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Evaluation under long-day conditions of 4*x*–2*x* progenies from crosses between potato cultivars and haploid Tuberosum-*Solanum chacoense* hybrids

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Summary

Twelve 4*x* families (obtained from a sub-set of crosses between seven 4*x*–potato cultivars and three 2*x* haploid Tuberosum-*Solanum chacoense* hybrids) were evaluated at Hancock, Wisconsin (USA). The 4*x*–parents were elite cultivars selected for adaptation in three continents (Europe, South America, and North America). The 2*x* male clones were able to produce 2n–pollen grains by a mechanism akin to first-division restitution with crossover (FDR-CO). The estimation of the degree of heterosis for total tuber yield (TTY) was obtained by comparing the field performance of the progenies with their respective 2*x* and 4*x* parents. Haulm maturity (HM) and general tuber appearance (GTA) were also evaluated. For TTY, the 4*x*–2*x* families (as a group) outyielded both the 4*x* and 2*x* parental groups by 10.6% and 42.5%, respectively. In addition, 5 out of 12 families outyielded their corresponding 4*x*–parents. These best five families outyielded the group of 4*x*–parents by 40.6%. A considerable variability was observed for HM but, in general, the families were later maturing than the 4*x* cultivars. The identification of 4*x*–2*x* families with GTA within the range of the 4*x* commercial cultivars was another important observation. An overall lack of parent-offspring correlation was detected indicating that performance of the parents *per se* cannot provide a reliable prediction about the performance of the families. Therefore, progeny testing would be an imperative step for selection of parental clones at both ploidy levels. Our study indicated that haploid Tuberosum-*S. chacoense* hybrids are able to generate heterotic 4*x*–2*x* families for TTY in combination with good GTA. These results reinforce the view that selection of superior clones for the Northern Hemisphere can be feasible using germplasm with ~25% genomic contribution of this wild South American species.

Key words: *Solanum chacoense*, *Solanum tuberosum*, unilateral sexual polyploidisation, wild species, 2n–gametes

Introduction

Solanum chacoense Bitter is a wild diploid (2*x*) species distributed across a large area of South America. Its natural occurrence has been reported in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Hawkes, 1990). Habitats of this species range widely, from sea level to over 3500 m in the Andes mountains (Miller & Spooner, 1996). *S. chacoense* is highly polymorphic and its germplasm is a potential source of genes for improvement of numerous traits in the cultivated tetraploid (4*x*) potato. These traits include insect and disease resistance, heat tolerance, high tuber starch content and strong vegetative vigour (Bani-Aameur, Lauer, Villeux & Hilali, 1991; Brown & Thomas, 1994; Lynch *et al.*, 1997; Veilleux, Paz & Levy, 1997). Another useful characteristic of this species for plant breeding is that male-sterile Tuberosum haploids can hybridise with accessions of *S. chacoense* to produce male-fertile progeny. However, there are also some major problems associated with the adaptation of *S. chacoense* including the presence of very long stolons and late tuber initiation under field conditions in Northern temperate areas (Leue & Peloquin, 1977).

Three major breeding strategies have been used to introgress *S. chacoense* genes into Tuberosum germplasm: (1) doubling the chromosome number of *S. chacoense* for subsequent use in 4*x*–4*x* crosses; (2) 4*x*–2*x* mating with unilateral sexual polyploidisation (USP) and, (3) interdiploid crosses with bilateral sexual polyploidisation (Peloquin, Yerk, Werner & Darmo, 1989). Schemes (2) and (3) rely upon the production of 2*n*–gametes for recovery of the tetraploid level in the progenies. The frequency of 2*n*–

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pollen grains formed by first-division restitution with crossover (FDR-CO) was found to be reasonably high in *S. chacoense* (Leue & Peloquin, 1980). The FDR-CO gametes are considered to be more valuable than those obtained by the second-division restitution (SDR) mechanisms because a larger amount of the parental heterozygosity and epistatic interactions can be transferred to the progeny without disruption by recombination (Peloquin *et al.*, 1989).

Selection work was carried on *S. chacoense* germplasm for more effective tuberisation and 2*n*–gamete formation (Leue & Peloquin, 1980). It was observed that hybridisation between 2*n* gamete-producers of *S. chacoense* was a good method of obtaining new 2*n*–gamete producing individuals. Similar selection programmes with 2*x* haploid Tuberosum- *S. chacoense* hybrids for 2*n*–gamete production have been carried out in Italy (Barone, Carputo & Frusciante, 1993) and Brazil (Cunha, Pinto & Davide 1994; Morais & Pinto, 1996). USP- and BSP-derived genetic materials have allowed a further and more systematic exploitation of this germplasm by incorporating genome segments from distinct *S. chacoense* accessions into Phureja and haploid Tuberosum clones (Leue & Peloquin, 1980; Werner & Peloquin, 1991; Morais & Pinto, 1996). In addition, 4*x*–2*x* (FDR-CO) crosses involving haploid Tuberosum — *S. chacoense* germplasm have been also used in basic genetic studies to determine centromere-locus distances of important genes (Douches & Quiros, 1987; Wagenvoort & Zimnoch-Guzowska, 1992) and to ascertain the average heterozygosity transmitted through 2*n*–gametes to the progeny (Douches & Quiros, 1988; Barone, Gebhardt & Frusciante, 1995).

The USP breeding scheme has generated valuable 4*x*–2*x* families derived from 2*x* Phureja-haploid Tuberosum hybrid clones (for review see Tai, 1994). Good results have been also obtained with 4*x*–2*x* families derived from crosses between haploid Tuberosum and *S. berthaultii* Hawkes, *S. tarijense* Hawkes, *S. bukasovii* Juz. and *S. sparsipilum* (Bitt.) Juz. et. Buk. (Buso, 1986; Darmo & Peloquin, 1991; Serquen & Peloquin, 1996). However, few field tests have been conducted to evaluate the breeding potential of 4*x*–2*x* (FDR-CO) families obtained from crosses between adapted 4*x* cultivars and 2*x* haploid Tuberosum — *S. chacoense* hybrids. Promising results were obtained with interdiploid families from 2*x* (SDR) — 2*x* (FDR-CO) crosses involving *S. chacoense* or *S. chacoense* × *S. infundibuliforme* (Phil.) hybrids (Werner & Peloquin, 1991). In addition, three-way hybrids with 25% genomic contribution from *S. chacoense* outperformed other types of hybrids for tuber yield in assays conducted in Africa (Bani-Aameur *et al.*, 1991). Complex hybrids with *S. chacoense* genome were also more tolerant to tuber heat necrosis than the standard 4*x* cultivar used for comparison in Virginia, USA (Veilleux, Paz & Levy, 1997). In Brazil, selected families and clones derived from crosses of *S. tuberosum* × *S. chacoense* showed very good performance for traits such as yield and specific gravity (Morais & Pinto, 1996). The aim of the present study was to extend the evaluation of the potential value of 4*x*–2*x* (FDR-CO) crosses using (as female parents) 4*x* potato cultivars and as staminate parents haploid Tuberosum-*S. chacoense* hybrids.

Materials and Methods

Plant material

Three 2*x* haploid Tuberosum- *S. chacoense* hybrids ('T–480', 'T–704', and 'T–706') were used. The hybrid 'T–480' was obtained from the cross ['Chippewa' haploid–W1831 × *S. chacoense* 6–9]. The 2*x* hybrids 'T–704' and 'T–706' were full-sibs derived from the cross ['Merrimack' haploid–W3304 × *S. chacoense* 1–24–1]. All 2*x* clones produce 2*n*–pollen grains due the presence of the *ps* (parallel spindles) gene in homozygous condition. The *ps* gene controls 2*n*–gamete formation by a mechanism genetically equivalent to FDR-CO (Mok & Peloquin, 1975). A group of seven 4*x* cultivars representing a cross-section of elite genetic materials selected for adaptation in three continents (Europe, South America, and North America) were used as female parents. They were 'Aracy' (Brazil), 'Baronesa' (Brazil), 'Chiquita' (Brazil), 'Mantiqueira' (Brazil), 'Atlantic' (USA), 'Elvira' (Holland) and 'Spunta' (Holland).

4x–2x crosses and interploid families

Altogether, twelve 4*x*–2*x* families were obtained for field evaluation. The haploid-species hybrid 'T–704' was hybridised as male with all the seven 4*x* potato cultivars. 'T–706' was hybridised only to 'Chiquita, 'Elvira', and 'Spunta'. The hybrid 'T–480' was hybridised as male only to 'Aracy' and 'Chiquita'. Crosses were made in the greenhouse (at Madison-WI, USA) using fresh or refrigerated pollen that was applied to previously emasculated flowers. After crossing, plants were kept in a greenhouse with supplementary light conditions. The seeds were extracted when the fruits were at least 5 wk old. All the seeds were treated with 1500 ppm of giberellic acid for 24 h and rinsed in water before planting. Seeds of the families produced in the greenhouse were sown in jiffy-mix in 13 cm × 13 cm plastic trays. The seedlings were transplanted individually to 10–cm pots and kept under greenhouse conditions. The tubers were harvested about 158 days later. Two tubers of at least 20 plants per cross were used to constitute two family-bags, with one tuber per genotype per bag. Tubers of the 4*x*–2*x* families were treated with Rindite (1 mg kg^{-1} of tubers for 3 days) to break dormancy. After treatment, the tubers were left at room temperature until sprouting. These tubers were utilised in the field trials.

Field experiment and trait assessments

The field assay with the 4*x*–2*x* (FDR-CO)-derived families was set up at Hancock, WI in a randomised complete block design (RCBD) with two replications (20 hills per plot). For estimation of the degree of heterosis, a set of six 4*x* cultivars (used as female parents) and the 2*x* species-hybrid clones (used as male parents) were also planted in RCBD (with two replications) in the same experimental field but using 4–hill plots. These different plot sizes were used since the comparison was done between identical clones (i.e, the parents) vs. a group of 20 distinct genotypes (i.e., 20 hybrid clones from 4*x*–2*x* crosses). Tubers of the parental 4*x* cultivar 'Mantiqueira' (Brazil) were not available for this assay. The parental tubers (used as seed) were field-grown and larger than the 4*x*–2*x* family tubers (see Discussion). Plants were spaced 0.91 m between rows and 0.31 m between hills in a row. The total duration of the experiment was 110 days from planting to harvesting (June-October). Tubers were dug and harvested by hand. Three agronomic traits were evaluated. Total tuber yield (TTY) was estimated using only tubers over 2.5 cm in diameter. Tubers were weighed and plot means (in kg per hill) were used in the analysis of variance. Haulm maturity (HM) was based on a description of the vine appearance of the plot at 77 days from planting. The following scale was used for HM assessment 1 = completely senesced; 2 = partially senesced; 3 = prostrate, green, post-flowering; 4 = upright, green, post-flowering; 5 = upright, green, flowering or pre-flowering. General tuber appearance (GTA) was evaluated using a qualitative key from 1 = poor to 5 = excellent, with 0.5 increments.

Analysis of variance and parent-family correlation

The analysis of variance (ANOVA) for this experiment was partitioned into the sources of variation due to blocks, families, and experimental error. Tests of significance were conducted by comparing their mean squares with the respective error mean squares. The means of the 2*x* and 4*x* parent groups were contrasted with those of the 4*x*–2*x* families for the three traits. Correlation analysis of parent mean and family mean were done for each individual trait.

Table 1. *Analysis of variance of total tuber yield (TTY), haulm maturity (HM) and general tuber appearance (GTA) of families from 4x–2x crosses between 4x potato cultivars and haploid Tuberosum-*S. chacoense *hybrids evaluated at Hancock, Wisconsin, USA*

		Mean squares		
Source of variation	df[a]	TTY	HM	GTA
Block	1	0.132	3.375	0.260
Families	11	0.160*	0.496	0.579*
Error	11	0.052	0.193	0.192
CV[b] (%)		22.13	10.87	13.94

[a] df = degrees of freedom

[b] CV = coefficient of variation

* = Significant at 0.05 level

Results

Total tuber yield

The ANOVA indicated the presence of a significant difference for TTY among the 4*x*–2*x* (haploid Tuberosum-*S. chacoense*) families (Table 1). The family as a group outyielded both the 4*x* and 2*x* parental groups by 10.6% and 42.5%, respectively (Table 2). The overall mean of the hybrid families (1.04 kg per hill) was identical to that observed for 'Atlantic' (the only North American 4*x* cultivar involved in this set of crosses). Expressed as the percentage of the 4*x* parent, the yield of the families ranged from 48% to 210%. The average performance of the best five families was 1.32 kg per hill (a value identical to that observed for the best 4*x* parent — 'Aracy'). Furthermore, the best five families outyielded the 4*x* parent as a group by 40.6%. About 42% of the families outyielded their respective 4*x* parent. In addition, three families ['Spunta' × 'T–704'], ['Spunta' × 'T–706'], and ['Baronesa' × 'T–704'] outyielded 'Aracy' which was the best for TTY among the 4*x* parents assessed (Table 2).

General tuber appearance

The ANOVA indicated a significant difference among families for GTA (Table 1). The 4*x*–2*x* families had a slightly lower GTA mean score when compared with both the 4*x* and the 2*x* parents. A GTA score of three is the minimum limit of acceptance in many breeding programs. Therefore, 10 out of 12 families were considered phenotypically acceptable and would be saved for additional evaluation (Table 2).

Haulm maturity

The ANOVA indicated significant differences among families only at the 10% level for HM (Table 1). The two parental groups were quite similar in terms of HM scores indicating that previous selection against very late maturity was effective at the diploid level. However, the families (as a group) were later maturing than both the 4*x* and the 2*x* parent groups (Table 2). When considered individually, each family was later maturing than both groups of parents with only one exception, ['Aracy' × 'T–704'](Table 2).

Parent-family correlation

No significant parent mean-family mean correlation could be observed for HM and GTA (r-value ranged from –0.12 to 0.16). For TTY, a significant and negative correlation (–0.71) between the 4*x*–parent mean and the family mean was observed (Table 3).

Table 2. *Means of total tuber yield (TTY) in kg per hill, haulm maturity (HM) and general tuber appearance (GTA) of 4x–2x (Tuberosum-S.* chacoense*) families and their parents evaluated at Hancock, Wisconsin, USA*

Genotypes	Means		
	TTY	HM[a]	GTA[b]
2*x*–parents			
T–480	0.71	3.0	3.00
T–704	0.72	3.0	3.50
T–706	0.77	2.5	3.00
4*x*–parents			
Aracy	1.32	4.0	4.00
Atlantic	1.04	3.0	3.25
Baronesa	0.65	3.5	2.50
Chiquita	1.06	3.5	3.75
Elvira	0.64	3.0	3.50
Mantiqueira	—	—	—
Spunta	0.76	3.0	3.75
4*x*–2*x* families			
Aracy × T–480	1.05	5.0	3.00
Aracy × T–704	0.84	3.5	2.75
Atlantic × T–704	0.81	4.0	4.00
Baronesa × T–704	1.37	3.5	2.75
Chiquita × T–480	0.51	4.0	2.00
Chiquita × T–704	0.88	4.5	3.50
Chiquita × T–706	0.86	4.5	3.00
Elvira × T–704	1.26	3.5	3.50
Elvira × T–706	1.26	4.0	3.75
Mantiqueira × T–704	0.89	4.0	3.00
Spunta × T–704	1.43	4.5	3.00
Spunta × T–706	1.33	3.5	3.50
$LSD_{0.05\ among\ families}$	0.50	NS	0.96

[a] Haulm maturity (HM) based on a scale from 1 = senesced to 5 = still flowering

[b] General tuber appearance (GTA) based on a scale from 1 = poor to 5 = excellent

NS = Non-significant at 0.05 level

Discussion

Total tuber yield

The results suggest that 2*x* haploid Tuberosum - *S. chacoense* hybrids are promising genetic material with potential to increase total tuber yield in potatoes. It is important to mention that the yield potential of the 4*x*–2*x* families in our experiment was probably underestimated due to the lower weight of the greenhouse-grown tubers of the families (15–50 g) in comparison with those of the field-grown seed tubers of the parental clones (50 g or more). The fact that seed tubers were not homogenous between parental group and families, penalizing the 4*x*–2*x* progenies, may give some erroneous conclusions about the yield potential of these crosses. The levels of high-parent heterosis were variable and seemed to be dependent upon both the 4*x* cultivar and the 2*x* haploid Tuberosum-*S. chacoense* hybrid used as parental material as observed in pairwise comparisons (Table 2). Except for 'Atlantic', all 4*x* cultivars were originally selected for adaptation to distinct environmental conditions, which differed from those under which the present trial was conducted. However, some of the 4*x* cultivars performed similarly or even better than 'Atlantic' (Table 2). Some 4*x* cultivars that had poorer performance such as 'Baronesa' (Brazil), 'Elvira' (Holland), and 'Spunta' (Holland) gave rise to heterotic 4*x*–2*x* families. Surprisingly, the two families with the highest means (higher than the mean of the best 4*x* cultivar) were originated from crosses involving 'Baronesa' and 'Spunta' (Table 2). These results suggest that complementary genetic factors for TTY may be present in certain pairs of parental clones.

The TTY increase in 4*x*–2*x* families over their 4*x* parents can be attributed to an increase in allelic and non-allelic interactions. Preponderance of nonadditive genetic variance for tuber yield has been reported in potato (Mendiburu & Peloquin, 1977). In fact, as pointed out by Mendiburu, Peloquin & Mok (1974) losses and gains, respectively, of allelic and non-allelic interactions rather than inbreeding can explain haploid depression as well as vigour in tetraploid potatoes. The increase in yield of 4*x*–2*x* families over the 4*x* parent may also be explained by the introgression of allelic diversity and more favourable 'linkats' (i.e. linkage blocks of favourable genetic factors) (DeMarly, 1979).

The identification of heterotic families for TTY is in agreement with previous investigations using the USP breeding scheme. The heterosis values reported here are difficult to compare with those reported in the literature since a large number of distinct haploid-species and 4*x* parents have been evaluated as parents in 4*x*–2*x* crosses (Tai, 1994; Buso, Boiteux, Tai & Peloquin, 1999). Previous reports with genetic material similar to our families are those derived from interdiploid 2*x*(SDR)–2*x*(FDR-CO) crosses with *S. chacoense* or *S. chacoense* × *S. infundibuliforme* hybrids. The results indicated that best five 4*x* families outyielded the best five 4*x* cultivars by 57% and 69%, at two distinct locations in Wisconsin (Werner &

Table 3. *Parent mean-family mean correlation coefficients (r) of total tuber yield (TTY), haulm maturity (HM), and general tuber appearance (GTA) of 11 families from 4x–2x crosses between 4x potato cultivars and haploid Tuberosum - S.* chacoense *hybrids evaluated at Hancock, Wisconsin, USA*

Parent	TTY		HM		GTA	
	2*x*	4*x*	2*x*	4*x*	2*x*	4*x*
r	0.27	–0.71**	0.05	0.15	0.16	–0.12

** = significant at the 1% level

Peloquin, 1991). In the experiment reported here, the best five families outyielded the 4*x*–parent group by 40.6%. In another set of experiments in North Africa, three-way 4*x* hybrids (with 25% genomic contribution of *S. chacoense*) were able to outperform other hybrids for tuber yield in assays conducted in the fall (cooler) season (Bani-Aameur *et al.*, 1991). The same promising results were observed for yield and specific gravity in field trials in Brazil (Morais & Pinto, 1996). It is important to highlight that the results reported here considered the families as a group (i.e. degree of heterosis at family level). Therefore, superior clones with a degree of heterosis even higher than that reported here could potentially be identified in progenies derived from this set of crosses.

Heterosis, however, is not the only expected outcome in crosses involving wild species germplasm. There are several examples in the potato breeding literature where the lack of adaptation of a given wild species could erode field performance even in highly heterozygous genetic materials in which epistatic interactions have been preserved (Bani-Aameur *et al.*, 1991). However, this seems to be not the case for most of the 2*x* haploid Tuberosum - *S. chacoense* hybrids used in our study. This would indicate that previous selection work for adaptation and tuberisation under long days conditions was relatively effective (Leue & Peloquin, 1980).

General tuber appearance

The identification of 4*x*–2*x* families with GTA similar to commercial cultivars is a very important observation. Families with GTA scores above our selection limit (3) were observed in five out 11 families. Some 4*x*–2*x* families with significantly higher ratings for general tuber appearance have been observed in other haploid Tuberosum-wild species hybrids (Darmo & Peloquin, 1991). For improved results, it seems that selection of 2*x* hybrid parents for important GTA components (e.g. eye depth) would be a necessary step before using them as staminate parents in 4*x*–2*x* crosses. Results indicating that relatively few genes contribute to GTA suggest that selection for and fixation of desirable tuber characteristics will not be a difficult breeding task (Ortiz & Huaman, 1994).

Haulm maturity

Even though there is considerable variability for this trait, the families were later maturing than both parental groups. HM score higher than the parental groups could be some manifestation of hybrid vigour in the families. It is important to note that the two Tuberosum haploids ('Chippewa' haploid–W1831 and 'Merrimack' haploid–W3304) used to generate our 2*x* clones are also relatively late maturing (Buso, 1986). The 2*x* haploid-species hybrids used in the present set of crosses were medium-late maturing clones. Therefore, further breeding effort needs to be done to cross *S. chacoense* introductions to early-maturing haploids in order to generate genetic variability for this trait. This could be done more efficiently via development of new early-maturing haploid-species hybrids.

Parent-family relationships

The lack of correlation found between the 4*x* and the 2*x* parents and their respective offspring for total tuber yield is in agreement with previous results with other 4*x*–2*x* crosses (Tai, 1994). This indicates that when selecting for tuber yield, test crossing and progeny testing will be necessary since the performance of the parents *per se* will be uninformative. Likewise, unsatisfactory predictions have been reported for TTY in 4*x*–4*x* crosses using correlation coefficients between mid-parent value and progeny performance (Neele, Hab & Louwes, 1991). A somewhat surprising outcome was the significant and negative 4*x* parent-family correlation observed for TTY (Table 3). A possible explanation for this result is the relatively large number of unadapted 4*x* cultivars that were employed as female parents in our study. These elite cultivars were originally developed and selected for cultivation under distinct environmental conditions. The improved performance of the hybrid families with genomic contribution from more adapted Tuberosum germplasm (e.g. the cultivars 'Chippewa' and 'Merrimack') in the male parents could explain, in part, this negative correlation.

Conclusions

The overall results with haploid Tuberosum-*S. chacoense* hybrids pointed out the ability of the USP breeding scheme to produce families with higher TTY than their 4*x* parents. The results highlight the importance of the USP breeding scheme in introgressing high yield factors from wild species into the gene pool of the cultivated potato. Selection of clones from crosses between closely related but highly adapted cultivars has been the major strategy of several breeding programs. In this context, the resources present in the 2*x* wild germplasm have been used predominantly in breeding for simply inherited traits (Plaisted & Hoopes, 1989). This may be caused by the previous erroneous notion that yield-enhancing genes are not available in wild species (Tanksley & McCouch, 1997). The results with 4*x*–2*x* and 2*x*–2*x* crosses in potatoes clearly demonstrate that heterotic families could be obtained using wild and cultivated diploid germplasm (for a recent review see Tai, 1994). Likewise, 4*x*–2*x* families with 25% genomic contribution from *S. chacoense* had (as a group) a higher tuber yield than seven elite 4*x* cultivars obtained from different breeding programmes around the world. In addition, our results suggest that superior clone(s) for cultivation in temperate regions of the world can be obtained from this South American potato species.

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