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Inbreeding and true seed in tetrasomic potato. IV. Synthetic cultivars

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Abstract A true potato seed (TPS) synthetic cultivar from open pollination may broaden the genetic base in potato. A synthetic cultivar can also reduce the effect of inbreeding and maintain the productivity from generation to generation. Selected tetraploid parental genotypes, based on combining-ability tests, were chosen for isolated polycrosses to obtain tetraploid offspring. A series of experiments were undertaken to investigate the development of these TPS synthetic populations in two Peruvian locations: San Ramon, a rainfed, humid, mid-altitude environment, and La Molina, an arid, coastal environment under irrigation. Natural open-pollinated synthetics or control-mixture synthetics, involving two to six parents, had a similar tuber set but plant survival and tuber weight were higher in control synthetics including two or six parents. The results suggest that two-parent open-pollinated TPS synthetics may be a feasible option by selecting the right parents for the base population. A subsequent experiment showed that four-parent control synthetics (i.e. double crosses) were the best for tuber weight and size, followed by the two-parent control synthetics. Synthetic breeding populations could be shared with other breeders, who in cooperation with their local farmers may select promising genotypes for further cultivar release.

Keywords Broadening genetic base · Combining ability · Farmer participatory breeding · Open pollination · TPS

Introduction

True seed (TPS) offers a means to propagate the potato sexually. The advantages of this system with respect to tuber propagules have been reviewed elsewhere (Ortiz 1997; Simmonds 1997). Breeding potatoes for TPS requires a different approach on methods and cultivar types. TPS cultivars grown by farmers today are a heterogeneous collection of genotypes arising often from a cross between two heterozygous parents. However, TPS breeding targets phenotypically homogeneous cultivars.

In early articles of this series (Golmirzaie et al. 1998a, b) the influence of inbreeding in TPS was reviewed. This research showed that open-pollination in potatoes result from both selfing and outcrossing. This finding was corroborated by tuber yield and other quantitative characteristics of open-pollinated (OP) offspring, which rank between those of hybrids and selfed-offspring. The results also suggested that inbreeding and selection for developing parental materials appear to be limited in potato breeding. Synthetic cultivars have been recommended as an alternative mode for potato production using TPS (Atlin 1985; Ortiz 1998). Synthetic cultivars have been successfully used in maize, sugar beet or cross-pollinated forage crops (Simmonds and Smartt 1999; Khan 2000).

Potato clones are phenotypically uniform (homogeneous) owing to vegetative propagation, but their genotypes are heterozygous tetraploids. However, TPS cultivars are hybrids or arise from the open-pollination of clones or heterogeneous TPS hybrid offspring. Hence, TPS synthetic cultivars may be obtained from free intermating of at least two parental sources that are planted in an isolated field. These parents must be chosen after testing their combining ability. The aims of the present research were to investigate the potential of synthetic cultivars for TPS, the number of parents to be included in the synthetic, and the performance of synthetic cultivars arising from open or controlled pollinations.

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Materials and methods

Synthetic populations were obtained from open (OP) or controlled (hybrid) crosses. Six parents were used in combinations of 2, 4 and 6 to develop the source synthetic populations. These parents were selected from the TPS breeding population of the Centro Internacional de la Papa (CIP, Lima, Perú) according to their known combining ability (A. Golmirzaie, unpublished results). To obtain seed for each synthetic, the plots with the corresponding number of parents were isolated from other potatoes by three rows of maize. At the same time some reproductive characters were measured in these populations (e.g. berry number and weight), which were included in the next season, along with control hybrid crosses, in an experiment to determine the potential of synthetics vs hybrids in TPS. Four and six parental controls were developed using the multi-line concept for the respective TPS synthetic.

Two experiments were conducted at San Ramon (11°08′S, 800 m, rainfed humid mid-altitude Peruvian location on the Eastern slopes of the Andes) and La Molina (12°05′S, 240 m, arid coastal Peruvian location under irrigation) to study the effect of these open and controlled crosses in combination with various numbers of parents in the development of synthetic TPS populations. The seeds from the previous experiment were used for natural synthetics and the control crosses were made for two parents only. A subsequent experiment was conducted to further investigate the effect of increasing the number of parents in controlled crosses. The main objective of this new experiment was to determine the effect of the number of parents in the source population of a controlled-derived TPS synthetic.

In all experiments, the experimental layout was a randomized complete block design with three replications of 40 plants each. In each location, about 150 TPS of each synthetic population were planted in flats. After 6 to 8 weeks in the nursery, 120 random but vigorous seedlings were transferred to the field (40 seedlings per each single row plot) at each location. Data were recorded for flowering, plant vigor, vine earliness, berry number and weight, plant survival, and tuber set plus weight. Plant vigor was scored 50 days after planting (DAP), flowering was recorded at 60 DAP, and vine earliness 30 days before the anticipated day of harvest (90–100 DAP). The scale for these characteristics ranged from 1 to 7 or 9, where 1 indicated the poorest and 7 or 9 the best. At harvest, tuber number and yield (kg) were determined for all tubers and then for marketable tubers, over 50 g each. Berry number and weight (g) were also recorded before harvest. Individual, and combined – across locations, analyses of variance for the randomized complete block design and single degree of freedom contrasts were performed with MSTAT-C (Anon 1989) for all characteristics recorded in this research.

Results

Significant differences among the synthetic populations were observed for all characteristics recorded (Tables 1 and 2). Further results from investigations to develop two-parent synthetic TPS populations at San Ramon indicated that good flowering and a high berry set of heavy fruits could be possible in this humid, mid-altitude location. About 613 fruits with a total weight of 3,138 g were harvested in two parent-OP-synthetic TPS, while 95 fruits with a total weight of 446 g were harvested in four-parent-OP- synthetic TPS. The berry set in six-parent-OP synthetic TPS was 126 fruits with a weight of 600 g.

The genetic background of these synthetic populations was wide and the variation among synthetic offspring was significant, or highly significant, for all the characteristics investigated (Table 3). Four- parent synthetics (irrespective of being obtained through controlled or natural crosses) showed the same performance. However, control synthetics including two- or six-parents had better survival and tuber yield than their natural counterparts for plant survival at harvest and tuber weight (Table 4).

The performance of different synthetics according to the number of parent combinations in controlled crosses are given in Table 5, which indicates that two- and three-parent-derived controlled synthetics are very similar for most characteristics. The double-cross (or four-parent synthetics) was, however, significantly different than the other synthetics for marketable tuber weight, and showed the highest plant vigor and marketable tuber set. The results confirmed the need for the right parent selections, as well as including the appropriate number of parents for the development of high-yielding broadly adapted TPS synthetic cultivars.

Table 1 Analysis of variance of synthetic populations consisting of two and four parents

Source of variation	*df* [a]	Flowering	Berry number	Berry weight	Tuber weight
Replications	2	*	NS	NS	NS
Population[b]	6	**	**	**	**
(1)+(6) vs (7)	1	*	**	**	**
[(2)+((3)+(4)+(6)] vs (7)	1	**	**	**	**
[(1)+(2)+((3)+(4)+(5)+(6)] vs (7)	1	**	**	**	**
(1) vs (6)	1	**	**	**	**
Error	12				
Coefficient of variation (%)		8.3	20.6	4.6	2.5

NS, * and ** indicate non-significance, or significance at $P \leq 0.05$ or 0.01, respectively
[a] Degrees of freedom
[b] 1, 2, 3, 4, 5, and 6 consist of two parents, 7 consists of four

Table 2 Performance of synthetic populations consisting of two and four parents. Statistics for mean comparisons are indicated as single degree of freedom contrasts in Table 1

Population[a]	Flowering[b]	Berry number (#)	Berry weight (g)	Tuber weight (g plant^{-1})
1	2.3	38	148	253
2	3.7	51	195	346
3	5.0	256	1,220	326
4	1.7	88	393	326
5	4.3	110	549	474
6	6.3	649	3,238	589
7	5.7	648	3,269	588
Mean	4.1	263	1,287	415

[a] 1, 2, 3, 4, 5, and 6 consist of two parents, 7 consists of four
[b] Scale from 1: poor to 7: best

Table 3 Analysis of variance of controlled (C) and open-pollinated (OP) synthetic populations consisting of two, four and six parents

Source of variation	*df* [a]	Plant number at harvest	Tuber plant^{-1}	Tuber weight (kg plot^{-1})
Locations	1	**	NS	*
Reps/location	4	NS	NS	NS
Progenies	23	**	*	**
OP vs C/2 parents	1	**	NS	**
OP vs C/4 parents	1	NS	NS	NS
OP vs C/6 parents	1	**	NS	*
Coefficient of variation	(%)	21.4	24.1	32.2

NS, * and ** indicate non-significance, or significance at $P \le 0.05$ or 0.01, respectively
[a] Degrees of freedom

Table 4 Performance of controlled (C) and open-pollinated (OP) synthetic populations consisting of two, four and six parents. Statistics for mean comparisons are indicated as single degree of freedom contrasts in Table 3

Parent number	Plant number at harvest		Tuber plant^{-1}		Tuber weight (kg plot^{-1})	
	OP	C	OP	C	OP	C
2	19	24	241	321	10.9	11.8
4	21	25	277	307	11.2	11.3
6	19	26	234	342	9.8	12.3

Table 5 Performance of different combinations of parents in controlled crosses

Parent number	Earliness[a]	Plant vigor[a]	Univormity[a]	Plant number	Marketable tuber number	Marketable tuber weight (kg plot^{-1})
1[b]	3	3.7	5.7	20	73	6.3
2	5	5.7	4.5	23	153	7.3
3	5	5.5	4.5	18	145	6.8
4	5	6.8	4.9	23	172	10.3
1 parent vs (2+3+4 parents)	**	NS	*	NS	*	NS
(1+2+3 parents) vs. 4 parent	NS	NS	NS	NS	NS	*

NS, *, ** indicate non-significance, or significance at $P \le 0.05$ or ≤ 0.01, respectively
[a] Scale from 1: poor to 9: best
[b] One clone planted alone in isolation plot to obtain seeds

Discussion

Potato cultivars are clonally propagated from tubers but true seed may be obtained from artificial crosses, i.e. hybrids, or from open-pollination of clones or other phenotypically uniform TPS offspring (Ortiz 2000). Synthetic cultivars mixing two or more TPS offspring as the parent source may be alternatives for potato production from true seed (Golmirzaie et al. 1998a), particularly for locations where the seed industry is not well-developed, and hybrids are not available. A TPS synthetic cultivar from open-pollination may broaden the genetic base of crop production in potato (Ortiz 1997). It may allow potato farmers to save their seed for the next crop instead of purchasing new seed for each new planting. However, the availability of the synthetic generation for farmers will depend on seed production and the demand for this seed (Simmonds and Smartt 1999).

A synthetic cultivar is "a multiple hybrid between selected genotypes which combine well among themselves" (Khan 2000). Hence, general and specific combining-ability tests are needed to select parents for synthetic TPS cultivars ensuing from natural outcrossing (Ortiz 1998). The number of parents included in a synthetic cultivar has always been a matter for discussion among plant breeders. The first-generation synthetic (syn-1) results from all [k(k-1)/2] crosses between k parents. Simmonds and Smartt (1999) suggest that the parent number of a synthetic may vary, but not widely. If the parent number becomes large in a synthetic cultivar, its performance may approach that of OP population cultivars. Wricke and Weber (1986) provide a prediction formula for selecting parents of synthetic cultivars in tetrasomic polyploid species.

The early results of our experiments suggested that, by selecting the right source of parental material, it will be feasible to obtain the same or better results with a minimum number of parents in the source synthetic population and allowing it to open-pollinate in an isolation plot. These results further support the contention that the components of synthetics should be selected according to their combining ability. Further investigations demonstrated that four-parent controlled synthetics (i.e. double crosses) were the best for tuber weight and size, followed by the two-parent controlled synthetics in potato (Table 5). This was not surprising because in tetrasomic polyploid species inbreeding is reduced to 1/3 in double crosses (vs single crosses) (Wricke and Weber 1986). Hence, the best four-parent control synthetic should always have a higher tuber yield than the best two-parent control synthetic because this trait capitalizes on heterosis in tetrasomic potato (Ortiz 1998).

Synthetic cultivars are maintained and propagated by random mating, and this mixture of genotypes may provide genetic diversity in the cropping system through natural gene flow between these diverse genotypes (Ortiz 1997). In potato and other crops, genetic heterogeneity also provides flexibility (Amoros and Mendoza 1979), which may enhance resistance to diseases and pests in the crop pathosystem (Robinson 1996), and adaptability to environmental stresses. As suggested by genetic theory, advanced generations of a synthetic cultivar reduce the average inbreeding depression (Wricke and Weber 1986) but, if there are few parents, some deleterious inbreeding may occur while producing seed (Simmonds and Smartt 1999). Furthermore, a synthetic TPS cultivar may be partially inbred because of the mixture of selfing and outcrossing in polysomic tetraploid potato (Brown 1993).

These synthetic breeding populations could be further shared as a source of favorable alleles or for adaptive testing with other breeders. They may locally select promising genotypes for further cultivar release (Ortiz 2000), particularly with the participation of progressive farmers. In this regard, an interesting amount of variation in the breeding population will be needed for farmer-participatory selection. However, farmer's selection within adapted germplasm may be required for potato cultivar development in some regions because tuber yield per se in optimum environments does not appear to be an indicator of acceptability (Prain et al. 1992), or preferences may diverge between breeders and farmers (Thiele et al 1997). Culinary quality, of course, may also influence the selection of new germplasm by farmers and consumers.

Andean farmers grow potato through botanical seed propagation (or TPS) for disease elimination, stock rejuvenation, and the generation of new cultivars. These farmers also preserve potato genetic diversity by clonal propagation of tubers in the Andes. As suggested by Quiros et al (1992) "Andean potatoes form a large and plastic gene pool amplified and renovated by outcrossing followed in some cases by human selection of desirable genotypes". Hence, Ortiz (2000) recommends broadening the genetic base of potato with locally adapted, pest- and disease-resistant germplasm for the sustainable and environment-friendly production of this crop. The development of synthetic TPS cultivars having a wide genetic base will be an important genetic component towards this goal.

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