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Inbreeding and true seed in tetrasomic potato. III. Early selection for seedling vigor in open-pollinated populations

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Abstract Tuber yield in open-pollinated (OP) offspring of potato cultivars appears to be correlated with the proportion of hybrids within each population. OP true potato seed (TPS) from ten selected clones was tested in an experiment at two Peruvian locations, San Ramón (mid-altitude warm tropics) and Huancayo (highland cool tropics), to investigate the early selection effect on OP populations. Another experiment in La Molina (dry coast) was included to confirm the results from these other two locations. The results clearly showed that plant survival, tuber yield and berry number can be increased by a strong early selection. Likewise, the results suggested that the most-promising OP offspring for TPS production could be derived from tetraploid clones with a high rate of outcrossing. This experiment demonstrates that high tuber yield may be obtained in OP TPS cultivars with little effort, using early selection for seedling vigor in the nursery. Genetic interpretation of this response to early selection indicates that both the intensity of selection and non-additive genetic variation for tuber yield account for these observed gains.

Keywords Outcrossing · Selection intensity · Selfing · TPS · Tuber yield

Introduction

In recent years, reports have shown that harvesting tubers from true potato seed (TPS) looks promising as an alternative production system to the traditional harvesting of tubers from tuber planting, particularly in the developing world (Almekinders et al. 1996; Ortiz 1997). TPS provides healthy and cheap planting material, thereby saving production costs for tuber propagules, especially if imported. The cheapest materials for potato production from TPS are open-pollinated (OP) offspring. However, most of these OP seeds result from self-pollination (Arndt et al. 1990). Hence, controlled crosses have been recommended to avoid inbreeding depression (Simmonds 1997), which makes TPS costly.

Hybrid TPS has always been reported to outyield OP and selfed-offspring (Schonnard and Peloquin 1991; Golmirzaie et al. 1998a, b). Furthermore, the tuber yield of OP TPS appear to be linearly associated to the proportion of hybrid individuals in the population. Tuber yield in OP TPS was between that of hybrids (S_0) and inbred (S_1 and S_2) offspring (Golmirzaie et al. 1998a).

OP TPS result from both selfing and outcrossing by insect pollinators. The percentage of each depends on the outcrossing rate of the potato clone. Some partially male-sterile, advanced breeding material with Tuberosum cytoplasm may have at least 75% outcrossing rates, while this rate in male-fertile clones ranges from 1 to 74% in breeding materials (Brown 1993). In Andean potato landraces (Andigena cytoplasm) the outcrossing rate ranges from 13.2±9.9% to 44.9±3.9% (Brown and Huaman 1984). Any increase that can be made in the proportion of hybrids in OP TPS should increase the tuber yield potential.

An efficient and cost-effective TPS breeding program needs to be targeted, and includes a few primary traits: early generation selection, an optimal testing scheme, plus an effective delivery mechanism for the new cultivar. Also, the management of available information and an effective network of partnerships helps in the success of a breeding program. Hence, this research was undertaken to investigate how early generation-selection influences the plant survival of transplanted seedlings and the tuber weight harvested from TPS. The information provided in this article will also help research partners worldwide (including farmers) to apply this new knowledge when producing potato from true seed.

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Materials and methods

Two experiments were conducted at San Ramon (11°08′S, 800 m, humid mid-altitude in the Eastern Andes slopes) and Huancayo (12°07′S, 3280 m, highland in the Andes) to study the efficiency of an early selection on the OP TPS. A third experiment was undertaken at La Molina (12°05′S, 240 m, dry coast) to independently confirm the effect of early selection on TPS survival and tuber weight. The materials included in this research were OP TPS from ten clones (R-128.6, India 931, MS 35–22, CFS. 69.1, Desirée, Capiro, LT-6, DTO-28, DTO-33 and LT-5).

A random sample of 2250 OP TPS from each of these ten clones were sown independently in a greenhouse nursery at each location. The seed lot for each clone was divided into five groups of increasing seedling intensity (Table 1). After 8 weeks the 120 most-vigorous seedlings were transplanted into the field. The ensuing selection ratio is indicated in Table 1. The experimental layout was a complete randomized block design with three replications of 40-plants each. Cultural practices were those recommended for TPS management (Accatino and Malagamba 1982). The characteristics recorded were plant vigor (only at La Molina), plant survival after transplanting (as determined by the number of plants), tuber weight per plot and per plant (g), and berry number (only in Huancayo and San Ramon).

Factorial analysis was performed for the results obtained at Huancayo and San Ramon (combined across both locations) plus La Molina (individual analysis for this location). The Duncan Multiple Comparison Test at $P \leq 0.05$ was used to compare the selection intensity across OP offspring. Regression curves were fitted between either plant survival or tuber yield (dependent variables) and selection intensity (independent variable) with the data recorded at La Molina. A significant and positive trend was regarded as an indication of the gain from early seedling selection in the flat-nursery.

Table 1 Early selection intensity in the flat-nursery for open-pollinated offspring in potato

Number of seeds per flat	Number of seedlings transplanted to field	Selection of vigorous seedlings (%)
150	120	80
300	120	40
450	120	27
600	120	20
750	120	16

Results

All characteristics were significantly different between Huancayo and San Ramon (Table 2). Plant survival, berry set and tuber weight were highest at the former location. The selection intensity significantly affected plant survival, tuber weight per plot and berry set. The higher the selection intensity against weak seedlings the better the performance for these characteristics (Table 3).

The selection intensity equally affected all characteristics irrespective of the OP offspring included in this research (Table 2). However, the effect of the selection intensity may vary across locations, as suggested by the significant population size×location interaction. This result may also be accounted for by the distinct performance of the OP offspring across the two locations, as confirmed by a significant OP offspring×location interaction.

The highest selection intensity against the weakest seedlings (84%) resulted in significant gains of 33% in plant survival, 84% for tuber weight per plot, 21% for tuber weight per plant and 76% in berry set (Table 3), versus the lowest selection intensity of 20%. This lowest selection intensity has often been used while carrying out experiments with hybrid TPS transplants.

The data recorded in La Molina confirmed the observations from the trials at Huancayo and San Ramon. The selection intensity significantly affected plant vigor,

Table 2 Significant sources of variation after the analysis of variance for agronomic characteristics of ten open-pollinated offspring (OP) for early selection according to population size in two locations (San Ramón and Huancayo)

NS, * and ** indicate non-significance or significance at $P \leq 0.05$ and $P \leq 0.01$, respectively

Source of variation	Plant survival	Tuber weight per plot (g)	Tuber weight per plant (g)	No. of berries per plot
Locations (L)	**	**	**	**
Selection intensity (SI)	*	**	NS	**
Offspring (OP)	NS	NS	**	**
P×L	**	*	**	NS
P×SI	NS	NS	NS	NS
SI×L	**	**	**	**
SI×OP×L	NS	**	**	**
Coefficient of variation (%)	17.24	18.57	16.42	32.22

Table 3 Comparison of agronomic characteristics in ten open-pollinated offspring (OP) for early selection according to population size in two locations (San Ramón and Huancayo). Means followed by the same letter within each column are not significantly different according to the Duncan Multiple Comparison Test at $P \leq 0.05$

Selection of vigorous seedlings (%)	Plant survival	Tuber weight per plot (g)	Tuber weight per plant (g)	No. of berries per plot
80	18 d	5,158 d	673 c	29 b
40	21 c	5,760 d	700 b	28 b
27	22 bc	6,660 c	726 b	25 b
20	23 ab	8,136 b	792 a	41 a
16	24 a	9,481 a	816 a	51 a

Table 4 Analysis of variance (mean squares) for agronomic characteristics of ten open-pollinated offspring (OP) for early selection for seedling vigor according to population size in La Molina

** Indicates significance at $P \leq 0.01$

Source of variation	Plant vigor	Number of surviving plants	Tuber weight per plant (g)	Tuber weight per plot (g)
Replications	0.39	24.09	72,722.99	71,577,352
Selection intensity (SI)	6.92**	271.84**	59,143.95	357,704,741**
Offspring (OP)	13.16**	333.12**	1,424,981.59**	2,098,445,116
SI×OP	0.64	17.98	30,158.35	46,231,262
Coefficient of variation (%)	13.43	14.27	19.13	22.20

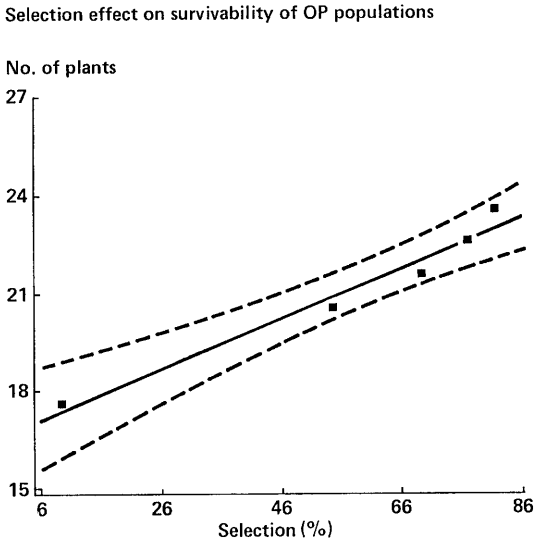

Fig. 1 Effect of selection intensity (i.e. 1 – % selection for seedling vigor) on plant survival in open-pollinated populations of potato (*dot lines* indicate the confidence belt at 5%) in La Molina

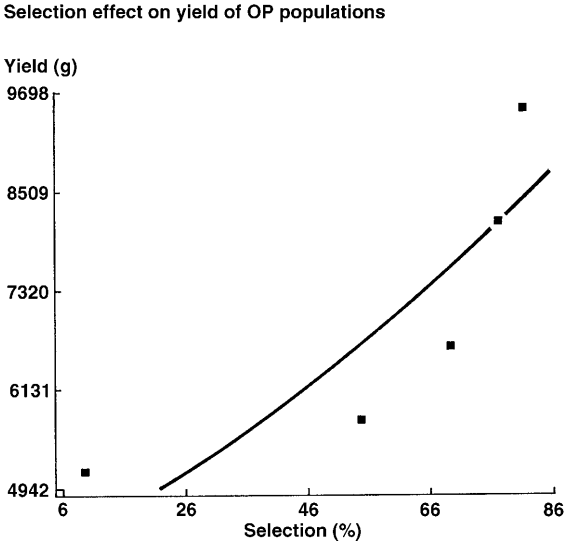

Fig. 2 Effect of selection intensity (i.e. 1 – % selection for seedling vigor) on tuber yield (g) in open-pollinated populations of potato in La Molina

plant survival and tuber weight per plot (Table 4). An almost linear trend was observed between plant survival and selection intensity for seedling vigor in the nursery (Fig. 1), while this trend was almost logarithmic for tuber weight per plot (Fig. 2). These results suggest that by increasing the amount of seed in the flat and transplanting the vigorous seedlings, which will be better adapted for survival in the field, tuber weight can be significantly enhanced in OP offspring.

Discussion

Early reports (Atlin and Wiersema 1986) indicated that nursery selection against weak plants in artificial mixtures of hybrid- (S_0: 25%) and self- (S_1 and S_2: 50% and 25%, respectively) generations of TPS offspring increased the frequency of hybrids to 71%. Further research showed that elimination of weak transplants during population-thinning reduced the frequency of inbred plants. The tuber yields of TPS mixtures, which originally included 25% or 50% of hybrids, were 96% and 99% of that recorded in hybrid offspring. Our results confirm the effectiveness of early selection in the TPS nursery, perhaps due to the increased percentage of hybrid offspring in the selected material that was transplanted to the field.

These results also showed that breeding methods depend on the propagation mode in crops like potato, in which asexual (tubers) and sexual (TPS) means are available to obtain propagules for further commercial production (Pallais 1986). Early generation selection in potato breeding has not been widely accepted or recommended by potato breeders, particularly in offspring derived from 4*x*–4*x* crosses (for a review see Tarn et al. 1992). However, the results from our experiments clearly show that early and strong selection for seedling vigor in the flat-nursery works in TPS, because the percentage of inbred offspring could be drastically reduced.

Marker genes such as tuber flesh color or embryo spot have been used to identify hybrids among OP offspring (Arndt and Peloquin 1990; Brown 1993). However, to be cost-effective for farmers using TPS for potato production, the selection protocol needs to be quite simple and easy to apply in large populations. Likewise, the characteristics to be improved must also be associated with hybrid vigor, e.g. tuber yield (for reviews on this subject see Ortiz 1997, 1998).

In polysomic tetraploids such as potato, the inbreeding of OP TPS will depend on the rate of selfing. Selec-

tion for seedling vigor in the flat-nursery may be regarded as mass selection after pollination, resulting in preferred hybrid TPS. Hence the response (R) to this early selection in the flat-nursery depends not only on the intensity of selection (*i*) but also on the inherited additive genetic variance (σ^2_A) and the digenic non-additive variance (σ^2_D) as determined by the equation

$$R = i\,[(1/2)\,\sigma^2_A + (1/6)\,\sigma^2_D]/\,\sigma_P\,,$$

where σ_P is the phenotypic standard deviation.

In tetraploids, R includes σ^2_D because tetrasomic polyploids (2n=4*x*) have gametes (n = 2*x*) that contain two alleles per locus, and selection operates also on the intra-allelic interaction among these alleles (Wricke and Weber 1986). In this regard, tuber yield in potato appears to be mostly influenced by non-additive, intra- and inter-locus interactions (Ortiz 1998). The observed gains from strong, early selection in TPS may be accounted for by capitalizing on both the intensity of selection and non-additive genetic variation, which enhances tuber yield in potato.

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