Open Pollinated Offspring for Producing Potatoes from True Seed

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Summary

Open pollinated (OP) offspring offers a cheap propagule for potato production from true seed (TPS). A series of trials in contrasting Peruvian locations including several generations derived by open pollination were carried out to determine the potential of OP for TPS. The results suggest that several generations of OP did not affect the performance of TPS for tuber characteristics. On average, F_1 hybrids out-yielded first generation OP offspring, but tuber yield per plot of advanced OP generations (OP_5) across locations did not differ significantly from that shown by F_1 hybrids. It seems that the effect of potential inbreeding in early OP generations was absent in advanced OP generations, maybe due to selection of heterozygous parents in the preceding generations. Results from sequential harvests showed that initiation and bulking of tubers are slower in advanced generations of OP than in the first OP generation, particularly in the warm tropics. Nonetheless, some OP TPS did not differ significantly for tuber yield across generations, suggesting that farmers may grow commercially selected OP offspring.

Résumé

Progéniture de pollinisation libre pour la production de la pomme de terre à partir des vraies semences biologiques

La progéniture de pollinisation libre offre du matériel de propagation moins cher pour la production de la pomme de terre à partir des vraies semences biologiques (TPS). Des séries d'essais comparant différentes localités péruviennes comprenant plusieurs générations issues de pollinisation libre (OP) ont été conduites pour déterminer le potentiel OP pour les TPS. Les résultats suggèrent que plusieurs générations de pollinisation libre n'ont pas affecté la performance des TPS pour les caractéristiques des tubercules. En moyenne, les rendements des hybrides F_1 ont premièrement surpassé la génération de la progéniture OP, mais les rendements des tubercules par parcelle des générations avancées de pollinisation libre (OP_5) n'ont pas été significativement différents des rendements des hybrides de la F_1 à travers les différentes localités. Il semble que l'effet de la consanguinité potentielle dans les premières générations de pollinisation libre était absent dans les générations avancées OP, due probablement à la sélection des parents hétérozygotes dans les générations précédentes. Des résultats des récoltes chronologiques ont montré que l'initiation et la tubérisation sont lents dans les générations avancées OP plus que dans les premières générations OP, plus particulièrement dans les zones chaudes des tropiques. Cependant, quelques TPS de l'OP n'ont pas été significativement différents pour les rendements de tubercules à travers les générations, suggérant que les agriculteurs peuvent produire de façon commerciale la progéniture de pollinisation libre sélectionnée.

Introduction

There are 3 kinds of potato: i. the single-sprouted tuber from which more tubers can grow, ii. a true seed from whose ensuing plants tubers will be harvested, and iii. a plant from which the true potato seed (TPS) will be harvested for commercial production (23). TPS receives nowadays great attention in the developing world because of many advantages that include pathogen-free potato propagules; particularly for locations prone to pests affecting seed health or importing expensive tubers from overseas that may account up

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to 60% of the costs, and easy of transport because a few hundred grams of TPS replaces 2 t of tubers for planting 1 ha (19). However, TPS requires more care than tubers since it appears to be more susceptible to weeds, water stress and some soil-borne pests in the early growth stages (27).

TPS may fit well into potato cropping systems because date of planting will not depend on the physiological age of the tubers. TPS needs however a longer growing period: 15 to 20 extra days viz. a viz. tubers. Hence, TPS cultivars showing early tuber initiation and fast tuber bulking rate under heat are two of the main traits in TPS breeding (12). Nonetheless, true potato seed (TPS) is an alternative to tubers for producing potato in pest-prone environments where farmers are unable to harvest healthy planting materials or imported seed-tubers are expensive

Hybrids from crosses between tetraploid parental sources are the most popular for TPS offspring, which should be phenotypically uniform, if they are to be recommended to farmers as new cultivars (5, 19, 27). Tetraploid potatoes are highly heterozygous but owing to their vegetative propagation are true-to-type unless mutation occurs. Hence, tetraploid parental sources are usually selected after progeny testing when showing uniform offspring (6, 11).

Farmers may still be reluctant to adopt TPS for producing potatoes because of the costs –mostly hand labor for emasculating flowers and pollinating to get hybrid seeds. A cheaper option will be to use open-pollinated (OP) TPS (22). Indian breeders recommended ‘MST-1’ as a potential OP TPS (28). Tuber yield was similar to that of hybrid TPS or commercial potato cultivars. Most of the other results show however that experimental hybrids always out-yield OP in potato (27 and references therein). Most of these reports included only one or a maximum of two OP generations, while equilibrium for gene frequency in a tetrasomic polyploid species such as potato needs more generations.

It seems that OP in potato ensues from selfing and sib-mating rather than only from outcrossing. Selfing occurs mostly in OP from selected clones, and both selfing as well as sib-mating plus outcrossing at different rates in F_1 TPS offspring. Recent results suggest that either selecting for vigorous seedlings in the nursery prior to transplanting or synthetic OP cultivars may provide high tuber yields (9, 10). Early nursery selection capitalizes on heterozygote individuals in the offspring (2, 7, 8), while synthetics rely on reducing inbreeding after open pollination (10).

This research includes a serie of trials in contrasting Peruvian locations with several generations derived by open pollination carried out to determine the potential of OP for TPS as well as the effect of earliness, as determined by date of harvest, in hybrid and open-pollinated (OP) TPS propagules.

Materials and methods

The first experiment consisted of OP generations ensuing from F1 TPS offspring selected in a warm humid tropic environment (San Ramón). These OP generations were advanced through testing and selecting the most outstanding plants up to OP_5 from six selected TPS breeding materials along with their original F_1 hybrids from a breeding population of the Centro Internacional de la Papa (CIP). The first experiment included these five OP generations and the original hybrid source for the six TPS breeding materials. The OP seeds were always obtained at San Ramón season after season by using the previous generation as parental source, i.e., F_1, OP_1 and so on, were the parents of OP_1, OP_2 and so on. Following this approach, any bias owing to environmental effects was avoided in each generation. The second experiment included selfed offspring (S_1), hybrid offspring (F_1) open pollinated offspring from clones and F_1 (OP and F_1 OP, respectively hereafter) from six TPS parents. The third experiment comprised OP generations derived each from six original TPS experimental hybrids whose original source was the same CIP lowland tropic breeding population (6).

The experiments were conducted at CIP experimental stations in San Ramón and Huancayo (first and third experiments only). San Ramón (11º 08’ S, 800 m), where most of CIP breeding work for TPS was undertaken, is a humid location in the eastern Andean slopes whereas Huancayo (12º 07’ S) is in the Peruvian highlands (3280 m). Ortiz and Golmirzaie (20) provide more details of both Peruvian locations.

The field layouts were always randomized complete block designs with 2 or 3 reps of 40 plants. Because of sequential harvest the analysis of variance was that of a split-plot design in the third experiment, where the genetic background was the main plot and the date of harvest was the sub-plot.

A total of 200 TPS of each offspring were soaked in a solution of 1500 ppm giberellic acid for 24 h, and thereafter planted in flats at a greenhouse nursery using plastic trays containing a 1 sand: 2 peat: 1 soil (by volume) substrate. After the seedlings were 3 to 5 cm tall, they were transferred into peat pots and grown to about 15 cm height, when 40 full-sib seedlings were transferred after eight weeks to single-row plots in the field. The traits recorded vary with the experiment because of the characters included by TPS breeders at each stage of population development. The common trait was tuber yield, but in early stages they also recorded data for plant survival and vigor, berry set and weight. In more advanced stages tuber yield became the principal character. In the second experiment, the characters recorded were tuber yield (kg.plant^{-1}), days to flowering, flowering intensity, flowering duration and pollen production. Flowering intensity scale ranged from 0 (no buds) to 9: (very abundant), for flowering duration from 1 (very short) to 9 (very long), and for pollen production from 0 (none) to 5 (abundant). Phenotypic correlations were calculated among all these traits. Tubers were recorded in the third experiment using two sets according to big and small tuber size as per Peruvian farmers' commercial standards.

Results

While advancing OP generations (OP_2 onwards) during selection in San Ramón (data not shown), quantitative and qualitative characters were better than in the OP_1 generation, suggesting the possibility of removal of the performance depression owing to partial inbreeding by selecting the appropriate populations. Berry set in OP_3 ranged from 20 to 291, whereas berry weight (per plant) ranged from 58 g to 1 kg. Hence, this significant variation allowed selection of the right parental source in the OP_3 generation, which was the source of seeds for the OP_4.

There were significant differences for agronomic and tuber traits among F_1 and OP generations of six TPS offspring in the first experiment (Table 1).

The locations affected significantly the characters recorded, and the interactions influenced significantly tuber yield. Hence results were tabulated for each location (Tables 2 and 3).

Table 1

Mean squares of the analysis of variance for agronomic characteristics recorded in F_1 and five open-pollinated (OP) generations derived from six true seed populations (San Ramón and Huancayo)

Source of variation	Degrees of freedom	Plant at 45 days	Plants at harvest	Tuber yield per plant (kg)	Tuber yield per plot (g)
Location (L)	1	9248.0**	18157.6**	504513.3**	2014513611.1**
Replication/L	2	16.5	76.8**	3707.0	8415034.7
Generation (G)	5	29.9*	49.5**	27552.4**	29738194.4**
L x G	5	20.2	27.8	5104.4	11316736.1**
Population (P)	5	12.1	107.9**	16232.6**	30266944.4
L x P	5	2.4	31.6	7857.5*	20696736.1**
G x P	25	14.7	37.8**	5688.6*	6563036.1**
L x G x P	25	16.0	22.8**	4027.6**	4002161.1
Error	35	12.0	13.4	2880.6	3172141.9

* and ** significant at 5% and 1% respectively

Table 2

Average performance of F_1 and five open pollinated (OP) generations for agronomic characteristics in a cool highland environment (Huancayo)

Generation	Plant at 45 days	Plants at harvest	Tuber yield per plant (g)	Tuber yield per plot (kg)
F_1	35	35	341	11.5
OP_1	35	32	264	8.7
OP_2	36	31	247	7.7
OP_3	36	33	299	10.0
OP_4	33	31	220	6.8
OP_5	37	31	298	10.2
S.E.D.	^{z}	^{z}	13	^{z}

^{z} Non-significant source of variation for generations in analysis of variance

Table 3

Average performance of F_1 and five open pollinated (OP) generations for agronomic characteristics in warm lowland tropic environment (San Ramón)

Generation	Plant at 45 days	Plants at harvest	Tuber yield per plant (g)	Tuber yield per plot (kg)
F_1	26	23	278	7.2
OP_1	27	21	213	5.2
OP_2	27	19	195	4.4
OP_3	28	21	221	5.7
OP_4	27	21	178	4.2
OP_5	30	22	225	5.9
S.E.D.	1	1	13	0.5

The F_1 tuber yield was always better than its OP counterparts in both locations, but OP_5 was an outstanding TPS OP offspring for tuber yield and not significantly distinct –on average, for this characters than the F_1 hybrids. The effect of the heat stress was clear in the assessment at the warm location (San Ramón) (Table 3). The lower performance of the OP offspring in this location was accounted for by the start of tuberization rather than to plant survival. The results from this research suggest that selection within the breeding population for OP offspring with stable TPS performance may be feasible.

The parental sources were alike in the second experiment as revealed by its analysis of variance, which also indicated that the generations were significantly distinct for tuber yield, flowering intensity and duration. The F_1 and F_1 OP offspring were equal but better for tuber yield than S_1 and OP offspring (Table 4).

The generation-by-parental source interaction was only significant for tuber yield, because of the poor F_1 hybrid performance of one (C.223 LM86-B x C.241 LM86-B) out of the six TPS experimental breeding materials. A deeper analysis for each offspring confirmed these preliminary results, and suggested that the outstanding performance of the F_1 OP may be associated by residual heterozygosity in some offspring, while inbreeding depression in S_1 or OP may account for low yield in those offspring with poor performance for these generations. Selecting for offspring with outstanding F_1 OP allows other breeders to further select clones in this material or farmers to use this kind of offspring in potato production from TPS. Significant phenotypic correlations were observed between all characters except for pollen production (Table 5).

Table 4

Average performance for yield and other reproductive characteristics in hybrid, selfed and open pollinated (OP) offspring of six true potato seed parents

Generation	TY	DF[z]	FI	FD	PP
F_1	13.2	38	4.7	6.2	2.5
F_1 OP_1	12.1	37	5.7	8.0	2.2
OP_1	11.2	39	3.7	5.3	1.8
S_1	9.3	38	4.3	6.0	2.5
S.E.D.	0.4	z	1.0	1.2	z

TY= tuber yield ($t.ha^{-1}$), DF= days to flowering, FI= flowering intensity, FD= flowering duration, PP= pollen production

[z]Non-significant F-test among offspring

Table 5

Phenotypic correlations among tuber yield (g.plant^{-1}) and reproductive characteristics

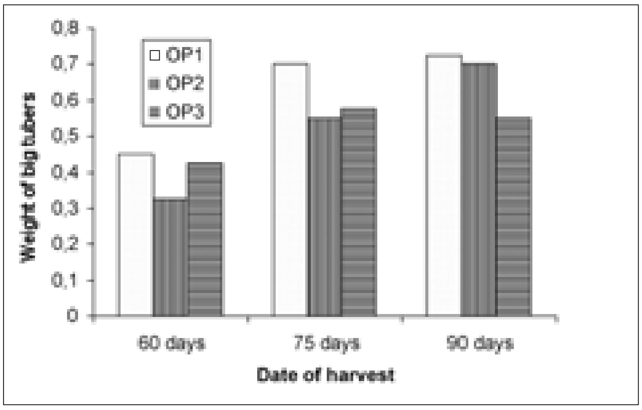
Trait	DF	FI	FD	PP
Tuber yield	-0.420	0.688	0.478	0.203
	(0.040)	(< 0.001)	(0.018)	(0.340)
Days to flowering (DF)		-0.491	-0.413	-0.015
		(0.015)	(0.044)	(0.943)
Flowering intensity (FI)			0.728	0.213
			(< 0.001)	(0.318)
Flowering duration (FD)				0.030
				(0.888)
Pollen production (PP)				

P[ρ= 0] indicated within brackets below correlation coefficient

The correlations between days to flowering and the other characters were negative, while those among the remaining traits (tuber yield, flowering intensity and duration) were positive. Hence, high tuber yielding offspring showed early flowering, which was also abundant and last for a long period.

The date of harvested affected significantly the performance of the OP offspring in experiment 3. The OP generation was only significant for weight of big tubers, which suggests that initiation of tuber bulking was slowed in advanced OP generations than in OP_1 when grown in the stressful hot environment of San Ramón but not in the cool highlands of Huancayo (Figure 1).

One single date harvest for all generations, therefore, may affect negative tuber yield in some OP genera-



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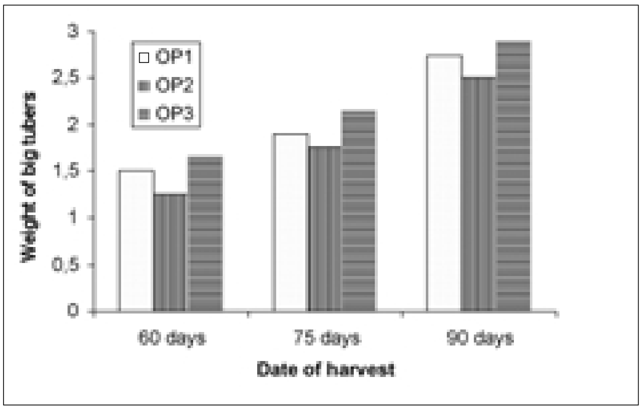
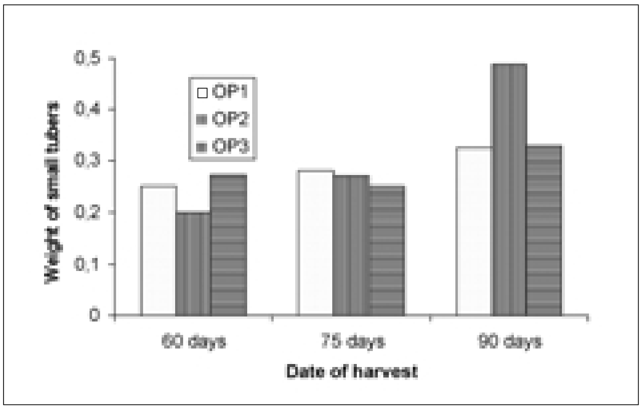


B

Figure 1: Weight of big tubers (kg) from OP_1 to OP_3 generations at three harvest dates (60, 75 and 90 days after planting): a. San Ramón, b. Huancayo. S.E.D.= 186 g.



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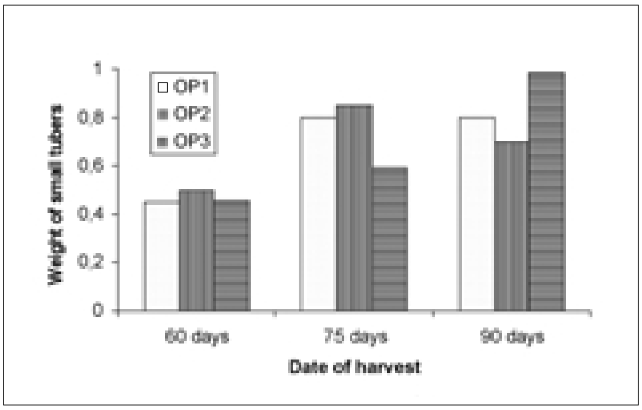
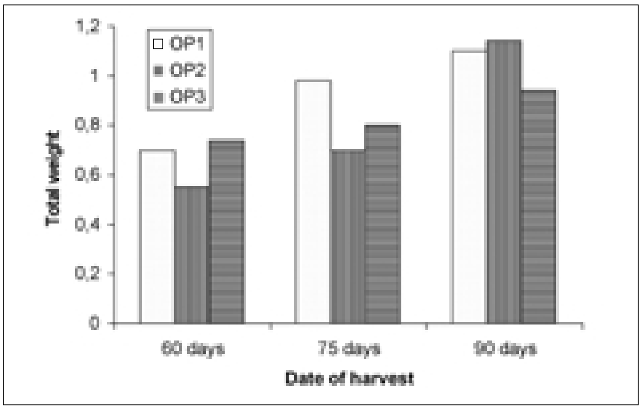


B

Figure 2: Weight of small tubers (kg) from OP_1 to OP_3 generations (60, 75 and 90 days after planting): a. San Ramón, b. Huancayo. S.E.D.= 53 g.

tions. Nonetheless, some offspring showed a stable tuber yield performance irrespective of the OP generation, making them a suitable material for TPS production by farmers –as shown by the non-significant interactions. The weight of small tubers –indicating late or slow bulking, was only affected significantly by the date of harvest but not by the genetic background or OP generation at both locations (Figure 2). The same was observed for total tuber yield in each or across both locations (Figure 3).



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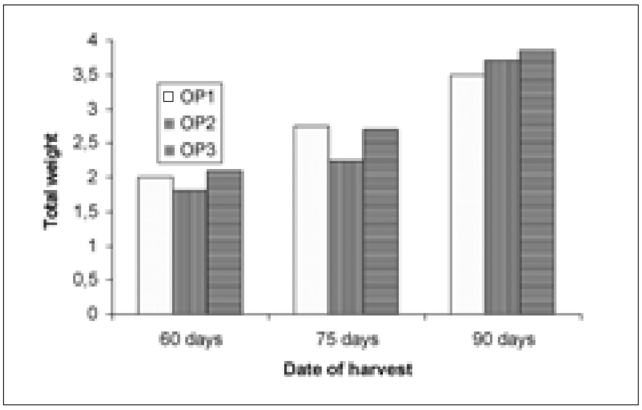

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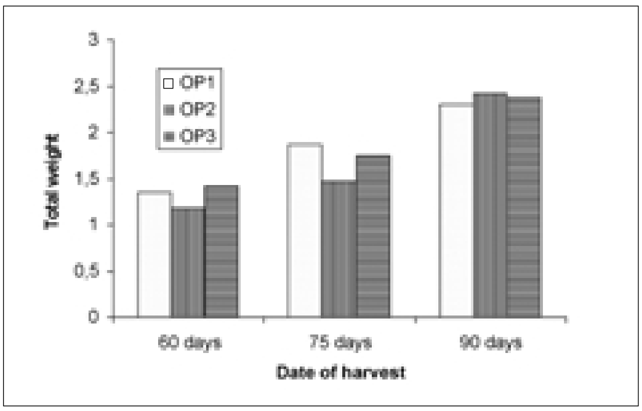

C

Figure 3: Tuber yield per plot (kg) from OP_1 to OP_3 generations (60, 75 and 90 days after planting): a. San Ramón, b. Huancayo, c. Combined. $S.E.D._{Location}$= 0.3 kg; $S.E.D._{Combined}$= 0.2 kg.

Discussion

Outcrossing rates define the genetic structure of an OP offspring because they may result from selfing (if male fertile) and sib-mating because of pollination by bumblebees within rows of sibs. High outcrossing rates may lead to most of the OP offspring being hybrids (19). In potato high tuber yield ensues from multi-allelism per locus in locally adapted genotypes (18). Hence, ensuring hybrids in OP offspring will ensure high tuber yield, either by selecting early for seedling vigor in the nursery (9) or through a synthetic genotype ensuing from hybridizing at least two F_1 TPS sources (10). In tetrasomic polyploid potatoes, gamete phase disequilibrium between loci will not be completely removed after one generation of random mating, which leads to a temporary reduction of the genetic variability. Hence, higher tuber yield in advanced TPS OP generations (e.g. OP_5) could occur because the offspring reached genetic equilibrium.

OP berry and seed set are correlated with pollen stainability because highly fertile male parents attract bumblebees (3), and hybrid plants had better seedling vigor, more flowers, high pollen stainability and large OP berry size (2, 7, 8), which suggest that through advancing OP generations, weak plants –ensuing from selfing or sib-mating, contributed less than hybrid plants to the next OP generation. Hence, advanced OP generations such as OP_5 could show high tuber yield, because of the heterozygosity remaining in the parental source (i.e., OP_4 plants from with OP_5 seeds were harvested).

The results from the first two experiments were not surprising because the F_1 hybrids were often the best for tuber yield. The poor tuber yield for only one F_1 hybrid in the second experiment could arise from inbreeding arising due to co-ancestry. Likewise, in the second experiment 2/3 TPS offspring the F_1 OP outyielded the OP from a single TPS parental source, which showed the advantage of the former multi-parent synthetic versus a uni-parental synthetic source resulting from both outcrossing and selfing. The rate of inbreeding in the multi-parent synthetic may be smaller because bumblebees may be attracted mostly by male fertile heterozygous plants shedding pollen, which is a trait significantly influenced by inbreeding depression (7, 8). These results support the advantage of synthetics ensuing from TPS offspring rather than a single clone for producing cheap OP TPS cultivars. The results also show the advances for tuber yield and key reproductive traits for producing OP TPS.

Selecting appropriate parental sources in the target environment and using them for producing multi-parent synthetics ensuing from OP of their F_1 generation may be one of the cheapest options for providing TPS cultivars to farmers in the developing world. This approach may become more important in locations with labor shortage because, as indicated by Ortiz and Peloquin (22), most of the TPS costs are associated to hand emasculation and hybridization. True seed for commercial production of potato seems to be therefore an attractive option for environments where sustainable seed tuber systems are difficult because of pest pressure or lack of a steady supply of high quality tubers (1). However, to fully exploit its potential, potato breeders need to provide TPS cultivars that will not be only a cheap planting material but also fit well in the cropping systems. In the warm tropics the major constraints are stresses such as heat –which affects tuberization, and pests (viruses, fungi, bacteria) (17). In such an environment, potato cultivar needs an early emergence, fast rate of tuber bulking and early maturity for harvest (13), plus genes protecting the crop against pests to avoid unhealthy propagules. Likewise, early tuberizing potato shows vine earliness because of fast leaf senescence (24). Hence the breeding materials need to include these traits into any TPS cultivar to be commercially feasible (16). The breeding materials originally developed by CIP for the warm humid lowland tropics possess these characters, and hence they are an important source to develop further TPS cultivars either as hybrid or OP seeds. Furthermore, it appears that general combining ability linked to additive genetic variance accounts significantly for inheritance of earliness in potato under heat (4), which suggests that genetic gains through selection for this trait are warranted.

The results from the third experiment clearly show that although tuber yield may be affected by early harvest of late maturing genotypes in the warm tropics, there was enough genetic variation assembled in the breeding population that suitable cultivars (either hybrids or OP) with the needed early tuberization and fast tuber bulking may be obtained from such a population (29). Early maturing cultivars may also provide extra benefits for competing against weeds after transplanting and for environment where reliable water supply systems are not always available, particularly because TPS cultivars with fast tuber bulking can be grown at the peak of the rains.

Conclusion

The cheapest material for TPS production are those derived from open pollination (14, 15), but tuber yields of OP TPS may be lower than those observed in hybrid seeds because they either result from selfing or sib-mating (2, 27). Inbreeding affects significantly tuber yield (9, 10, 25, 26) or pollen viability (3). Heterozygosity in the sporophyte affects however the gametophytic generation (21), which explains why tuber yield does not always decrease after successive OP generations (12). Selection of OP seedlings in the nursery according to its vigor may however yield a higher percentage of hybrid offspring thereby leading to higher tuber yields than in conventional OP TPS (9). Also a synthetic OP cultivar may provide a buffer against inbreeding (10), which clearly shows the potential of OP seed for potato production from true seed.

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AVIS

Nous rappelons à tous nos lecteurs, particulièrement ceux résidant dans les pays en voie de développement, que TROPICULTURA est destiné à tous ceux qui œuvrent dans le domaine rural pris au sens large.

Pour cette raison, il serait utile que vous nous fassiez connaître des Institutions, Ecoles, Facultés, Centres ou Stations de recherche en agriculture du pays ou de la région où vous vous trouvez. Nous pourrions les abonner si ce n'est déjà fait.

Nous pensons ainsi, grâce à votre aide, pouvoir rendre un grand service à la communauté pour laquelle vous travaillez.

Merci.

BERICHT

Wij herrineren al onze lezers eraan, vooral diegenen in de ontwikkelingslanden, dat TROPICULTURA bestemd is voor ieder die werk verricht op het gebied van het platteland en dit in de meest ruime zin van het woord.

Daarom zou het nuttig zijn dat u ons de adressen zou geven van de Instellingen, Scholen, Faculteiten, Centra of Stations voor landbouwonderzoekvan het land of de streek waar U zich bevindt. Wij zouden ze kunnen abonneren, zo dit niet reeds gebeurd is.

Met uw hulp denken we dus een grote dienst te kunnen bewijzen aan de gemeenschap waarvoor u werkt.

Dank U.