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Efficiency of potato breeding using FDR 2n gametes for multitrait selection and progeny testing*

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Summary. The objective of this research was to compare the efficiency of the 4x × 2x breeding scheme with the traditional 4x × 4x method with respect to potato improvement. The basis for such a comparison was the parental value of four 2x and four 4x male parents from the International Potato Center (CIP) as measured by multitrait selection and progeny testing. The 2x parents produced 2n pollen by parallel spindles at anaphase II, which is genetically equivalent to a first division restitution (FDR) mechanism. Both 2x and 4x parents were crossed with four common 4x female parents. Thus, 32 families were evaluated over 2 years at four Peruvian locations. A selection index which considered tuber yield, tuber number, average tuber weight and specific gravity was used for multitrait selection. Three FDR 2x parents had better selection index scores than the 4x parents over the four locations. Estimates of broad-sense heritability for total yield using different number of replications and locations were calculated by using the variance components. The 4x × 2x breeding scheme was found to be better than the traditional 4x × 4x method since fewer replications and locations are required to evaluate tuber yield in 4x × 2x progenies than in 4x × 4x progenies. The FDR 2x parents were also better material than the 4x parents for testing combining ability for tuber yield of the 4x progenitors. This could be the result of the mode of FDR 2n pollen formation. The pollen of FDR 2x parents is more heterozygous, but more homogenous than n pollen from 4x parents.

Key words: Selection index – Phenotypic correlations – Genotypic correlations – Heritabilities – 4x × 2x crosses

Introduction

Peloquin et al. (1989) suggested that the 4x × 2x breeding scheme is highly effective for the improvement of the cultivated tetrasomic potato ($2n=4x=48$). They indicated that the use of haploids ($2n=2x=24$) and 2n gametes (gametes with the sporophytic chromosome number) results in a better exploitation of the genetic resources available in potato. The use of haploids allows potato breeders to take advantage of disomic inheritance and consequently breeding at the 2x level, and also to increase the allelic diversity by using wild *Solanum* relatives. Moreover, the production of 2n gametes permits the resynthesis of the 4x potato by either bilateral (2x × 2x crosses) or unilateral tetraploidization (4x × 2x crosses). The production of 2n pollen, which is genetically controlled by a single meiotic recessive, *ps* (Mok and Peloquin 1975a), makes the latter approach feasible; i.e., 2x potatoes with *ps*/*ps* genotypes produce 2n pollen that is equivalent to a first division restitution (FDR) mechanism.

The objective of the research reported in this article was to compare the efficiency of the 4x × 2x breeding method with the traditional 4x × 4x approach. The criterion for such comparison was the parental value of FDR 2x and 4x parents from the International Potato Center (CIP) as measured by multitrait selection and progeny testing.

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Materials and methods

A sampling of parental clones from the International Potato Center (CIP) 2x and 4x breeding programs were intermated in 4x × 2x and 4x × 4x crosses. Thirty-two families were produced from crosses between four female parents (Atzimba, I-1035, LT-8, and 78.13.13F2) with four FDR 2x clones and with four 4x males. The FDR 2x clones were selected on the basis of the production of FDR 2n pollen, acceptable tuber shape and size, and a specific resistance; i.e., 84.36.29 and 85.27.13 are both root-knot nematode (RKN)-resistant parents (Iwanaga et al. 1989), and MI-49.10 and 84.194.30 are both bacterial wilt-resistant clones (International Potato Center 1985). The 4x male parents were LT-7, 7XY.1, CEW-69.1 (CIP 575049) and Tollocan, which have been previously used as parental clones for potato production from true seed (TPS) (Mendoza 1987).

The families were evaluated under short daylength conditions in four locations in Peru during 1989 and 1990. The locations are between latitudes 6 and 12 S, and represent the major agroecological zones of Peru: La Molina, arid; Huancayo and Huaraz, highlands; San Ramon, mid-elevation tropics.

Yield trials were performed using randomized complete block designs (RCBD) with two replications of 15 genotypes per family. The material was harvested 90 days after planting in San Ramon and after 120 days in the other three locations.

Data recorded on a plot (family) basis were: (1) total and marketable tuber yield (tubers weighing more than 50 g) per plant (in kg), (2) total number of tubers per plant, (3) average tuber weight, dividing the total tuber yield per plant by total number of tubers per plant, (4) specific gravity (mass density), by weighing the tubers in air (x) and in water (y). Thus, specific gravity $= x/(x-y)$.

Statistical analysis

Analysis of variance using RCBD in each location and combined over locations for each trait was performed (Nevado and Ortiz 1985).

The genetic analysis and estimation of parental value were done following a line × tester mating design. The analysis of variance was calculated assuming the random model for all of the factors. The general combining ability (GCA) effects and their respective standard errors were calculated using the procedure of Singh and Chaudary (1979) for the line × tester mating design.

The pooled mean squares for both male and females obtained from the analysis of variance of the line × tester mating design were used for estimation of one-quarter of the additive genetic variance (V_a), and the expected mean square of the male × female interaction source for one-sixth of the non-additive genetic variance (V_d) (Thompson and Mendoza 1984). Narrow sense heritabilities among full-sib families were estimated using the formula $h^2_{NS} = V_a/V_p$ where $V_p = V_G + V_{GE}/E + V_e/r\,E$ with r and E being the number of replications and environments, respectively, V_G the total genotypic variance (among family variance), and V_{GE} the genotypic × environmental variance (family-by-environment variance).

Covariance analysis between all pairs of characters was performed. Genetic and phenotypic correlations between each pair of characters x and y were estimated according to Baker (1986). Thus, the genetic correlation is $r_{Gxy} = Cov_{Axy}/(V_{Ax} \cdot V_{ay})^{1/2}$, and the phenotypic correlation, $r_{Pxy} = Cov_{Pxy}/(V_{Px} \cdot V_{Py})^{1/2}$, where Cov_{Axy} and Cov_{Pxy} were estimates of the additive and phenotypic covariance, respectively, and V_{Ax}, V_{Ay}, V_{Px}, and V_{PY} were the estimated additive and phenotypic variance components, respectively. An index of the form $I = b^1 X_1 + b_2 X_2 + b_3 X_3 + b_4 X_4$, where the b's are the weights for each trait and the X's are the estimates of genotypic values based upon phenotypic values for tuber number (X_1), specific gravity (X_2), average tuber weight (X_3), and tuber yield (X_4), was constructed for use in the comparison of 4x and FDR 2x parents for multitrait selection. The equation $Ga = Pb$ where G is a matrix of genetic variance and covariances, a is a vector of economic values, P is a matrix of phenotypic variances and covariances, and b is a vector of index coefficients was solved to derive the b values that maximized the correlation between the genotypic and index values (Baker 1986). An equal economic value was given for each tuber trait.

Genotypic, environmental and G × E interaction effects were compared for 4x × 2x and 4x × 4x crosses by separating the mean squares from the analysis of variance (Wright 1971). Broad sense heritability, H^2_{BS}, was estimated as $VG/(V_G + V_{GE}/E + V_e/E\,r)$. Likewise, estimates of heritability (narrow-sense) were calculated for 4x and FDR 2x males and for females in crosses with FDR 2x and 4x parents according to the procedures described by Hallauer and Miranda (1981) for the factorial design (Design II). The estimates of the components of variance were used to simulate $H^2_{BS(4x-2x)}$ and $H^2_{BS(4x-4x)}$ using different number of replications and locations. This provided a basis for comparison of the efficiency in the evaluation of 4x × 2x versus 4x × 4x progenies.

Results

Genetic parameters for the different traits evaluated in the heterogenous population are shown in Table 1. Tuber set had the highest broad-sense heritability among the tuber traits. The other four tuber traits had broad-sense heritability estimates below 0.50. Narrow-sense heritability was higher for average tuber weight than for the other tuber traits. Moreover, the ratio non-additive/additive variance estimates for specific gravity and average tuber weight were equal to 0, i.e., V_d was 0 for both traits. Non-additive variance was smaller than additive variance for tuber set. Otherwise, non-additive variance was significantly higher than additive variance for total tuber yield.

Phenotypic and genetic correlations between tuber traits are indicated in Table 1. A selection index for multitrait selection was derived using the genotypic and phenotypic variances and covariances to compare the performance of 4x and FDR 2x male parents in crosses with 4x females for the transmission of several traits to their offspring. The index (I) took the form: $0.471\,X_1 + 152.316\,X_2 - 89.447\,X_3 + 0.303\,X_4$ where X_1, X_2, X_3, and X_4 were tuber set, specific gravity, average tuber weight and total tuber yield, respectively.

The parental value of 4x and FDR 2x for the tuber traits evaluated (Table 2) indicates that FDR 2x clones such as 84.36.29 and 85.27.13 gave the highest yielding progenies, with 85.27.13 having progenies with fewer tubers and a larger size than 84.36.29. Both of these clones and another FDR 2x, 84.194.30, were the parents with the highest specific gravity in their offspring. The highest yielding 4x parent, 7XY.1, was the worst for specific gravity among all of the parents evaluated. However, all of

Table 1. Genetic (above diagonal) and phenotypic (below diagonal) correlations, narrow-sense (h^2) and broad-sense (H^2) heritabilities (in the diagonal), ratios of non-additive (V_d)/additive (V_a) variances, and selection index for tuber traits in potato

Trait	Tuber set	Specific gravity	Average tuber weight	Total yield
Tuber set	H^2 0.665±0.177 h^2 0.390±0.238	0.290	−0.821	0.835
Specific gravity	0.149	H^2 0.143±0.195 h^2 0.332±0.479	−0.411	−0.049
Average tuber weight	−0.591	−0.095	H^2 0.448±0.230 h^2 0.532±0.342	−0.408
Total yield	0.718	0.038	0.018	H^2 0.396±0.214 h^2 0.121±0.069
V_d/V_a	0.763	0.000	0.000	4.135

Selection index: 0.471 tuber set +152.316 specific gravity −89.447 average tuber weight +0.303 total yield

Table 2. Parental value based on progeny testing[a] of 4x and FDR 2x for several traits evaluated in four locations of Peru during 1989–1990

Parent	Tuber set	Specific gravity	Average tuber weight	Total yield	Selection index
FDR 2x:					
84.36.29	16.437	1.073	0.062	0.882	165.898
84.194.30	14.637	1.076	0.064	0.776	165.296
MI-49.10	10.834	1.062	0.072	0.601	160.604
85.27.13	12.812	1.072	0.074	0.820	162.946
4x:					
LT-7	11.622	1.075	0.084	0.748	161.927
7XY.1	12.750	1.056	0.075	0.793	160.383
Tollocan	12.428	1.069	0.078	0.714	161.919
CEW-69.1	11.094	1.065	0.080	0.729	160.507
$LSD_{0.05}$	1.511	0.012	0.012	0.125	

[a] Means over four locations (1989–1990), using two replications of 15 genotypes in each environment

the 4x parents had larger tubers in their offspring than the FDR 2x clones. The FDR 2x clones, 84.36.29, 84.194.30, and 84.27.13, had the highest selection index for tuber traits.

Phenotypic correlations were significant and positive between tuber set/specific gravity ($r = 0.656$), tuber set/total tuber yield ($r = 0.713$), and specific gravity/total tuber yield ($r = 0.705$) among the 4x × 2x progenies. A significant and negative phenotypic correlation for tuber set/average tuber weight ($r = -0.658$) was only estimated for the 4x × 2x progenies. The phenotypic correlation between tuber set/total tuber yield ($r = 0.719$) was significant and positive for 4x × 4x progenies. However, the phenotypic correlations tuber set/specific gravity ($r = -0.608$) and specific gravity/total yield ($r = -0.658$) were significant and negative for 4x × 4x progenies.

Significant differences for tuber yield were detected between locations and families (Table 3). The source of variation, families, was broken into two components. 4x × 4x and 4x × 2x families, in the analysis of variance for tuber yield. Significant differences were only found among 4x × 2x families (Table 3). Likewise, another source of variation, the interaction family × location, was broken down in the same way, and a significant interaction with the environment was detected for 4x × 2x families. Moreover, each family group was partitioned into its components male, female, and male × female interaction in both main and interaction source of variation. The interaction 4x female × FDR 2x male × location was significant for yield.

The progenies from the FDR 2x parents were on average better in Huaraz and La Molina than the 4x parents, meanwhile the 4x males were better than the FDR 2x parents in Huancayo and San Ramon (Table 4). The FDR 2x clone 84.36.29 produced high-yielding and stable offspring. The FDR 2x clone 84.36.29 was significantly better for tuber yield than the four 4x male parents. The only 4x parent with a positive GCA estimate for tuber yield, but not one larger than its standard error, was 7XY.1. The best female parent for tuber yield was 78.13.13F2 in crosses with 4x males and LT-8 in crosses with FDR 2x males (Table 5).

Broad-sense heritability, the coefficient of genetic variation, and narrow-sense heritability for tuber yield were higher for 4x × 2x crosses than for 4x × 4x crosses (Table 6). Broad-sense heritability estimates for tuber yield were simulated for a different number of locations and replications using the components of variance from Table 6. Figure 1 illustrates that the use of ten replications in the evaluation of progenies from 4x × 4x crosses

Table 3. Analysis of variance for tuber yield (kg/plant) between 4x × 2x and 4x × 4x families evaluated at four locations in Peru during 1989–1990

Source	df	Sum of squares	Mean square	*F*
Location	3	13.476	4.492	20.80**
Reps/location	4	0.426	0.106	1.65 ns
Families:	31	5.812	0.187	1.65*
4x × 4x (1)	15	2.430	0.162	1.43 ns
Males 4x	3	0.112	0.037	0.37 ns
Females 4x	3	0.645	0.215	0.90 ns
Male × female	9	1.673	0.186	2.09 ns
4x × 2x (2)	15	3.347	0.223	2.56**
Males FDR 2x	3	1.392	0.464	2.50 ns
Females 4x	3	1.166	0.389	2.90 ns
Male × female	9	0.789	0.088	1.13 ns
(1) vs. (2)	1	0.035	0.035	0.55 ns
Family × Location:	93	10.500	0.113	1.76**
(4x × 4x) × L	45	5.095	0.113	1.16 ns
4x M × L	9	1.357	0.151	1.57 ns
4x F × L	9	1.331	0.148	1.53 ns
4x M × 4x F × L	27	2.407	0.089	0.92 ns
(4x × 2x) × L	45	3.913	0.087	2.63**
2x M × L	9	1.157	0.129	1.65 ns
4x F × L	9	0.653	0.073	0.96 ns
2x M × 4x F × L	27	2.103	0.078	2.36**
(1) vs. (2) × L	3	1.492	0.497	7.76**
Pooled error:	124	7.891	0.064	
Error 4x × 4x	60	5.840	0.097	
Error 4x × 2x	60	1.998	0.033	
Remainder	4	0.053	0.013	

* $P<0.05$; ** $P<0.01$; ns, non-significant

Table 4. General combining ability for tuber yield (kg/plant) of 4x male and FDR 2x male parents using four female testers evaluated in four locations of Peru during 1989–1990

Parent	Location				
	Huaraz	La Molina	Huan-cayo	San Ramon	Total
4x Males	0.610	0.944	1.009	0.421	0.746
LT-7	0.064	−0.085	0.043	−0.060	−0.010
7XY.1	−0.298*	0.124	0.294*	0.021	0.035
Tollocan	−0.139	−0.047	−0.080	0.093	−0.044
CEW-69.1	−0.162*	−0.050	0.021	0.077	−0.029
FDR 2x	0.877	0.974	0.871	0.356	0.769
84.36.29	0.211	0.115	0.135	0.035	0.124*
84.194.30	0.137	0.212*	−0.264*	−0.013	0.018
MI-49-10	−0.117	−0.251*	−0.122	−0.137	−0.157*
85.27.13	0.302*	−0.018	−0.026	−0.013	0.062
S.E. (g_m)		0.077			0.045
S.E. ($g_m - g'_m$)		0.109			0.063
Mean	0.744	0.939	0.940	0.388	0.758

* $P<0.05$

Table 5. General combining ability for tuber yield of 4x females using 4x and FDR 2x as tester stocks[a] at four locations in Peru during 1989–1990

4x female	4x males (tbr, dms, adg)	FDR 2x males (adg, tbr, phu, stn, chc, spl, vrn).
Atzimba (dms, adg, tbr)	0.042 (2)	0.062* (2)
India-1035 (tbr, dms, adg)	−0.109* (4)	−0.160* (4)
LT-8 (tbr, dms, adg)	−0.013 (3)	0.081* (1)
78.13.13F2 (tbr, phu, dms, adg)	0.080 (1)	0.018 (3)
S.E. (g_f)	0.052	0.032
S.E. ($g_f - g'_f$)	0.073	0.045
Mean	0.746	0.769

[a] Species involved in the parentage of the clones: *S. tuberosum* Group. Tuberosum (tbr), Gp. Andigena (adg), Gp. Phureja (phu), Gp. Stenotomum (stn), *S. demissum* (dms), cf. *S. chacoense* (chc), *S. sparsipilum* (spl), and *S. vernei* (vrn)

Table 6. Components of variances, and narrow- and broad-sense heritability for 4x × 4x and 4x × 2x populations

Component	4x × 4x	4x × 2x
Broad-sense		
V_G	0.006 ± 0.008	0.017 ± 0.010
V_{GE}	0.008 ± 0.014	0.027 ± 0.009
V_E	0.076 ± 0.049	0.074 ± 0.049
H^2	0.302 ± 0.395	0.610 ± 0.359
CV_G (%)	10.3	17.0
Narrow-sense		
V_m	−0.006 ± 0.003	0.020 ± 0.009
V_f	0.002 ± 0.005	0.009 ± 0.007
V_{fm}	0.012 ± 0.010	0.001 ± 0.005
V_{mL}	0.008 ± 0.008	0.006 ± 0.007
V_{fL}	0.007 ± 0.008	−0.001 ± 0.005
V_{mfL}	−0.004 ± 0.014	0.225 ± 0.010
h_m^2	−0.037 ± 0.019	0.161 ± 0.086
h_f^2	0.095 ± 0.095	0.099 ± 0.081

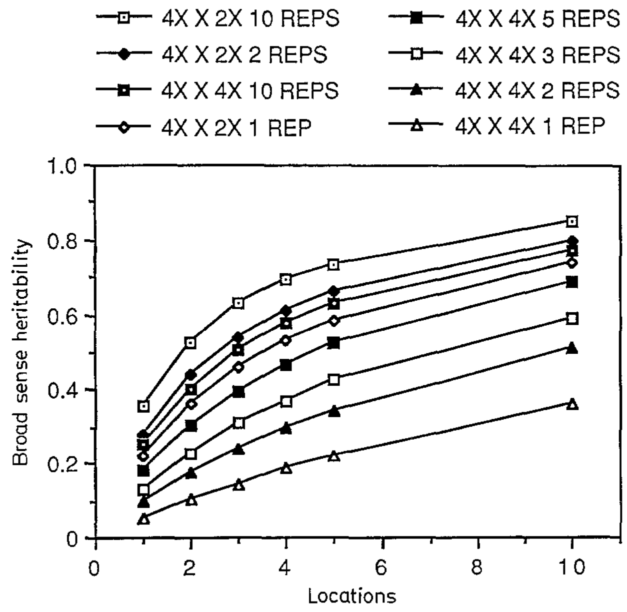

Fig. 1. Broad-sense heritabilities for tuber yield using a different number of locations and replications for the evaluation of 4x × 2x and 4x × 4x progenies

would be comparable to two replications in the evaluation of 4x × 2x progenies.

The comparison of the parental value, based on progeny testing, for tuber yield of clones from three cycles of selection is presented in Table 2. The FDR 2x from the third cycle, 85.27.13, performed better as a parent in 4x × 2x crosses than the other two clones selected in the previous cycles. Moreover, 84.194.30, a progeny of MI-49.10 selected in the second cycle, had a significantly better parental value for tuber yield than its progenitor.

Discussion

Heritability estimates and breeding procedures

A population is characterized for a specific trait by the estimation of its mean and variances. The selection of parental material is related to the inheritance of the character to be improved. Population improvement is sometimes limited by the narrow genetic base of the population, which leads to estimates of additive variance close to 0, e.g., the narrow-sense heritability estimate for tuber yield in the 4x × 4x population in our experiment.

The estimation of narrow-sense heritability and the ratio V_d/V_a (Table 1) indicate that selection must be effective in a broad-base genetic population of potatoes for average tuber weight, tuber set, and specific gravity. Moreover, the fact that only additive effects control average tuber weight and specific gravity suggests that phenotypic individual selection must be effective for both traits. However, it would be important to introduce new germ plasm to improve specific gravity in our population. The low estimate of narrow-sense heritability for tuber yield and the predominance of non-additive genetic variance confirm that tuber yield is the result of intra- and inter-locus interactions in potato (Mendiburu and Peloquin 1977; Mendoza and Haynes 1974). A method which maximizes the transmission of such interactions from the parents to the offspring is the use of FDR 2n gametes in potato (Peloquin et al. 1989).

Genetic and phenotypic correlations

The correlated characters are important for the potato breeder because they are the result of either pleiotropic actions of genes and/or changes brought about by linkage. Two main causes of phenotypic correlation between traits have been identified: genetic and environmental. Falconer (1989) states that if both characters have a low heritability, the phenotypic correlation (r_P) is determined mainly by the environmental correlation, which includes not only the correlation between the environmental deviations but also the non-additive genetic deviations. However, if they have high heritability, e.g., tuber set, average tuber weight, and specific gravity, the genetic correlation (r_G) is more important, i.e., $r_G > r_P$ for tubger set/specific gravity, tuber set/average tuber weight, and specific gravity/average tuber weight.

Falconer (1989) also mentions that a large difference and particularly a difference of sign between r_G and r_P indicates that the genetic and environmental causes of variation affect the character through different physiological mechanisms, e.g., average tuber weight/total tuber yield. In this regard, Hay and Walker (1989) pointed out that tuber yield = plant population density × number of tubers per plant × average tuber weight. Moreover, they indicated that tubers on a plant compete with each other for the substrates they need for growth; thus, tuber size is also determined by tuber set. Therefore, the negative genetic correlation between tuber yield and average tuber weight would be the result of the positive and high correlation between tuber set and total tuber yield in the population studied. The negative genetic correlation between specific gravity and average tuber weight also indicates that the production of large tubers does not necessarily means high dry matter (specific gravity) content. In effect, Ifenkwe et al. (1974) reported that the relationship between tuber size and dry matter content (specific gravity) is of a quadratic nature, i.e., specific gravity increases with an increase in tuber size to a maximum and then falls with a further increase in size.

Index selection for comparison of 4x and FDR 2x parents

In our research the component characters, tuber traits, have been combined into a score or index in order to be able to compare the 4x and FDR 2x parents (Table 2). The index used is a genetic selection index, thus assuming that the characters are equally important and that they did not need economic weighting. The best parents according to the index are the FDR 2x clones that combine yield with adequate size and a higher specific gravity in their offspring than the 4x parents. The phenotypic correlation for each group (either 4x × 4x or 4x × 2x) also indicates that in the 4x breeding population, the selection for high tuber yield has been carried out, to the detriment of specific gravity, consequently resulting in high yielding progenies, but lones with low dry matter.

The use of the selection index has also served to identify parents that produced progenies with more balanced traits. The FDR 2x parents transmits about 80% of the intra- and inter-locus interactions to their offspring. Therefore, careful selection at the 2x level with the purpose of developing elite parental 2x lines which produce high FDR 2n pollen with a specific resistance and good tuber types must be applied in the 2x broad-base breeding population with a high dry matter content. A new selection index must also be used in the breeding of the 2x population in order to break the negative correlation between average tuber weight and tuber set.

A surprising result of this experiment occurred in the comparison of the parental value for tuber yield, both total and marketable, of three FDR 2x clones that were selected in three different cycles. In all of the cycles tandem selection was applied: i.e., first, for production of FDR 2n pollen; second, for general tuber appearance; third, for specific resistance. However, the results suggest that an improvement in the parental value over the three cycles for both total and marketable tuber yield has been achieved (Table 2).

Progeny testing using 4x × 2x and 4x × 4x crosses

The choice of parents is based mainly on either pedigree or combining ability analyses. Our results indicate that the parental value of FDR 2x clones for tuber yield can be determined using no more than four 4x testers.

Mok and Peloquin (1975b) indicated that the differences between progeny obtained from crosses between testers and lines being evaluated depend on the variability of the gametes from the tester and the variability of the gametes from the line. FDR 2n gametes from a 2x clone are more homogenous, while still being heterozygous, than n gametes of 4x parents, which leads to a more critical evaluation of the 4x being tested due to the fact that the variability of the gametes from the tester is minimized. In effect, our results (Table 5) demonstrate that general combining ability (GCA) estimates for tuber yield were positive and significantly different from zero for the 4x parents using FDR 2x tester stocks. Seen otherwise, only one female of the four evaluated had a GCA estimate significantly different from zero for tuber yield using 4x tester stocks.

The use of families with high yield and lower within-family variance would be effective in reducing the time and space in a potato breeding program. The 4x × 2x breeding approach offers this opportunity for the potato breeder. Our results indicate that the error variance of 4x × 2x families is three times smaller than the error variance of 4x × 4x families (Table 3). The error variance was not only the variance due to random plot-to-plot variation but also included the within-plot variance (or variance between the 15 individuals within the family). As has been suggested by Concilio (1986) the possibility of early generation selection is not only methodology dependent, but also depends on the kind of genotypes involved. High yielding and more uniform progenies resulted from the 4x × 2x crosses. Therefore, the possibility of using only a few individuals to assess the worth of a 4x × 2x cross to be used in potato breeding seems to be feasible in an early generation selection program.

An important step in potato breeding is the evaluation of the advanced selections. Broad-sense heritabilities were simulated in order to determine the number of replications and locations necessary for a potato breeding program using either 4x × 4x and 4x × 2x crosses (Fig. 1). The results clearly indicate that the 4x × 2x approach would reduce costs, since fewer replications would be necessary for the evaluation of offspring derived from crosses of 4x parents with FDR 2x clones.

The last step in potato breeding is the introduction of an advanced selection that has been extensively evaluated as a new cultivar. A potential cultivar must be as high yielding and as stable as the cultivar to be replaced, but also must have additional properties such as quality and disease resistance, as well as good tuber appearance. The results presented here for tuber traits and elsewhere for disease resistance (Iwanaga et al. 1989) clearly indicate that the 4x × 2x breeding approach fulfills these requirements.

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