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Performance of true potato seed families. 1. Effect of level of inbreeding[1]

GISELA C. SHONNARD[2] and S.J. PELOQUIN

Departments of Horticulture and Genetics, University of Wisconsin, Madison, WI 53706, USA
[2]Current address: L-452, Lawrence Livermore National Laboratory, 7000 East Ave., Livermore, CA 94550, USA

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Summary

Successive generations of open pollinated (OP) true potato seed (TPS) families represent a low-cost planting material. This study was conducted to determine whether inbreeding occurred during two successive OP generations and, if so, whether it adversely affected the performance of transplant families from true seed. Potato seedling transplants from 4x × 2x hybrid, OP_1, OP_2, S_1 and S_2 families were compared for plant vigour, flowering, pollen stainability, OP fruit set, tuber yield and specific gravity. Hybrids were consistently superior, while S_2 families were inferior. The performance of OP_1, OP_2 and S_1 families did not differ significantly for most traits. The accumulation of inbreeding in successive OP generations was limited by reduced OP seed production on selfed plants; thus, a synthetic TPS variety propagated by open pollination may be feasible.

Introduction

The production of potatoes from true seed (TPS) can cut the costs of planting materials and reduce the disease and storage problems associated with seed tubers. If farmers can afford hand-pollinated TPS, highly heterozygous 4x × 2x hybrids can be utilized; such hybrids consistently outyield OP families when grown from seedling transplants (Kidane-Mariam et al., 1985; Li, 1983; Macaso-Khwaja & Peloquin, 1983). True seed of open pollinated (OP) families, which is of interest due to its lower cost, results largely from self-pollination. Selfing rates have been estimated at 69% (Brown & Huaman, 1984) and 80% (Glendinning, 1976) in 4x Andigena materials. Inbreeding in potato leads to reduced germination percentage, vigor, flowering, male fertility, and OP fruit set, and may lead to the loss of weak lines through failure to set seed (Arndt & Peloquin, 1990; Atlin, 1985; Glendinning, 1976; Krantz & Hutchins, 1929). Continued self-pollination results in large inbreeding depression, since the potato is a polysomic tetraploid with largely non-additive genetic variance for tuber yield (Krantz, 1946; Mendiburu & Peloquin, 1977; Mok & Peloquin, 1975). However, contrary to expectations, researchers have found that yields did not decrease after

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two (Atlin, 1985; Macaso, 1983) and even three (Kidane-Mariam et al., 1985) successive generations of open pollination.

Since the hybrid plants in an OP_1 population can have disproportionately high OP seed set (Arndt & Peloquin, 1990), relatively few S_2 seeds may be produced. The OP_2 progeny could, therefore, contain relatively few S_2 plants and may consist mainly of S_1 plants and a few outcrosses, similar to the OP_1 progeny. Thus, the inbreeding accumulating in successive OP generations may be limited by the reduced fitness of the more inbred individuals. This suggests that farmers could maintain their own true seed supply over a number of years in the form of a synthetic variety, produced by randomly mating several parents selected for adaptation and combining ability, and multiplied by open pollination.

In this study, 4x × 2x hybrid, first and second generation OP (OP_1 and OP_2) and first and second generation selfed (S_1 and S_2) families from seedling transplants were tested to study the changes in performance due to inbreeding occurring in two successive OP generations.

Materials and methods

Plant materials. Five 4x clones from the Wisconsin breeding programme (Merrimack, Rhinered, W231, W639 and W953) and 4x × 2x hybrid, open pollinated (OP_1) and self pollinated (S_1) transplant families, derived from each of these clones, were planted in 1984 to generate materials for this study. All hybrid and selfed seeds had been generated by controlled pollinations, while OP seeds were from natural pollinations by bumblebees in the breeding nursery. The 2x male parent, M6 (*psps/sy3sy3*), was a Phureja-haploid Tuberosum hybrid which is capable of almost complete transmission of the parental genotype to its 4x progeny (Douches & Quiros, 1986; Okwuagwu & Peloquin, 1981). In 1984, new 4x × 2x hybrid, OP_1 and S_1 seeds were obtained from the five 4x clones, while OP_2 and S_2 seeds were produced on the respective transplant families. Between 26 and 62 plants per OP_1 family and between 13 and 45 plants per S_1 family were available for producing OP_2 and S_2 seeds. Due to the extremely limited flowering and low male fertility of the S_1 plants, no S_2 seeds of Rhinered or W953 were produced; the W953 OP_1 plants produced no OP_2 seeds.

Field design and plant evaluations. A yield trial was conducted on seedling transplant families in 1985 at two Wisconsin locations, Hancock (H) and Rhinelander (R). Six-week-old seedlings from the 4x × 2x hybrid, OP_1, OP_2, S_1 and S_2 families were transplanted to the field, one plant per hill, after all danger of frost was past (June 6, H; June 18, R). These five types of families will be referred to as 'generations'. The spacing between rows was 91 cm, while spacing between hills was 46 cm (H) and 41 cm (R). A randomized complete block design (RCBD) with two replications was planted at both locations. An experimental unit consisted of a row of 14 hills. Each of the centre 12 plants was evaluated for the following traits (numbers in parentheses refer to days after transplanting at each location):

1. Vigour, 1 = weak to 5 = vigorous, average of values recorded on two dates (35d, 74d H; 29d, 77d R);
2. Flowering, 0 = no flowers to 5 = abundant flowers, higher of values recorded on two dates (35d, 74d H; 50d, 77d R);
3. Pollen stainability in acetocarmine glycerol, 0 = 0%, 1 = 1-10%, 2 = 11-30%,

3 = 31-50%, 4 = 51-100% stainable pollen (flowers collected when evaluating flowering);

4. OP fruit set in g/plant (on harvest date);
5. Tuber yield in kg/plant (125d H; 106d R);
6. Specific gravity = tuber weight in air / tuber weight in air − weight in water.

Specific gravity was determined for materials at Rhinelander only.

Statistical analysis. The data were tested for *normality* by doing calculations on both single plant data and on plot means (means of all plants within an experimental unit). The error deviates of the *individual plant values* did not follow a normal distribution for any of the traits; however, the error deviates of the *plot means* were normally distributed for all traits except OP fruit set. OP fruit set had a highly skewed distribution, because a large number of plants set no OP fruit. When calculations were performed on transformed values of plot means, $\log_{10}$(OP fruit set + 1), the error deviates were normally distributed. Therefore, ANOVAs, using a factorial treatment design, were conducted on plot means (transformed plot means for OP fruit set). All ANOVAs were analyzed according to a fixed effects model. Statistical Analysis System (SAS) was used for the data analyses (Anon., 1985) unless otherwise indicated.

Because W953 OP_2, W953 S_2 and Rhinered S_2 families were entirely missing, separate ANOVAs were conducted on two complete subsets of the data. *Subset 1* contained data from the three parents (Merrimack, W231 and W639) with all five generations present and was analyzed as a 2 × 3 × 5 factorial (2 locations, 3 parents, 5 generations). *Subset 2* contained data from the three generations (4x × 2x hybrid, OP_1 and S_1) for which all five parents were represented, and was analyzed as a 2 × 5 × 3 factorial (2 locations, 5 parents, 3 generations). Traits analyzed included vigour, flowering, pollen stainability, OP fruit set, and tuber yield.

For specific gravity, determined at Rhinelander only, both the mean value of a plot (row of 12 plants), and the uniformity within a plot, were of interest. ANOVAs were calculated on plot means to test for differences in specific gravity among families. *Subset 1* was analyzed as a 3 × 5 factorial (3 parents, 5 generations), while *Subset 2* was analyzed as a 5 × 3 factorial (5 parents, 3 generations). In order to test for differences in the variability of specific gravity among plots, pairwise F tests for homogeneity of pooled, within-plot variances were conducted (Steel & Torrie, 1980, p. 112).

$$\text{Pooled variance} = \sum_{i=1}^{m} (n_i - 1)s_i^2 \Big/ \sum_{i=1}^{m} (n_i - 1)$$

where i = number of plots, i = 1 to m; n_i = number of plants in the ith plot and s_i^2 = variance of specific gravity of the ith plot. The F test was used to determine whether the pooled, within-plot variances of all plots with the same parent (or generation) differed from the pooled within-plot variances of all plots with another parent (or generation).

Spearman's rank correlation coefficients were calculated on ranks of individual plant data for all pairs of traits (pooled over locations, replicates, parents, and generations). This test was used instead of a Pearson's correlation since it does not require the assumption of a bivariate normal distribution (individual plant data were not normally distributed).

A *cluster analysis* was used to test the similarity in performance of the 4x × 2x hybrid, OP$_1$, OP$_2$, S$_1$ and S$_2$ generations (Subset 1) for vigour, flowering, pollen stainability, OP fruit set and yield. The data for two locations, two replicates, and three parents were standardized and the stepwise (nearest neighbour) method of BMDP (Dixon, 1981) was used to group the observations into clusters.

Results

ANOVA – Main effects. There were significant main effects for a number of traits in both Subset 1 (all five generations for the three parents, Merrimack, W231 and W639) and Subset 2 (all five parents for the three generations, 4x × 2x hybrid, OP$_1$ and S$_1$). For traits where F tests from the ANOVA were significant, levels within main effects were compared using a Fisher's protected LSD for unequally replicated means (Steel & Torrie, 1980, p. 191; Table 1, Subset 1; Table 2, Subset 2).

The effect of *location* was significant for vigour ($P < 0.05$), OP fruit set ($P <$

Table 1. Subset 1; means by location, parent, and generation for five traits recorded on a per plant basis of 4x × 2x hybrid, OP$_1$, OP$_2$, S$_1$, and S$_2$ seedling families from three female parents at Hancock and Rhinelander.

	Number of plants	Vigour[a] (1 – 5[d])	Flowering (0 – 5[d])	Pollen[b] stainability (0 – 4[d])	OP fruit[c] set (g/plant)	Tuber yield (kg/plant)
Location						
Hancock	325	3.3 a	2.0	2.0 (199)	99 a	0.50 a
Rhinelander	286	2.9 b	1.2	2.8 (131)	12 b	0.21 b
Parent						
Merrimack	210	3.2	1.4	2.0 b (98)	23 b	0.33
W231	200	3.1	1.5	2.2 b (106)	73 a	0.37
W639	201	3.1	1.9	2.7 a (126)	81 a	0.40
Generation						
4x × 2x	137	3.6 a	2.1 a	2.4 (86)	109 a	0.56 a
OP$_1$	131	3.2 b	1.5 b	2.2 (73)	87 a	0.37 b
OP$_2$	115	3.0 b	1.7 ab	2.4 (62)	47 b	0.32 b
S$_1$	125	3.2 b	1.7 ab	2.2 (72)	24 b	0.34 b
S$_2$	103	2.6 c	0.9 c	2.3 (37)	9 c	0.20 c
Mean		3.1	1.6	2.3 (330)	58	0.37

[a] LSD$_{0.05}$ for unequally replicated means, different letters in a column represent significant differences among levels within a main effect. LSD values were calculated for traits with significant F test only.

[b] Number in parentheses is number of plants with pollen samples.

[c] Calculations performed on transformed data: log$_{10}$ (OP fruit set + 1); values in table represent means of untransformed OP fruit set data.

[d] For details of scoring scale, see text.

0.01), and yield ($P < 0.01$) for Subsets 1 and 2, and for pollen stainability ($P < 0.05$) for Subset 2. Values for pollen stainability were higher at Rhinelander, while values for all other traits were higher at Hancock (Tables 1 and 2). The effect of *parent* was significant ($P < 0.01$) for pollen stainability and OP fruit set for both subsets, and for flowering ($P < 0.05$) for Subset 2. W639 progenies were superior for all of these traits (Tables 1 and 2). *Generations* had a significant effect ($P < 0.01$) on vigour, flowering, OP fruit set, and yield for both subsets. The 4x × 2x hybrids consistently had the highest, while the S_2 progenies had the lowest values for all of these traits. The OP_1 had higher values for OP fruit set than the OP_2 or S_1 progenies; for all other traits, the OP_1, OP_2 and S_1 progenies did not differ significantly (Tables 1 and 2).

ANOVA – Interactions. Some two and three way interactions were found to be significant ($P < 0.05$). In general, the interaction mean squares were much smaller than those of the corresponding significant main effects and, often, ranks did not change. However, for each significant two way interaction, simple effects were evaluated and the most pertinent features are reported below (data not shown). The *location* × *parent* (L × P) interaction was significant only for pollen stainability in

Table 2. Subset 2; means by location, parent, and generation for five traits recorded on a per plant basis of 4x × 2x hybrid, OP_1, and S_1 seedling families from five female parents at Hancock and Rhinelander.

	Number of plants	Vigour[a] (1 – 5[d])	Flowering (0 – 5[d])	Pollen[b] stainability (0 – 4[d])	OP fruit[c] set (g/plant)	Tuber yield (kg/plant)
Location						
Hancock	335	3.5 a	1.9	1.9 b (201)	121 a	0.62 a
Rhinelander	303	3.0 b	1.3	2.8 a (146)	13 b	0.25 b
Parent						
Merrimack	139	3.5	1.8 ab	2.1 b (78)	33 b	0.41
Rhinered	112	3.3	1.1 c	2.1 b (50)	65 b	0.44
W231	130	3.4	1.6 ab	2.1 b (76)	92 a	0.44
W639	124	3.2	1.9 a	2.8 a (77)	102 a	0.43
W953	133	3.2	1.5 b	2.3 b (66)	58 b	0.50
Generation						
4x × 2x	218	3.6 a	1.9 a	2.3 (131)	115 a	0.58 a
OP_1	210	3.1 b	1.3 b	2.4 (100)	76 b	0.35 b
S_1	210	3.2 b	1.5 b	2.1 (116)	16 c	0.39 b
Mean		3.3	1.6	2.3 (347)	69	0.44

[a] $LSD_{0.05}$ for unequally replicated means, different letters in a column represent significant differences among levels within a main effect. LSD values presented for traits with significant F test only.

[b] Number in parentheses is number of plants with pollen samples.

[c] Calculations performed on transformed data: $\log_{10}$ (OP fruit set + 1); values in table represent means of untransformed OP fruit set data.

[d] For details of scoring scale, see text.

Subset 1 and for OP fruit set in Subset 2; low values for W231 at Hancock indicate that pollen fertility of progeny from this parent may be more sensitive to the higher temperatures present there, while low values of OP fruit set for all parents at Rhinelander may have been due to the short growing season. Significant *location* × *generation* (L × G) interactions were found for vigour for Subset 1 and for yield for both subsets. Very high vigour ratings of S_1 families at Rhinelander, and low mean values and low variances for yield at Rhinelander as compared to Hancock, contributed to the L × G interactions. Significant *parent* × *generation* (P × G) interactions were present for vigour and pollen stainability in Subset 1 and for OP fruit set in Subset 2. The P × G interaction was influenced by high vigour ratings for Merrimack S_1 and W639 OP_2 progenies (ratings were as high as the values for the respective hybrids). For pollen stainability, the different generations changed ranks greatly among parents. The P × G interaction for OP fruit set may have been due to the larger variability in fruit set among the OP_1 families than among the hybrid or S_1 families from different parents. Three way, *location* × *parent* × *generation* (L × P × G) interactions were significant for vigour, OP fruit set and yield in Subset 1 and for pollen stainability in Subset 2.

Table 3. Means and variances by parent and generation for specific gravity of 4x × 2x hybrid OP_1, OP_2, S_1 and S_2 seedling families from three female parents (Subset 1), and of 4x × 2x hybrid, OP_1 and S_1 seedling families from five female parents (Subset 2) at Rhinelander.

	Subset 1			Subset 2		
	number of plants	specific gravity		number of plants	specific gravity	
		mean	variance[a] × 10^{-4}		mean	variance × 10^{-4}
Parent						
Merrimack	99	1.0644	1.03 a	65	1.0633	0.91 a
Rhinered				51	1.0614	1.03 ab
W231	78	1.0610	3.80 b	54	1.0613	2.70 c
W639	89	1.0659	1.49 a	56	1.0695	1.73 bc
W953				64	1.0631	1.24 ab
Generation						
4x × 2x	66	1.0635	1.44 a	108	1.0619	1.37 ab
OP_1	53	1.0690	1.01 a	88	1.0679	1.07 a
OP_2	44	1.0639	3.20 b			
S_1	56	1.0620	2.64 b	94	1.0620	2.02 b
S_2	47	1.0610	1.88 ab			
Mean		1.0639	1.99		1.6037	1.49

[a] Different letters in a column represent significant differences ($P \leq 0.05$) among levels within a main effect. For means, LSD tests are not presented for parent or generation in Subset 1 due to the significant P × G interaction; for variances, differences were determined with pairwise F tests for homogeneity of variances. Means are weighted by number of plants per plot. Variances represent pooled within-plot variances.

Specific gravity. For specific gravity (Table 3), significant differences among plot means were tested with an ANOVA, while pairwise F tests were used to evaluate within-plot variances (pooled over replicates and either parents or generations). For Subset 1 only, the two main effects of parent and generation, as well as the P × G interaction for *mean* specific gravity were significant ($P < 0.01$). Since mean specific gravity values for generations changed ranks among the three parents, and the P × G interaction was large in comparison with main effects, comparisons among means (LSD values) for parents and generations were not reported (Table 3). The mean specific gravity of a particular generation can be expected to vary among transplant families depending on the parent. It may, however, be possible to identify parents or generations for which mean specific gravity may be more predictable: the hybrid families had more similar values than OP or selfed families, and families with Merrimack as a parent all had similar values for mean specific gravity.

Pairwise F tests indicated significantly different *pooled within-plot variances* for specific gravity among parents, as well as generations in both subsets ($P < 0.05$). Families with W231 as a parent had the highest, while the hybrid and OP_1 families had the lowest variances for specific gravity.

Spearman's correlation. Spearman's rank correlation coefficients for all pairwise comparisons were calculated on ranks of individual plant values (Table 4). The correlation coefficients between pollen stainability and all other traits were very low,

Table 4. Spearman's rank correlation coefficients for pairs of traits, calculated on a per plant basis, of 4x × 2x hybrid, OP_1, OP_2, S_1 and S_2 seedling families from three female parents (Subset 1) above in each line, and of 4x × 2x hybrid, OP_1 and S_1 seedling families from five female parents (Subset 2) below in each line, at Hancock and Rhinelander.

	Vigour (1 – 5[a])	Flowering (0 – 5[a])	Pollen stainability (0 – 4[a])	OP fruit set (g/plant)	Tuber yield (kg/plant)
Vigour		0.718** 0.734**	0.069 0.072	0.488** 0.446**	0.695** 0.700**
Flowering			0.055 0.127*	0.504** 0.500**	0.573** 0.559**
Pollen stainability				0.146** 0.185**	−0.093 −0.115
OP fruit set					0.433** 0.412**
Specific gravity[b]					0.109 0.039

*, ** $P \leq 0.05$ and 0.01, respectively.

[a] For details of scoring scale, see text.

[b] Specific gravity was recorded at Rhinelander only. Correlation coefficients were calculated only with respect to tuber yield.

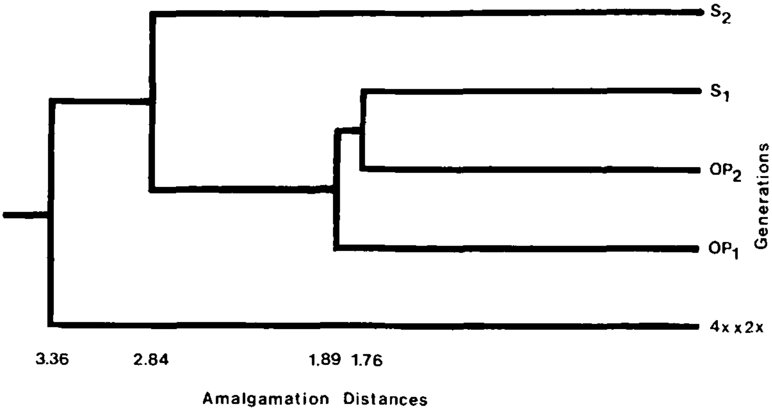

Fig. 1. Subset 1 – Dendrogram for a stepwise (nearest neighbour) cluster analysis of five seedling generations, based on standardised values for five traits (recorded for transplant families from three female parents at Hancock and Rhinelander).

while the highest correlations ($P < 0.01$) were present between vigour and flowering ($r_s = 0.718^{**}$, Subset 1; 0.734**, Subset 2) and vigour and yield ($r_s = 0.695^{**}$, Subset 1; 0.700**, Subset 2). There was no significant correlation between yield and specific gravity.

Cluster analysis. The dendrogram and amalgamation distances from the cluster analysis indicated the degree of similarity among the five generations included in Subset 1 (Figure 1). The OP_1, OP_2 and S_1 generations were the most similar in performance and formed one cluster. The S_2 families fell into the next larger cluster, while the performance of the 4x × 2x hybrid families was quite distinct.

Discussion

Effects of location and parent. The *location* main effects and interactions (Tables 1 and 2) were generally due to the poor performance and low variability of the transplant families in the less favourable environment (limited irrigation, shorter growing season) at Rhinelander as compared to Hancock, while the consistently higher pollen stainability values at Rhinelander may be due to the lower temperatures at that location. The *parent* main effect was significant for flowering, pollen stainability, and OP fruit set (Tables 1 and 2). The W639 progeny were superior for these traits. A consistent ability to set large amounts of OP fruit is important for parents to be used for OP true seed production; however, the significant P × L and P × G interactions found in this study for pollen stainability and OP fruit set indicate the need for caution. OP fruit set, of OP families in particular, varied greatly, possibly depending on the proportion of hybrid vs. selfed plants present in the OP family; in addition, the environment (temperature, length of growing season, abundance of pollinators) can have an effect. For specific gravity (Table 3), the transplant families with W231 as a parent were the most variable. Such parents could be selected against when cooking quality of tubers from TPS families is of concern.

Effect of generation on constitution of OP families. The 4x × 2x hybrids were consistently superior to both the OP_1 and the S_1 families, while the OP_1 and S_1 families had similar performance for all traits except OP fruit set (Tables 1 and 2) and variance of specific gravity (Table 3).

The similar performance of the OP_1 and S_1 families indicates that although *OP_1 progeny* included some hybrids due to outcrossing, they probably consisted mainly of S_1 plants. The OP fruit set data are in agreement with this hypothesis; S_1 families (with no hybrid plants) set significantly fewer OP fruit than OP_1 families (which may have included hybrid plants). Arndt & Peloquin (1990) found that the identifiable hybrid plants, which constituted only 5% of the OP_1 population, produced a disproportionately high quantity of the second generation OP fruit, namely 78% and 49% in the two seasons tested. This may explain why, for the five parents tested, the OP_1 families (which can vary in the proportion of hybrid vs. S_1 plants present within a family) were more variable for quantity of OP fruit set than the hybrid and S_1 families.

The similar performance of OP_2 and S_1 families indicates that the *OP_2 progeny*, a mixture of hybrid, S_1 and S_2 plants, contained a large proportion of S_1 plants also. Hybrids in the OP_2 generation resulted from occasional outcrosses of either hybrid or S_1 plants. S_1 plants among the OP_2 generation resulted from selfing of hybrid plants among the OP_1; since the hybrids have the potential for high OP fruit set, a large proportion of the OP_2 may have consisted of such S_1 plants. S_2 plants in the OP_2 generation could only have resulted from selfing of S_1 plants, which generally have low OP fruit set.

The hypothesis that both OP_1 and OP_2 populations consisted of a large proportion of S_1 plants was supported by results from the cluster analysis (Figure 1). This analysis clusters groups with similar performance together; similar performance may reflect similar inbreeding levels. The performances of the OP_1 and OP_2 progenies were very similar to that of the S_1 progeny, which consisted entirely of S_1 plants. The S_2 progeny (100% S_2 plants – more inbred) and the 4x × 2x hybrids (100% hybrid plants – less inbred) were separated by much larger distances from the OP_1 and OP_2 progenies in the cluster analysis.

Limited inbreeding depression in OP families. The above data indicate that the effective rate of inbreeding over the two successive OP generations in this study may have been limited by the reduced OP seed production on selfed plants. The performance of progeny from two successive OP generations did not decrease, contrary to the inbreeding depression that would have been predicted on the basis of published selfing rates of 70-80% in potatoes (Brown & Huaman, 1983; Glendinning, 1976). That the OP_2 families did not differ significantly in performance from the OP_1 and S_1 families, suggests that production of potatoes as a synthetic variety from successive generations of OP seed may be possible. This may be especially feasible when the original parents are selected for general combining ability (GCA) for yield. In a comparison of 20 F_1 TPS families with four successive generations of their OP progenies, no inbreeding depression was observed for those progenies derived from crosses where parents were selected for GCA for yield and tuber uniformity (Anon., 1988).

Relevance of correlations. Very low correlations were observed for all comparisons involving pollen stainability (Table 4). Environmental factors could have had a large effect on this trait. Very low pollen fertility may limit OP fruit set (Arndt et al., 1990), but once pollen fertility reaches a sufficient level, other factors might become limiting.

Significant positive correlations between yield and flowering as well as between yield and OP fruit set, although not high, indicate that selection for increased yield would not interfere with selection for increased OP true seed production in these families (Table 4). The highest correlations, those observed between vigour and flowering and between vigour and yield, might result in increased tuber yields and flowering in the OP families used in this study, if only the most vigorous seedlings were transplanted. Differences in height of the hybrid, OP, and selfed seedlings were apparent even at three weeks of age. The following examples suggest that selection for vigour may have positive effects on yield in a wider range of TPS materials. Atlin (1985) demonstrated that differences in seedling vigour may be used to increase the proportion of hybrids in OP populations. He started with a mixture of 25% F_1, 50% S_1 and 25% S_2 seedlings, roughly simulating the proportions he expected in an OP_2 population. By visually selecting the most vigorous 25% of the seedlings at 20 days after planting, he obtained a population consisting of 71% F_1, 28% S_1 and only 1% S_2 seedlings. In another study (Anon., 1986), by selecting for seedling vigour prior to transplanting, the authors were able to increase significantly the yields of OP families derived from ten clones from 5 kg/plot (80% selection intensity) to 9.5 kg/plot (16% selection intensity).

Potential of OP families. Although the 4x × 2x hybrids were the highest yielding and most vigorous of the materials tested, hand-pollinated seeds are expensive and are not always available. In such cases, production from successive OP generations may result in greater economic yields due to the negligible costs of planting materials. Clones whose OP families have yields equivalent to some hybrid families have been identified (Anon., 1988; Arndt, 1986; Sadik, 1983). Such clones, especially ones with good GCA for yield and high OP seed production, could be intercrossed to produce a synthetic variety. The low OP seed production observed on inbred plants appears to limit the inbreeding accumulating over successive OP generations. Visual selection for vigour at the seedling stage may increase the proportion of hybrid progeny and result in increased flowering and higher yields.

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