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Direct estimation of the effects of meiotic recombination on potato traits via analysis of 4*x*-2*x* progenies from synaptic mutants with 2n-pollen formation by FDR without crossing-over

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Abstract Diploid potato clones with 2n-pollen formation by first-division restitution without crossing-over (FDR-NCO) are ideal testers to estimate the breeding value of elite 4*x* cultivars by virtue of transmitting their genotypes practically intact to their progenies. This characteristic facilitates genetic analysis, since meiotic recombination would take place only in the 4*x* parent and not in the diploid parent. We evaluated (under short-day conditions) families from complete factorial crosses between four 4*x* cultivars and five 2*x*(FDR-NCO) clones. Families were compared with two standard 4*x* cultivars ('Bintje' and 'Delta') for total tuber yield (TTY), commercial yield (CY), haulm maturity (HM), plant vigor (PV), plant-top uniformity (PU), eye depth (ED), number of tubers per hill (NTH), and the CY/TTY index (CTI). For TTY, the contrasts family group (310 g/hill) vs 'Delta' (430 g/hill) and the family group vs 'Bintje' (210 g/hill) were significant. Only 25% of the families were different from 'Delta' and 20% of them outyielded 'Bintje'. For CY, differences were observed between families (240 g/hill) vs 'Delta' (340 g/hill) and families vs 'Bintje' (150 g/hill). The two best families had 53% CY over 'Bintje'. Surprisingly, only one family had a higher NTH than 'Bintje'. No differences were observed for HM. Seventy five and 30% of the families had an ED similar to 'Delta' (ED = 2) and 'Bintje' (ED = 1), respectively. A multivariate analysis indicated that 63% of the data variability could be explained by two factors. TTY, CY, and PV had high loading on the first factor, whereas ED, PU and HM had high loading on the second factor; CTI and NTH had equal sizes on both factors. High TTY and PV were associated with high NTH and CTI. Deep eye, PU, and late maturity were associated with high NTH and reduced CTI. The distributions of factor scores of the entries indicated that some 2*x* parents had strong influences (irrespective of the direction of their effects) on the crosses. Six crosses due to two 2*x* males were in the 'Bintje' quarter with negative scores for both factors (implying low TTY, poor vigor, and low NTH). Also three crosses due to another 2*x* clone were distributed in the quarter of positive factor 1 and negative factor 2. These crosses plus another one were in the same quarter of 'Delta' (implying high yields, low ED, low PU, and early maturity). The FDR-NCO clones provide a homogeneous sample of heterozygous 2n-gametes allowing the unique opportunity to estimate the relative contribution of the random meiotic products (from the 4*x* parents) and the 'somatic' 2*x* genome for the phenotypic expression of quantitative traits. The interesting result was that measurable effects (favorable or not) on the data variability were mainly determined by the genomic contribution of the haploid-species hybrids. Three out of five 2*x*-male parents showed rather strong effects on progenies. No such effects were observed on the four 4*x*-female parents.

Key words *Solanum phureja* · First-division restitution without crossing-over · Potato · Unilateral sexual polyploidization · 2n-gametes

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Introduction

The unilateral sexual polyploidization (USP) breeding scheme has been implemented in potato via two major strategies. The simplest, and so far the most successful one, involves the employment of haploid-species hybrids as staminate parents in 4*x*-2*x* crosses where the 2*x* parent

forms 2n-pollen via the meiotic mutant *ps* (= *'parallel spindles'*). This mutation controls the formation of 2n-pollen grains by a process akin to first-division restitution with crossing over (FDR-CO). The FDR-CO gametes can transmit to the offspring approximately 80% of the heterozygosity and a large proportion of the interlocus interactions (Peloquin et al. 1999). The results from several breeding programs using the 4*x*-2*x*(FDR-CO) scheme indicated its tremendous potential for potato improvement (Peloquin et al. 1989). In fact, the tuber yield of 4*x*-2*x*(FDR-CO)-derived progenies regularly exceeds those of the respective 4*x* parents (Tai 1994; Ortiz 1998). Furthermore, individual diplandrous clones (i.e., selected within the 4*x*-2*x* families) had significantly higher yields than the corresponding 4*x* cultivar, as well as similar scores for tuber appearance (Buso et al. 1999c).

The second strategy involves the combination of two meiotic mutants *ps* and *sy-3* (= *'synaptic 3'*). Individuals with the *sy-3/sy-3* genotype were found in segregating populations from crosses between two diploid *ps/ps* clones (Okwuagwu and Peloquin 1981). The peculiar characteristic of this genetic combination of meiotic mutants is the almost complete lack of chiasmata observed per meiocyte. In some *sy-3/sy-3* clones, only univalents are present at metaphase-I nuclei. These univalents are distributed randomly into telophase-I nuclei. This phenomenon would ordinarily lead to almost complete male sterility. However, the combination of *sy-3/sy-3* with *ps/ps* leads to the formation of a high frequency of functional 2n-pollen grains. The 'parallel spindles' mechanism in the second division ensures a 'balanced' incorporation of two sets of chromosomes in each pair of 2n-microspores. These synaptic pollen grains are, therefore, the result of a process akin to FDR without crossing over (FDR-NCO). The FDR-NCO gametes are unique breeding tools since they are able to incorporate a virtually intact genotype (approximately 98%) of the 2*x* parent into all the 2n-gametes (Douches and Quiros 1988). Diploid clones with doubly recessive genotype (*sy-3, sy-3/ps, ps*) are, therefore, considered ideal 'testers' because they are able to contribute a set of highly homogenous (non-recombinant) gametes (Peloquin 1983; Peloquin et al. 1999). This characteristic facilitates genetic analysis, since meiotic recombination would take place only in one parent and not in the other. In addition, the preponderance of non-additive gene action for important quantitative traits such as tuber yield has been reported in the cultivated potato (Plaisted et al. 1962; Mendoza and Haynes 1974a; Tai 1976; Killick 1977; Mendiburu and Peloquin 1977). These observations imply that the 2*x* clones producing 2n-pollen by FDR-NCO mechanisms would be the best parents in the unilateral sexual polyploidization (USP) breeding scheme since these gametes can transmit virtually all the heterozygosity and epistasis (Peloquin et al. 1999).

The ability of the USP strategy to generate high yielding 4*x* progenies has been well documented employing almost exclusively *4x-2x* (FDR-CO) crosses under long-day conditions (Tai 1994). Therefore, the aim of the present work was to evaluate the merit of families derived from 4*x*-2*x* crosses (exclusively with staminate clones with 2n FDR-NCO pollen) under a subtropical environment. In addition, the complete factorial 4*x*-2*x*(FDR-NCO) mating design allows a unique genetic opportunity to estimate what proportion of phenotypic expression of a given trait is due to random meiotic products (from 4*x* parents) and the somatic genome (via FDR-NCO gametes of the 2*x* parent).

Material and methods

Plant material

Twenty 4***x***-2***x*** families were obtained from a factorial mating design between four 4***x*** cultivars and five *2x* clones. All five *2x* clones ('M-6', 'SY-7', 'SY-8', 'SY-11' and 'SY-12') were 2n-pollen producers by a mechanism equivalent to FDR-NCO. These clones are full-sibs originated from crosses between two elite Phureja-haploid Tuberosum hybrids: clone 'I' (*Solanum phureja* 'PI 243462' × 'Katahdin' haploid US-W1) × clone 'J' (*S. phureja* 'PI 225696' × 'Chippewa' haploid US-W42). The 4***x*** cultivars employed in the factorial crosses were 'Baronesa' (Brazil), 'Belladona' (German), 'Spunta' (Holland) and 'Elvira' (German origin with seed tuber production in Holland).

Crosses and seed tuber production

True seeds were obtained from all 4*x*-2*x* cross combinations. The seed tuber production was done under greenhouse conditions. Ten-day old seedlings were transplanted to plastic bags (18 × 9cm) filled with autoclaved soil. The tubers were harvested 3 mounths after transplanting. Between 24 to 49 plants (genotypes) per family were obtained with a range of 2–6 tubers/plant. The tubers were kept separately according to the mother plant. The seed tubers were kept in cold storage (5^{o}C) up to 2 months before field planting.

Field assay

Two family bags were constructed per family by choosing two tubers of each of 20 plants (genotypes) and by putting one tuber in each bag. The family bags were used to set up the field experiment. This experiment was conducted during the hot-rainy season (October–January) at the experimental field of the CNPH/EMBRAPA (17^{o} latitude South and about 1020 m above sea level). A randomized complete block design with two replications was used. Each plot had 20 hills, with a spacing of 0.85 m between rows and 0.35 m between hills in a row. Plots were fertilized with 2 ton/ha of the formula 4-14-8 before planting. The plots were also fertilized with 200 kg/ha of ammonium sulfate when the hilling up was done. Supplementary irrigation was provided only when needed.

Trait evaluation

Each entry was evaluated for eight traits. Total tuber yield (TTY) was estimated (in g/hill) by taking all tubers of each plot (harvested by hand) and weighing them. Commercial tuber yield (CY) was estimated using only tubers ≥ 33 mm in diameter. Haulm maturity (HM) was evaluated as the number of days from the planting date until the date when 50% of the plants in the plot were completely senesced. Plant vigor (PV) was assessed visually based on the vine appearance, using a scale from 1 = poor to 5 = very good vigor.

Plant uniformity (PU) was evaluated using a scale from 1 = uniform to 5 = non-uniform. Eye depth (ED) was scored using a scale from 1 = shallow to 5 = very deep. The number of tubers per hill (NTH) was assessed by counting the total number of tubers in three randomly selected plants in a plot. The plot mean (i.e., the total number of tubers divided by three) was used in the analysis of variance. The last trait was the CY/TTY index (CTI) that was calculated by dividing the commercial yield by the total tuber yield in per plot basis.

Analysis of variance

The male and female parents were selected in this experiment based upon previous information on agronomic characteristics (e.g., yellow flesh and ability to form tubers under long-day conditions in the case of the 2*x* parents, and tropical adaptation in the case of the 4*x* parents). The source of variation due to treatments was subdivided into among-families with 19 degrees of freedom (*df*). The sources of variation among families (i.e., factorial mating design) for the experiment were partitioned into the sources of variation due to males (2*x* hybrid clones – 4 *df*), females (4*x* cultivars – 3 *df*) and male × female interaction (12 *df*). The two first values provide an estimate for general combining ability (GCA) of male and females, respectively. The male × female interaction provides an estimation of the specific combining ability (SCA). Tests of significance for males and females were obtained by using male × female interaction mean squares. Female × male interactions were obtained by testing their means squares against the error mean squares. To allow useful comparisons between the 4*x*-2*x*(FDR-NCO) strategy and the conventional 4*x*-4*x* breeding scheme two additional contrasts (with 1*df* each) were also investigated: (1) the 4*x*-2*x*(FDR-NCO) families vs the standard cultivar 'Delta', and (2) the 4*x*-2*x*(FDR-NCO) families vs the standard cultivar 'Bintje'.

Factor analysis

Factor analysis was carried out to investigate the interrelationship between the eight evaluated traits. This multiple-trait information was used to study the behavior of the progenies derived from the factorial crosses and the two standard 4*x* cultivars. Factor analysis was carried out using the overall mean of all eight traits for the families and the standard cultivars. The purpose of the factor analysis was twofold. (1) To extract factors from the original data of multiple traits such that the variability of all traits can be accounted for or explained by only few factors. (2) The extracted factors can be then rotated by the method of VARIMAX to provide a biologically meaningful interpretation of the results.

Results

Total tuber yield

There was a significant difference among treatments (i.e., among 4*x*-2*x* families and 4*x* standard cultivars) and replicates (Table 1). The contrast between the 4*x*-2*x* family group (310 g/hill) versus the standard cultivar 'Delta' (430 g/hill) was significant at the 5% level. However, only 5 out 20 families were significantly different from 'Delta'. The contrast between the 4*x*-2*x* families vs 'Bintje' (210 g/hill) was also significant at the 1% level. A total of 20% of the 4*x*-2*x* families significantly outyielded 'Bintje' (Table 2).

Commercial tuber yield

The ANOVA results indicated a significant difference among treatment means (Table 1). There was also a significant difference between the 4*x*-2*x* families (240 g/hill), and the cultivar 'Delta' (340 g/hill) was significant at the 5% level. The contrast 4*x*-2*x* families versus 'Bintje' (150 g/hill) was significant at the 1% level. 'Bintje' was significantly outyielded by 15% of the 4*x*-2*x* families. The best two cross combinations ('Spunta' × 'SY-8') and ('Baronesa' × 'SY-12') had a superiority of 53.3% over 'Bintje' (Table 2).

Index commercial/total tuber yield

No significant differences were observed among treatment means and contrasts for this trait (Table 1).

Number of tubers per hill

Significant differences were observed among treatments and among families for NTH (Table 1). The contrast between the 4*x*-2*x* families vs 'Delta' was not significant.

Table 1 Analyses of variance for total tuber yield (TTY), commercial yield (CY), CY/TTY index (CTI), number of tubers per hill (NTH), eye depth (ED), plant vigor (PV), plant-top uniformity (PU), and haulm maturity (HM) for 4*x*-2*x*(FDR-NCO) families and the cultivars 'Bintje' (var. 1) and 'Delta' (var. 2). Experiments were conducted at Brasilia-DF, Brazil. For trait description see Materials and methods

Source of variation	*df*	Mean squares							
		TTY	CY	CTI	NTH	ED	PV	PU	HM
Replication	1	0.030*	0.020	0.000	6.828	0.023	0.000	0.205	131.273*
Treatment	21	0.014*	0.013*	0.020	48.213*	1.919**	0.797*	0.685	29.662
Families	19	0.011*	0.011*	0.022	47.467*	1.804**	0.709*	0.731	31.074
Males (GCA)	4	0.014	0.011	0.011	37.115	6.662*	0.338	0.938	60.600
Females (GCA)	3	0.023*	0.011	0.023	168.269*	0.425	0.892	0.292	32.533
M x F (SCA)	12	0.007	0.011	0.025	28.628	0.529	0.787*	0.771	20.867
Families vs var. 1	1	0.020*	0.016*	0.016	10.880	5.344**	3.219**	0.268	6.171
Families vs var. 2	1	0.026**	0.050*	0.050	0.023	0.962*	0.076	0.268	27.505
Error	21	0.005	0.005	0.015	19.781	0.308	0.333	0.443	28.416
CV (%)		22.9	29.6	16.4	32.8	21.6	17.9	23.4	6.1

*, ** = significant at the $P = 0.05$ and $P = 0.01$ level, respectively

Table 2 Means of total tuber yield (TTY), CY/TTY index (CTI), number of tubers per hill (NTH), commercial yield (CY), eye depth (ED), plant vigor (PV), plant uniformity (PU), haulm maturity (HM) of 4x-2x (FDR-NCO) progenies and two standard 4x cultivars ('Bintje' and 'Delta'). Experiments were conducted at Brasilia-DF, Brazil. For trait description see Materials and methods

Genotypes	Traits							
	TTY	CY	CTI	NTH	ED	PV	PU	HM
Belladona × SY-7	240	200	0.80	8.8	1.50	3.50	2.50	88
Belladona × SY-8	320	250	0.78	11.7	2.50	3.50	2.00	86
Belladona × SY-11	200	150	0.77	13.0	4.00	3.00	4.00	94
Belladona × SY-12	130	90	0.68	10.3	3.00	2.50	2.50	86
Belladona × M-6	350	250	0.73	15.2	3.00	2.50	3.00	84
Spunta × SY-7	250	220	0.87	9.8	1.50	3.00	1.50	84
Spunta × SY-8	420	380	0.89	9.8	1.50	4.00	2.50	88
Spunta × SY-11	310	260	0.85	12.7	4.00	3.00	3.50	96
Spunta × SY-12	290	220	0.77	6.7	2.50	3.00	2.50	86
Spunta × M-6	290	200	0.70	9.8	3.00	3.00	3.50	86
Elvira × SY-7	320	210	0.67	15.2	1.50	3.00	3.00	84
Elvira × SY-8	350	240	0.68	16.0	2.50	2.50	3.50	86
Elvira × SY-11	330	250	0.75	23.7	4.00	4.50	2.50	86
Elvira × SY-12	260	210	0.77	13.7	3.00	2.50	3.00	84
Elvira × M-6	410	290	0.72	28.0	3.50	3.50	2.50	88
Baronesa × SY-7	310	220	0.71	14.3	2.50	4.00	3.00	96
Baronesa × SY-8	320	250	0.78	10.7	1.00	4.00	2.50	86
Baronesa × SY-11	310	100	0.39	10.8	4.00	3.00	3.50	94
Baronesa × SY-12	440	380	0.85	19.3	3.00	4.00	3.50	88
Baronesa × M-6	420	340	0.82	4.3	2.00	3.50	3.00	86
Delta (standard)	430	340	0.80	13.3	2.00	3.50	2.50	84
Bintje (standard)	210	150	0.72	10.8	1.00	2.00	2.50	86
$LSD_{0.05}$	150	150	NS[a]	9.3	1.15	1.20	NS	NS

[a] NS = not significant

Likewise, the contrast between families and 'Bintje' was not significant. In fact, only one 4*x*-2*x* family had NTH significantly higher than 'Delta' (Table 2).

Eye depth

There was a significant difference among treatment means when both families and clones were taken into account (Table 1). The average score of 'Bintje' was a perfect 1 (Table 2). The average score for 'Delta' was 2. A total of 75% of the 4*x*-2*x* families had ED scores within the range of 'Delta', and a total of 30% of the families had ED scores in range of 'Bintje' (Table 2).

Plant vigor

There was a significant difference among families for PV (Table 1). About 45% of the 4*x*-2*x* families had a PV significantly superior to 'Bintje' and all of them were in the range of 'Delta' (Table 2).

Plant uniformity

No differences were found among treatments for this trait (Table 1). The average score of 2.5 was observed for both 'Bintje' and 'Delta'. The family range was 1.5–4.0 (Table 2).

Haulm maturity

No significant difference among treatments was observed for HM (Table 1). The average values of 'Bintje' and 'Delta' were almost identical, 86 and 84 days, respectively. The range observed in the 4*x*-2*x*(FDR-NCO) families was 84–96 days (Table 2).

Combining ability analysis

The sources of variation due to males (GCA males) were significant (at the 1% level) only for eye depth. The sources of variation due to females (GCA females) were significant (at the 5% level) for TTY and NTH. The source of variation due to male × female interaction (SCA) was significant for PV (Table 1). No source of variation was significant for CY, CTI, PU and PM.

Factor (multivariate) analysis

TTY, CY and PV had a high loading on the first factor whereas PU, ED and HM had a high loading on the second factor (Table 3). CTI and NTH had equal sizes of loading on both factors. High TTY and PU were associated with high NTH and high CTI values. ED, PU and late maturity were also associated with a high NTH and reduced CTI. The distribution of factor scores of 20 crosses and two cultivars on the two rotated factor axes are shown in Fig. 1. The distribution of crosses indicated a relationship to one another and to the two cultivars. Some male parents showed strong influences on the be-

Table 3 Loading of eight traits on two factors obtained from factor analysis with a Varimax rotation of axes, and the percentage (%) of total variance accounted for by the two factors

Traits	Factor 1	Factor 2
Total tuber yield (TTY)	0.88	0.03
Commercial yield (CY)	0.93	–0.24
CY/TTY index	0.51	–0.52
Number of tubers per hill	0.45	0.45
Eye depth	0.02	0.86
Plant vigor	0.79	0.06
Plant (top) uniformity	–0.05	0.76
Haulm maturity	–0.04	0.72
% Total variance explained	34.11	29.65

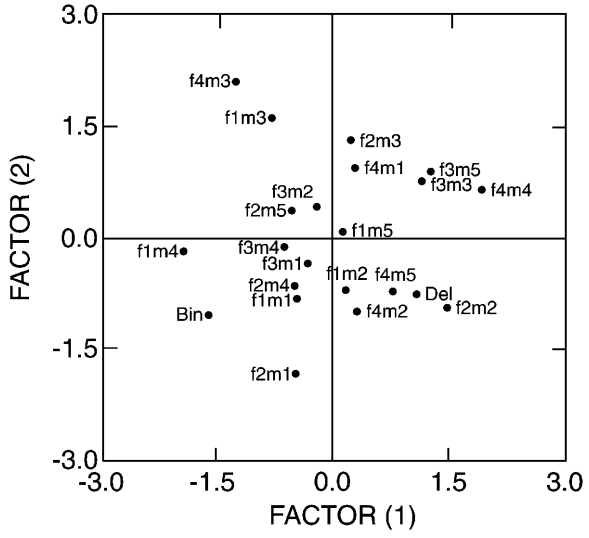

Fig. 1 Distributions of 20 progenies and 'Bintje' (*Bin*) and 'Delta' (*Del*) on the two rotated factor axes. Female parents in the crosses were 'Belladona' (*f1*), 'Spunta' (*f2*), 'Elvira' (*f3*), and 'Baronesa' (*f4*). Male clones in the crosses were 'SY-7' (*m1*); 'SY-8' (*m2*); 'SY-11' (*m3*); 'SY-12' (*m4*), and 'M-6' (*m5*)

havior of crosses. Three crosses due to 'SY-7' (with female parents 'Belladona', 'Spunta' and 'Elvira') and three crosses due to 'SY-12' (with same three female parents) are in the quarter of negative scores of both factors. These crosses are in the same quarter as the cultivar 'Bintje'. Also three crosses due to 'SY-8' (with female parents 'Belladona', 'Spunta' and 'Baronesa') are distributed in the quarter of positive factor 1 and negative factor 2. These crosses and another one ['Baronesa' × 'M-6'] are in the same quarter of the cultivar 'Delta'. The 'Bintje' quarter is low on both factors implying low yield, poor vigor, and low tuber number. The 'Delta' quarter, on the other hand, has a high yield, shallow eye, lack of uniformity, and some levels of early maturity. The interesting result is that three out of the five 2*x*-male parents showed rather strong effects on progenies. No such effects were observed on the four 4*x*-female parents.

Discussion

The identification of high yielding families is a somewhat expected outcome with FDR-NCO clones, because of the large amount of favorable allelic interactions that can be transmitted to the progenies (Peloquin et al. 1989). These findings parallel those of several other breeding experiments using progenies from Phureja-haploid Tuberosum clones with 2n-pollen grain formation by the FDR-CO mechanism (for a review see Tai 1994). Our results indicated that the 4*x*-2*x*(FDR-NCO) scheme could also generate high yielding progenies under short day conditions in Brazil. The families outyielded the standard cultivar 'Bintje' by 47.6% for TTY and by 60% for commercial yield. It is important to highlight that families were not superior to 'Delta'. However, it is noteworthy that 25% of the families did not differ significantly from 'Delta' for either TTY or CY. These results are striking considering the smaller size of the 4*x*-2*x* family seed tubers and that the 2*x* clones were selected for tuber production exclusively under long-day conditions. Furthermore, the data reported here are for families as experimental units. Comparing progenies from interploid (4*x*-2*x*) crosses with elite parental clones may be misleading, since the effects of transgressive segregants are 'diluted' within families. Our results suggest the possibility of within-family selection of transgressive clones, which could have a better performance than the standard cultivars. This notion has been confirmed in comparative assays between elite 4*x* cultivars and several 4*x*(FDR-CO) and 4*x*(FDR-NCO) diplandrous clones evaluated under long-day conditions (Buso et al. 1999c).

The 'yield stasis' associated with the conventional 4*x*-4*x* breeding scheme in potato has been attributed to a combination of factors (Mendoza and Haynes 1974a; Douches et al. 1996). The recent trend of developing early maturing cultivars (in spite of the strong positive correlation between TTY and late vine maturity) has been one of the major explanations for the lack of improvement for yield in the conventional 4*x*-4*x*(intra-Tuberosum) scheme (Douches et al. 1996). Here, no association between TTY and HM was observed ($r = 0.06$). In addition, our multivariate analysis indicated that the 4*x*-2*x*(FDR-NCO) breeding scheme could provide a positive contribution in breaking the relationship between late maturity and high TTY. For instance, three crosses due to 'SY-8' (with female parents 'Belladona', 'Spunta' and 'Baronesa') as well as the family ('Baronesa' × 'M-6') were distributed in the quarter of positive factor 1 and negative factor 2 (same quarter of the cultivar 'Delta'). This quarter was characterized by high yields, shallow eye, lack of plant-top uniformity, and some levels of early maturity.

Some specific parents and cross combinations deserve special mention in terms of TTY performance. For instance, the German cultivar 'Elvira' and the Brazilian cultivar 'Baronesa' contributed four of the top five families for this trait. The best family ('Baronesa' × 'SY-12') yielded 109% more than 'Bintje' for TTY. The perfor-

mance of the Dutch cultivar 'Spunta' should be highlighted for CY. 'Spunta' was present in two out of five top families for CY. The family ('Spunta' × 'SY-8') yielded 100% more than 'Bintje', 89% of tubers having 33 mm or more in diameter (i.e., CTI = 0.89). Improvement in the percent of CY is a major factor increasing the profitability of a given cultivar (Douches et al. 1996). For CY, the family ('Baronesa' × 'SY-12') was slightly superior to the higher yield standard 'Delta' (380 vs 340 g/hill, respectively). Non-complementation of parents in some cross combinations has been the rule in progenies derived from distinct meiotic mutants (Mok and Peloquin 1975; De Jong and Tai 1977). A similar phenomenon was observed in our assay where families with exceptionally poor performance were also observed, but were restricted to only a few cases (Table 2).

Recent experiments comparing the relative genetic merit of FDR-CO vs FDR-NCO families indicated that both clones may have equivalent value for several traits including TTY (Buso et al 1999a, b). Therefore, both types of clones could be used as parental materials if high TTY is the exclusive breeding objective. It is important to note that four out of the top five TTY families were similar to 'Bintje' in NTH; three of them were similar to 'Bintje' in terms of ED score, and no overall differences were observed for HM. These preliminary results suggest that the 4*x*-2*x*(FDR-NCO) breeding scheme may have, at least, similar levels of multitrait selection efficiency. These observations parallel the results obtained with the 4*x*-2*x*(FDR-CO) scheme in Peru (Ortiz et al. 1991), USA (Buso et al. 1999c, d) and Poland. In this latter case, clones combining multiple disease resistance genes and desirable tuber quality could be selected (Zimnoch-Guzowska et al. 1999). Moreover, the USP scheme with FDR-CO clones was found to be five-times more effective than the conventional 4*x*-4*x*(intra-Tuberosum) crosses in developing parental clones and cultivars (Zimnoch-Guzowska et al. 1999).

The observation indicating no differences in plant-top uniformity in the comparison between families and highly selected cultivars is noteworthy. However, this is a somewhat expected result taking into account that the 2x FDR-NCO clones can provide a homogeneous sample of 2n-gametes (Peloquin 1983). On the other hand, our experimental data indicating a similar performance of families and cultivars for NTH was a rather surprising outcome. This trend is in opposition to previous investigations conducted under long-day conditions (De Jong and Tai 1977; Schroeder 1983). The large number of tubers per plant has been one major drawback of the USP scheme (using Phureja germplasm) in the Northern Hemisphere. This problem seems not to be relevant under subtropical/short-day conditions in Brazil. A possible explanation for these differences is the existence of genotype by environment interaction for NTH in 4*x*-2*x* families of Phureja origin. Comparative assays in the different hemispheres using identical families/genotypes would provide more insight into this topic.

The influence of the mode of 2n-gamete formation on combining ability estimates among 2*x* haploid-species hybrids in 4*x*-2*x* crosses has been well recognized. Apart from few exceptions (Mok and Peloquin 1975; Neele et al. 1991), most of the experimental data obtained with 2*x* hybrids producing 2n-pollen by the FDR-CO mechanism indicated GCA as significant source of variation for tuber yield and several other traits of importance for potato breeding (for review Tai 1994). In our experiment the 4*x* female GCA was found do be significant for TTY and NTH, and the male GCA was significant for ED. A significant SCA was observed only for PV. These results, indicating that the overall GCA variances are more important than SCA, suggest that progeny testing may not be necessary for the evaluation of important yield/tuber quality traits, which could simplify the selection process. Reduced genetic relationship between staminate and stylar parents tends to be reflected in significant GCA variances (Veilleux and Lauer 1981). This is true in our assay, since even the 4*x* parents of the haploid-species hybrids are not highly related with the group of cultivars used as parents. Previous results with FDR-NCO clones indicated only the male GCA for TTY as significant (at the 10% level), as well as the SCA for ED and HM (Buso et al. 1999b). This latter experiment was conducted under similar environmental conditions, but employing a slightly different set of four 4*x* females (all but 'Baronesa' and 'Belladona') and an almost identical set of five 2*x* FDR-NCO clones (Buso et al. 1999b). Therefore, no trend has yet become apparent in terms of generalizing on the parental effects of FDR-NCO clones for this collection of traits.

One notion that is emerging from empirical studies is that major effect loci (more likely deleterious alleles) for yield are in proximal regions of the potato chromosomes (Tai and De Jong 1997; Buso et al. 1999a). These regions have comparatively less meiotic recombination, which demands the development of alternative strategies for introgressing genetic diversity into these chromosomal sites. In this context, one would expect an inherent superiority of both 4*x*-2*x*(FDR-CO) and 4*x*-2*x*(FDR-NCO) breeding schemes in comparison with the conventional 4*x*-4*x* crosses, since both can transmit almost intact heterozygosity at proximal loci (Peloquin et al. 1999).

The FDR-NCO clones provide a homogeneous sample of heterozygous 2n-gametes for testing the parental value of 4*x* clones (Peloquin 1983). Factorial 4*x*-2*x* crosses using 2*x* (FDR-NCO) male parents allow the singular opportunity to estimate the relative contribution of the random meiotic products (from the 4*x* parents) and the 'somatic' (non-recombinogenic) male genome to the phenotypic expression of quantitative traits. The distributions of factor scores of the entries indicated that three out of the five 2*x*-male parents showed rather strong effects on progenies. No such effects were observed, however, on the four 4*x*-female parents. These preliminary results suggest that meiotic recombination in the 4*x* female group had an inexpressive effect on the phenotypic

variation of these 20 progenies. This 'neutral meiotic effect' in the female parents could be explained by a combination of factors including reduced allelic/genetic diversity of these highly selected 4*x* cultivars and the presence of important genetic factors in non-recombinogenic regions of the potato chromosomes (Tai and De Jong 1997; Buso et al. 1999a). In our assay all measurable effects (favorable or not) on the data variability were mainly determined by the genomic contribution of the haploid-species hybrids. Additional experiments using distinct sets of families will be necessary to ascertain which would be the predominant genetic trend.

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