and TAI (1991). Each 2x male was successfully crossed with three to five 4x female parents. Of the possible total of 50 crossing combinations, 45 were available for analysis.

Analyses of variance were carried out for each of the six traits and reported in the companion paper (DE JONG and TAI 1991). Means of all 45 progenies tested in the experiments were used in an analysis based on a mathematical model modified from the conventional model for investigating factorial experiments. The new model is described in the last section. The aim of the present study is to evaluate the

Table 1. Estimates of mean effect (μ_i) and sensitivity measure (B_i) of 2x parents

	Tuber no.		Mean tub. wt.		Total yield		Mark. yield		Sp. gravity		Chip. score	
	μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i
W5295.7	183.97	2.28	117.60	1.54	21.27	.59	14.23	.85	91.59	1.14	47.48	.80
W5337.3	191.45	−3.56	109.97	−.84	20.30	.95	13.73	1.40	86.35	1.63	42.85	1.35
H412-1	158.97	−.45	119.39	.36	18.37	1.35	12.80	1.03	87.85	.39	47.74	−.03
8664-6	232.3	−.13	92.37	.76	21.24	.26	11.77	.25	89.70	.54	46.23	.83
BPH32-5	196.9	1.05	109.43	1.18	21.04	.99	13.40	.52	83.43	.80	44.22	1.53
BPH32-17	158.62	−.37	130.31	.31	20.34	−.79	14.07	.01	86.56	1.05	45.72	.61
BPH32-40	166.14	2.01	123.38	1.26	20.22	.81	14.34	1.29	87.55	1.10	43.27	1.21
BPH32-46	205.63	1.72	105.82	1.03	21.36	.75	13.85	.89	86.56	.84	43.90	.93
BPH37-8	159.54	.84	36.33	2.36	21.33	1.03	15.71	1.16	88.66	1.28	48.16	1.57
429	219.79	3.26	89.30	.67	19.51	2.30	10.28	1.87	93.21	.50	54.14	−.03

Table 2. Estimates of tester effect (g_j) of 4x parents

Tester	Tuber number	Mean tub. weight	Total yield	Mark. yield	Specific gravity	Chipping score
'Raritan'	−7.29	2.38	−1.82	−1.46	2.66	−4.06
'Superior'	−4.76	−.12	.06	.03	.65	−1.06
'Trent'	13.05	−9.40	−.26	−.88	3.84	4.15
'Shepody'	−1.52	6.10	.79	1.69	−2.21	−.53
'Katahdin'	.51	1.06	1.22	.62	−4.94	1.51

potential of ten 2x parents in 4x—2x crosses by hybridizing them with five 4x parents which served as "testers". The mean effect (μ_i, i = 1, 2, . . . , 10) indicates the overall potential of a 2x parent. The sensitivity measure (B_i, i = 1, 2, . . ., 10) indicates the degree of response of the 2x parents to the 4x testers. A tester effect (g_j, j = 1, 2, 3, 4, 5) was also estimated for each of the 4x parents. Mean effects and sensitivity measures of 2x parents and tester effects of 4x parents were then used to calculate fitted values of all possible progenies according to the proposed model i.e. $y_{ij} = \mu_i + B_i g_j$. The representability of the model on observed results was measured by the correlation between fitted and observed values of 45 progenies tested in the experiments.

To study the relationship between the conventional model (1) and the new modified model (2), estimates of SCA (i.e. s_{ij}) effect in (1) were obtained by the difference between observed cross mean and estimate of $\mu_i + g_j$ ($= \mu + g_i + g_j$). A correlation analysis was then carried out between estimates of s_{ij} in (1) and $b_i g_j$ [$= (B_i - 1) g_j$] in (2).

Results

Means of all 45 progenies tested in the two-year experiments were analyzed for each of the six traits according to the modified model for incomplete factorial mating design. Two parameters, mean effect (μ_i) and sensitivity measure (B_i), were estimated for each of the ten 2x parents (Table 1). The tester effect (g_j) was estimated for each of the five 4x parents treated as testers (Table 2). Fitted values of all possible hybrid families were obtained by $y_{ij} = \mu_i + B_i g_j$, i = 1, 2, . . ., 10, j = 1, 2, . . ., 5. Correlation coefficient between fitted and observed values of the 45 progenies tested in the experiments was determined for all traits (Table 3). Variance components due to the mean effect (μ_i) and linear response ($B_i g_j$) in the model were also estimated for all traits based on estimated values of the parameters (Table 3).

High correlations (r_1 values in Table 3) were obtained between observed and fitted values of all traits. The variance component due to mean effect (μ_i) was much larger than that due to linear response ($B_i g_j$) for tuber number and mean tuber weight of the hybrid families. The contribution of the linear response parameter to the variation of progenies for these two traits was small. Total yield and chipping score had a larger variance component due to linear response than that for mean effect. The variance component due to linear response, al-

Table 3. Correlation between observed and fitted values (r_1), between estimates of $b_i g_j$ and s_{ij} parameters (r_2) and estimates of variance components for μ_i and $B_i g_j$ effects

Trait	r_1*	r_2*	Variance components	
			μ_i	$B_i g_j$
Tuber no.	.93	.77	708.93	191.10
Mean tub. wt.	.89	.60	230.34	37.64
Total yield	.79	.52	.94	1.38
Mark. yield	.89	.50	2.27	1.43
Chip. score	.89	.54	7.90	10.44
Sp. gravity	.95	.59	11.10	8.17

* Correlation coefficient significantly different from zero when it is larger than .38 at the 1 % level.

Table 4. Correlation between estimates of mean (μ_i) and sensitivity measure (B_i) of six traits of the 2x parents

		Tuber no.		Mean tub. weight		Total yield		Mark. yield		Chipping score		Specific gravity	
		μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i	μ_i	B_i
Tuber no.	μ_i		.17*	−.95	−.17	.29	.27	−.70	.05	.29	−.36	.22	−.11
	B_i			−.16	.69	.14	.33	−.18	.21	.47	−.42	.51	−.23
Mean tub. wt.	μ_i				.34	.03	−.42	.87	−.19	−.33	.51	−.30	.35
	B_i					.48	.06	.40	−.04	.19	−.06	.22	.30
Total yield	μ_i						−.40	.43	−.37	−.13	.41	−.31	.71
	B_i							−.45	.86	.37	−.29	.54	−.26
Mark. yield	μ_i								−.21	−.45	.71	−.56	.68
	B_i									.42	.11	.40	−.15
Chip. score	μ_i										−.25	.79	−.56
	B_i											−.47	.69
Sp. gravity	μ_i												−.65
	B_i												

* Correlation coefficient significantly different from zero when it is larger than .63 and .83 at the 5% and 1 % levels, respectively.

though smaller than that for mean effect, was of a substantial magnitude for marketable yield and specific gravity.

The $B_i g_j$ effect showed highly significant correlation with s_{ij} effect for all traits (r_2 in Table 3). The sizes of the correlation coefficient were ranged from moderate to moderpately high.

Correlation analyses between all possible pairs of μ_i and B_i effects are given in Table 4. For yield and yield components, negative correlations were observed between μ_i values of tuber number and mean tuber weight (r = −.95**), and tuber number and marketable yield (−.70*). Positive correlations were obtained between μ_i values of mean tuber weight and marketable yield (.87**), and between B_i values of tuber number and mean tuber weight (.69*), and total yield and marketable yield (.86**). Both the μ_i values (.79*) and B_i values (.69*) of specific gravity were positively correlated with the corresponding ones of chipping score. The μ_i values of both total (.71*) and marketable yields (.68*) were positively associated with B_i values of specific gravity. The μ_i value of marketable yield was also correlated to the B_i values of chipping score (.71*). Another interesting correlation was the negative correlation (−.65*) between μ_i and B_i values of the chipping score. All other correlations were not significant.

Results in Table 3 showed that the mean effects of 2x parents dominated the variation of hybrid families for tuber number and mean tuber weight. The 2x parents BPH32-17, BPH37-8 and BPH32-40 showed a low μ_i value for tuber number and a high μ_i value for mean tuber weight. They represent better parents to produce progenies with ideal yield components, i.e. a low number of tubers with a good size grade. The opposite was true for 8664-6, 429 and BPH32-46. These parents produced progenies with a large number of small tubers.

The parameters μ_i and B_i should be jointly used to judge the merit of the 2x parents for the rest of traits. Diploid parents with above average μ_i and low absolute B_i values are expected to produce good progenies without requiring a specific type of 4x parent as a crossing partner. The results in Table 1 suggest that good progenies would be produced by 8664-6 for high total yield, by BPH32-17 for high marketable yield, and by 429 for high specific gravity and high chipping score.

The merit of 2x parents with relatively high absolute B_i values should be judged with care. They can only produce superior progenies when crossed with a suitable 4x parent. The results in Tables 1 and 2 can be used for this purpose. For example, BPH32-40 and BPH37-8 had high mean effects with positive B_i values for marketable yield. Shepody was a 4x parent showing a large positive tester effect. Progenies produced by crossing these two 2x parents with Shepody can be expected to have progenies with a high marketable yield. A similar situation exists by crossing W5295-7 and BPH37-8 with Raritan and Trent for high specific gravity, and BPH37-8 with Trent for high chipping score.

Most of the B_i values were positive. Thus, the results in Table 2 reveal that, in general, Shepody contributed to lower tuber number, higher mean tuber weight, and higher total and marketable yields than other 4x parents. It also contributed to low specific gravity and to a lesser extent, to low chipping score. Trent contributed to high specific gravity and chipping score but it was a poor parent for yield components and yield. None of the five 4x parents were superior testers for all traits.

It is interesting to note that the 2x parent 8664-6 had relatively small B_i values which were among the low ones for all traits. BPH37-8 had relatively high positive B_i values for all traits except tuber number. H412-1, the only SDR 2x parent, had lowest μ_i values on tuber number and total yield. It had a moderate μ_i for tuber size and a below average μ_i for marketable yield. It also had small B_i values for tuber number, mean tuber weight, specific gravity and chipping score.

Discussion

Reports on relationship between 2x parents and their 4x—2x progenies indicate a lack of agreement between rankings of parents and progenies for such traits as tuber number, total yield and marketable yield (McHale and Lauer 1981, Veilleux and Lauer 1981, Schroeder 1983). Schroeder (1983) also found no relationship for total yield between 4x—2x families and 4x, 2x and mid-parent means, but significant correlation for average tuber weight between progenies and 2x parents. The study by De Jonge and Tai (1991) revealed a low degree of determination of 4x and 2x parents on the performance of their hybrid families for all six evaluated traits. It appears that progeny test experiments are required to assess the merit of parents and cross combinations in a 4x—2x breeding program.

A problem of using the factorial mating design to evaluate hybrid progenies is that some of the crossing combinations may not be obtainable. Evaluating the parental value of a large number of 2x clones by crossing them with a number of 4x parents also requires a large amount of work (Ortiz et al. 1988). These authors suggest the use of a single 4x parent with a low GCA as tester. One would also have to ensure that such a tester does not have a strong SCA effect with all 2x clones. The mathematical model used in the present study represents a modification of the conventional model for the factorial mating design. A linear relationship is imposed on the SCA effect, i.e. $s_{ij} = b_i g_j + \sigma_{ij}$. There are two advantages of the modified model over the conventional one. The identification of a desired parent is not only by its GCA effect but also by its sensitivity to the mating partner. The analytic procedure allows a certain degree of missing matings in the design. The new model, however, should be used in a special situation where parents of two mating groups are not equally treated. In the present study, advanced breeding lines from a 2x breeding population were desired to be evaluated for their value in future breeding work in 4x—2x combinations. The 4x parents thus served as a representative sample of the 4x parental stocks for the purpose of evaluating the 2x parents. Results from the present study indicated that the linear component $b_i g_j$ is correlated, but not completely so, with the SCA effect in the conventional model. The fitness of the new model, however, is reflected by the high correlation between observed and fitted values of all six traits (Table 3).

The mean effects of 2x parents dominate the variation of the two yield components, and are comparable to or larger than those of the effects due to linear response for the other four traits. The results imply the important role of GCA of the 2x parents. The importance of GCA for 2x parents on yield and yield components of 4x—2x families have been reported in many papers (Mendiburu and Peloquin 1977, De Jong and Tai 1977, McHale and Lauer 1981, Veilleux and Lauer 1981, Schroeder 1983, Ortiz et al. 1988).

The linear response (i.e. $B_i g_j$) effect of the modified model is contributed by the GCA of 4x testers (g_j) plus the linear response of 2x on the g_j effects ($b_i g_j$), i.e. $B_i g_j = b_i g_j + g_j$. For a trait subjected to a high level of influence by the $B_i g_j$ effect, the relative importance of g_j and

b_ig_j in B_ig_j depended on the degree of variation of the B_i values. Only the GCA of 4x testers play an important role when all B_i values of 2x parents are close to unity. The B_i values for all six traits show a substantial variation between 2x parents (Table 1). The importance of specific combining ability (SCA), as measured by the linear component (b_ig_j), cannot be neglected for the four traits with a large variance component due to B_ig_j effects.

The results of μ_i and B_i estimates of 2x parents and g_j estimates of 4x parents can be combined to evaluate the merits of the parents and the hybrid families in terms of regressing the 2x parents on the 4x testers. It may be argued that the results in Table 1 and Table 2 are more difficult to interpret in terms of combining abilities of the parents than the conventional model for studying factorial mating experiments. They can, however, be easily used to identify superior parents and families. A 2x parent with a high μ_i and a close to zero B_i can be used in 4x—2x crosses without a critical concern of the choice of the 4x parent. A 2x parent with above average μ_i and high B_i can be used to produce superior progeny via 4x—2x hybridization only when crossed with a complementary 4x parent. The tester effect of the 4x parents should be treated as an independent variable in a regression equation and jointly evaluated with the B_i coefficient of the 2x parent.

The μ_i and B_i estimates of six traits are not entirely independent to one another. It is interesting to observe that the μ_i values of two yield components are negatively associated whereas their B_i values are positively related. No correlation was observed between μ_i and B_i of each of these traits. This suggests independent genetical control on the performances of μ_i and B_i for yield components. There were complicated relationships between quality (specific gravity and chipping score) and yield traits. This suggests the necessity of a careful strategy on selecting 2x parents with optimum μ_i and B_i values for all concerned traits to cross with 4x parents.

Zusammenfassung

Untersuchungen an Kartoffelhybriden aus Kreuzungen: diploid × tetraploid II. Nachkommenschaftsanalyse

Aus einer Kreuzungsserie von jeweils 10 als männliche Partner dienenden diploiden Eltern mit 5 tetraploiden Eltern entstanden insgesamt 45 Hybrid-Nachkommenschaften (4x—2x). Die nach einem zweijährigen Versuch mit diesen Hybriden gewonnenen Mittelwerte von 6 Ertragsmerkmalen wurden für eine Nachkommenschaftsanalyse herangezogen. Zusätzlich wurde aus der unvollständigen Zweiwege-Tafel für die 2x-Eltern ein Regressionskoeffizient ermittelt. Ziel dieses Modellansatzes ist es, den züchterischen Wert von 2x-Eltern für 4x-Eltern anhand ihrer mittleren Effekte (μ_i) und ihrer Regression auf die 4x-Eltern (B_i) zu schätzen. Die 4x-Eltern wurden in diesem Modell als Tester betrachtet und bezüglich ihrer allgemeinen Kombinationseignung (g_j) verglichen. Die mittleren Effekte (μ_i) der 2x-Eltern waren die wesentliche Ursache für die Variation der Knollenzahl und des Knollengewichts bei den Hybrid-Nachkommenschaften. Ebenso beeinflußten sie die Variation des Gesamtertrages, des Ertrages an marktfähiger Ware, der Farbe der Chips and des spezifischen Gewichts in starkem Maße. Aber auch der Regressionskoeffizient (B_i) wies einen starken Einfluß auf die zuletzt genannten Eigenschaften auf. Die Kenntnis von μ_i und B_i ist für die Selektion von überlegenen 2x-Eltern und in Verbindung mit g_j der 4x-Eltern für die Auslese von 4x—2x-Hybrid-Nachkommenschaften mit bestimmten Eigenschaften von Nutzen. Die Schätzwerte von μ_i und B_i standen bei den untersuchten Merkmalen in einer komplizierten Wechselbeziehung zueinander.

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