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Effects of 2n-pollen formation by first meiotic division restitution with and without crossover on eight quantitative traits in 4x-2x potato progenies

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Abstract The 2n-pollen grains formed by first-division restitution without crossover (FDR-NCO) are unique breeding tools, since they can transmit almost 100% of non-additive genetic effects from the parent to the progeny. FDR-NCO gametes are considered superior to those formed by FDR with crossing over (FDR-CO), which can pass on to the progenies approximately 80% of the heterozygosity and a large fraction of the epistasis. However, 2n-pollen formation by FDR-NCO mechanism requires the incorporation (in homozygous condition) of at least two recessive alleles. In the present work, 40 tetraploid families derived from complete 4x-2x factorial crosses were evaluated under short-day conditions to verify whether or not the postulated genetic superiority of FDR-NCO over FDR-CO gametes holds true for eight quantitative traits in potato. Families were derived from crosses between four 4x commercial cultivars, and a random sample of ten diploid *Solanum phureja*-haploid *S. tuberosum* hybrids producing 2n-pollen by either FDR-CO or FDR-NCO. The results indicated no significant superiority of FDR-NCO over FDR-CO families for total tuber yield (TTY) and six other traits (haulm maturity – HM; plant vigor – PV; plant uniformity – PU; eye depth – ED; number of tubers per hill – NTH; and commercial over total yield index – CTI). Based upon cytological observations, the FDR-CO and FDR-NCO gametes are expected to be genetically equivalent for all loci between the centromeres and the chromosomal site of maximum recombination. In our experiment, differences between FDR-CO- and FDR-NCO-derived progenies were not observed for TTY. Therefore, our results can be interpreted as additional evidence for the hypothesis that genes with major effect on TTY expression might have a physical location between centromeres and proximal crossovers in the potato chromosomes. In addition, a similar trend was observed for HM, PV, and ED but apparently not for commercial yield – CY (i.e., tubers with more than 33 mm in diameter).

Key words Combining ability · First-division restitution with crossing over (FDR-CO) · First-division restitution without crossing over (FDR-NCO) · *Solanum phureja* · 2n gametes

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Introduction

The 4x-2x crosses with unilateral sexual polyploidization (USP) and the 2x-2x crosses with bilateral sexual polyploidization (BSP) are two alternative breeding strategies available for improvement of the cultivated potato via introgression of genetic diversity from the diploid gene pool (Peloquin et al. 1990). Both USP and BSP breeding schemes rely upon the production of numerically unreduced gametes with a sporophytic (2n) chromosome number (Mendiburu and Peloquin 1976; 1977a, b). Premeiotic, meiotic, and postmeiotic abnormalities have been identified as the most frequent genetic causes of 2n-gamete formation (Veilleux 1985). First-division restitution (FDR) and second-division restitution (SDR) are the two major mechanisms of 2n-gamete production reported in *Solanum* spp. (Peloquin et al. 1989a; Tai 1994). A large collection of natural mutants affecting the meiotic process during microsporogenesis, which can lead to the formation of 2n-pollen grains, is now available for employment in

applied potato breeding (Veilleux 1985; Peloquin et al. 1989a; Tai 1994; Qu Dongyu et al. 1996).

The genetic control of 2n-pollen grain formation has been studied intensively. Single recessive genes have been reported to govern this process (Mok and Peloquin 1975; Okwuagwu and Peloquin 1981), but the estimate of the number of genes involved in 2n-pollen grain formation may vary from 1.55 to up to 3.75 (Qu Dongyu et al. 1996). These apparently controversial results indicate that the estimate of the number of genes controlling this process seems to be dependent upon the criterion used for phenotypic evaluation, environmental conditions, as well as on the particular set of crosses under consideration (Mok and Peloquin 1975; Okwuagwu and Peloquin 1981; Qu Dongyu et al. 1996). Two meiotic mutants have been particularly useful in potato breeding using the USP scheme: the mutant allele *ps* ('parallel spindles') from *S. phureja* × haploid Tuberosum hybrids (Mok and Peloquin 1975) and the mutant allele *sy-3* ('synaptic-3') also from *S. phureja* × haploid Tuberosum hybrids (Okwuagwu and Peloquin 1981). The genotype *ps*/*ps* controls the production of 2n-pollen by a process akin to first-division restitution with crossing over (FDR-CO) (Mok and Peloquin 1975). These gametes are capable of transferring to their progenies about 80% of the heterozygosity and a large fraction of the epistasis present in the 2x parent (Hermsen 1984). Clones with the genetic constitution *ps*/*ps*, *sy-3*/*sy-3* (i.e., double homozygous) can produce 2n-gametes by a process essentially equivalent to a first division restitution without crossing over (FDR-NCO) (Hermundstad and Peloquin 1987). A diploid FDR-NCO clone will transmit almost intact the heterozygosity and epistasis to the progeny by reason of the almost complete absence of chiasma formation in *ps*/*ps*, *sy-3*/*sy-3* plants (Peloquin 1983; Peloquin et al. 1989b).

In this context, since non-additive genetic effects are reported to be the major components associated with tuber yield in potato (Plaisted et al. 1962; Mendoza and Haynes 1974; Mendiburu and Peloquin 1977a; Ortiz and Peloquin 1994), clones with 2n-gametes formed by the FDR-NCO mechanism would be the best choice for use as staminate parents in the USP strategy. This is due to the postulated transmission by FDR-NCO gametes of a larger amount of potentially favorable intralocus and interlocus interactions to the offspring without loss by recombination (Peloquin 1983; Hermsen 1984; Hutten et al. 1994). However, field experiments conducted to verify the relative genetic value of FDR-NCO vs. FDR-CO gametes indicated that the higher level of heterozygosity (approx. 20%) and epistasis transmission by 2x FDR-NCO parental clones was apparently not enough to produce significant differences for total tuber yield, marketable yield, specific gravity, and general tuber appearence (Masson 1985; Buso 1986). These experiments comparing FDR-CO vs. FDR-NCO families were carried out in Europe (Masson 1985) and mainly at Wisconsin, USA (Masson 1985; Buso 1986). Therefore, there is so far no clear evidence that 4x-2x progenies derived from clones with the FDR-NCO mechanism of 2n pollen formation are genetically superior to those derived from 2x FDR-CO clones for this collection of traits under long-day conditions in Europe and Northern temperate regions.

The main objective of the work presented here was to expand the comparative analysis of the genetic merit of 2n-pollen-producer clones by either FDR-CO or FDR-NCO mechanisms. For this purpose, we evaluated, under subtropical (short-day) conditions in Brazil, eight quantitative traits in a group of 40 tetraploid families derived from 4x-2x crosses involving a complete factorial mating design between a random sample of ten 2x clones (*S. phureja*-haploid *S. tuberosum* hybrids) and four tetraploid cultivars. Our work provides information on the performance of 4x-2x progenies derived from a different set of crosses with a genetic analysis of a larger collection of traits. In addition, this experiment is the first of this kind conducted under short-day (subtropical) conditions.

Materials and methods

Plant material

Forty 4x-2x families were obtained from a factorial mating design between four 4x cultivars and ten 2x clones. Six of these diploid clones were 2x FDR-CO ('H-3', 'H-4', 'H-5', 'L-10', 'L-11', and 'M-5') and four were 2x FDR-NCO ('M-6', 'SY-8', 'SY-11', and 'SY-12'). They originated from crosses of two elite Phureja-haploid Tuberosum hybrids: clone 'I' (*S. phureja* 'PI 243462' × 'Kathadin' haploid US-W1) × clone 'J' (*S. phureja* 'PI 225696' × 'Chippewa' haploid US-W42). These 2x clones were selected for 2n-pollen production and tuber development at Wisconsin, USA (i.e., long-day conditions). The 4x cultivars employed in the factorial crosses were 'Chiquita' (Brazil), 'Aracy' (Brazil), 'Spunta' (Holland) and 'Elvira' (German origin with seed tuber production in Holland).

Crosses and true seed production

Seeds were obtained from all 4x-2x crosses. After fruit harvesting, a sample of each true seed lot was tested by the nucleic acid spot hybridization method (Owens and Diener 1981) for the presence of potato spindle tuber viroid (PSTVd). This was done because PSTVd has not been detected in Brazil thus far (Fonseca and Boiteux 1997). Seed samples identified as PSTVd-free were then sent to Brazil.

Seed tuber production

The seed tuber production was done in greenhouses in the National Center for Vegetable Crops Research (CNPH)-EMBRAPA (Brazilian Corporation for Agricultural Research) located at Brasilia-DF, Brazil. Ten-day-old seedlings were transplanted to plastic bags (18 × 9 cm) filled with autoclaved soil. The tubers were harvested approximately 3 months after transplanting. Between 24 and 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 (4°–5°C) up to 2 months before field planting.

Field assay

Two family-bags were composed 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° latitude South and about 1,020 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. In addition, the plots were fertilized with 200 kg/ha of ammonium sulfate when the hilling was done. Supplementary irrigation was provided only when needed since the experiment was conducted in the rainy season.

Trait evaluation

Each entry was evaluated for the following traits. (1) Total tuber yield (TTY) – all tubers of each plot were harvested by hand and weighed. Plot averages as tuber yield per hill were used in the analysis of variance. (2) Commercial tuber yield (CY) – for this trait only tubers over 33 mm in diameter were weighed. Plot means were used in the analysis of variance. (3) Haulm maturity (HM) – maturity 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. (4) Plant vigor (PV) – the plots were assessed visually based on the vine appearance using a scale of 1 = poor to 5 = very good vigor. (5) Plant uniformity (PU) – this trait was evaluated using a scale of 1 = uniform to 5 = non-uniform, on a plot basis. The PU assessment reflects haulm size/volume and height. (6) Eye depth (ED) – this trait was visually scored, on a per-plot basis, using a scale from 1 = shallow to 5 = very deep. (7) Number of tubers per hill (NTH) – was assessed by obtaining the total number of tubers in 3 randomly selected plants in a plot. The plot mean (i.e., the total number of tubers divided by 3) was used in the analysis of variance. (8) Commercial over total yield index (CTI) – this index was calculated by dividing the commercial yield by the total tuber yield in each plot.

Analysis of variance

The source of variation due to treatments was divided into among families from 4x-2x crosses, which was further subdivided into two groups: among families from 2x FDR-CO and among families from 2x FDR-NCO as well as a contrast between 2x FDR-CO vs. 2x FDR-NCO-derived families. The sources of variation due to 2x males (male GCA), females (female GCA), and males × females (SCA) were obtained when all 40 families were taken into account as well as within each group (i.e., FDR-CO and FDR-NCO) of families. Analysis of variance also included data from 11 4x-4x families and two commercial 4x cultivars (clones) that were used as standards. However, it is important to note that the data and statistical contrasts involving these 4x-4x families and the 4x clones/cultivars were part of a multipurpose experiment the results of which, for the sake of clarity, will not be discussed in this present study, being described elsewhere.

Results

Total tuber yield

There was a significant difference among both treatments and 4x-2x families for TTY (Table 1). The mean values for TTY of families from the 4x-2x crosses are presented in Table 2. The subdivision of the 4x-2x families into two groups according to the mode of 2n-pollen formation in the 2x parent (i.e., FDR-CO vs. FDR-NCO) revealed two points: (1) there was a significant difference only among families from 2x FDR-NCO and (2) the 2x FDR-NCO group yielded an average of 0.32 kg/hill, while the 2x FDR-CO group yielded 0.27 kg/hill. But, the contrast between the two types of families was not significant for this trait.

Commercial tuber yield

The ANOVA results indicated the presence of a significant difference among treatment means and among 4x-2x family means for CY (Table 1). In addition, there was a significant difference among family means from the 4x-2x (FDR-NCO) group and among families from the 4x-2x (FDR-CO) group. The means of CY of families from 4x-2x crosses are presented in Table 3. The ANOVA indicated that the family group mean from 2x FDR-NCO (0.26 kg/hill) was significantly higher than the family group mean from the 2x FDR-CO (0.22 kg/hill).

Commercial over total tuber yield index

For this trait, no significant differences were observed among treatments (Table 1). The average value for the FDR-CO family group was 0.83, and the average value for the FDR-NCO family group was 0.81. The index means for each family are presented in Table 4.

Number of tubers per hill

This followed the same trend of CTI with no significant differences being observed among treatments (Table 1). The average value for this trait in the FDR-CO group was 14.3 tubers/hill. For the FDR-NCO group this value was 15.5 tubers/hill. The means for this trait are presented in Table 5.

Eye depth

A significant difference was observed for ED among treatment means (Table 1). In addition, a significant difference was observed among families from 4x-2x crosses. There was also a significant difference among families of both the 2x FDR-CO and 2x FDR-NCO groups. However, no difference was observed in the contrast between the two group means. The average ED score was 2.27 and 2.97 for the FDR-CO and

Table 1 ANOVA results using 4x-2x FDR-CO and 2x FDR-NCO families evaluated for eight agronomic traits at Brasilia-DF, Brazil

Source of variation		Mean squares							
	df	Total yield	Commercial yield	Index commercial/ total yield	Number of tubers	Eye depth	Plant vigor	Plant uniformity	Maturity
Replication	1	0.002	0.000	0.006	39.045	0.085	0.151	0.009	116.236
Treatment	52	0.016**	0.013**	0.009	24.382	2.153**	0.935**	0.638	100.583**
Among families	50	0.016**	0.014**	0.009	24.213	2.140**	0.967**	0.662	101.420**
Families from 4x × 2x	39	0.013**	0.012**	0.011	17.763	2.456**	0.845*	0.672	109.101**
Males	9	0.020*	0.019*	0.014	17.062	4.422*	0.633	0.550	224.467**
Females	3	0.047**	0.037**	0.002	35.627	4.433	1.950	0.500	185.483*
Males × females	27	0.007	0.007	0.010	16.012	1.581*	0.793*	0.731	62.159*
2x FDR-CO families	23	0.010	0.009*	0.005	14.931	1.650*	0.681	0.507	120.793**
Males	5	0.012	0.013†	0.012	15.226	2.471	0.833	0.633	275.900**
Females	3	0.027**	0.022*	0.007	20.889	3.021	1.056	0.500	178.917
Males × females	15	0.007	0.005	0.002	13.629	1.104	0.556	0.467	57.467*
2x FDR-NCO families	15	0.015**	0.015**	0.019	20.931	3.231**	1.126**	0.967	92.667**
Males	3	0.027†	0.027	0.021	14.028	6.031	0.375	0.583	184.667
Females	3	0.020	0.016	0.004	25.624	2.698	1.042	1.000	115.333
Males × females	9	0.009	0.011*	0.024	21.673	2.476**	1.403**	1.083	54.444
FDR-NCO vs FDR-NCO	1	0.001	0.030*	0.010	35.390	9.370	0.390	0.030	86.700
4x × 4x families	10	0.029**	0.022**	0.003	49.581	1.027	1.527**	0.682	81.282*
4x × 4x vs 4x × 2x families	1	0.010	0.001	0.020	22.089	0.930	0.150	0.060	3.250
Clones	1	0.001	0.003	0.010	18.778	4.000*	0.250	0.001	12.250
Families vs clones	1	0.001	0.001	0.001	38.439	0.960	0.001	0.070	147.070*
Error	52	0.006	0.005	0.009	24.558	0.854	0.439	0.721	31.120
CV %		27.0	31.1	11.6	34.5	37.3	17.7	32.3	6.2

†,*,** Significant at 10%, 5% and 1% levels, respectively

Table 2 Means of total tuber yield (kg/hill) of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	0.33	0.16	0.24	0.22	0.24	0.30	0.37	0.19	0.39	0.27	0.27
Aracy	0.21	0.27	0.21	0.33	0.20	0.28	0.32	0.24	0.40	0.13	0.26
Spunta	0.28	0.23	0.17	0.23	0.22	0.25	0.34	0.27	0.31	0.29	0.26
Elvira	0.41	0.20	0.34	0.26	0.40	0.41	0.46	0.41	0.34	0.34	0.36
Means[a]	0.31	0.22	0.24	0.26	0.26	0.31	0.37	0.28	0.36	0.26	0.29

[a] $LSD_{0.05}$ for family means = 0.15

FDR-NCO family groups, respectively. The means for the ED score are presented in Table 6.

Plant vigor

There was a significant difference among families for plant vigor (Table 1). In addition, there was a significant difference among 4x-2x families. There was also a significant difference among families of the 2x FDR-NCO group. The average score for the FDR-CO group was 3.83 and for the FDR-NCO group 3.72. The contrast between the FDR-CO and FDR-NCO family groups was not significant for this trait. The means of the PV rating are presented in Table 7.

Plant uniformity

For this trait, no differences were found among treatments (Table 1). The average PU score for the FDR-CO group was 2.68 and for the FDR-NCO group 2.62. The means for PV are presented in Table 8.

Haulm maturity

There was a significant difference among treatments for HM (Table 1). There was also a significant difference among families of the 4x-2x crosses. For this trait a significant difference was observed among the FDR-CO and FDR-NCO families. The average HM value

Table 3 Means of commercial yield (kg/hill) of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen-producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	0.28	0.12	0.20	0.17	0.20	0.25	0.33	0.13	0.35	0.21	0.22
Aracy	0.18	0.20	0.18	0.27	0.16	0.21	0.29	0.18	0.35	0.10	0.21
Spunta	0.26	0.19	0.14	0.19	0.19	0.21	0.17	0.21	0.28	0.25	0.21
Elvira	0.37	0.15	0.27	0.23	0.35	0.34	0.41	0.34	0.29	0.25	0.30
Means[a]	0.27	0.16	0.20	0.21	0.23	0.25	0.30	0.22	0.32	0.20	0.24

[a] $LSD_{0.05}$ for family means = 0.14

Table 4 Means of the index commercial/total yield index of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen-producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	0.86	0.75	0.83	0.76	0.84	0.84	0.89	0.71	0.89	0.77	0.81
Aracy	0.85	0.75	0.82	0.82	0.84	0.74	0.89	0.76	0.87	0.78	0.81
Spunta	0.91	0.83	0.82	0.84	0.87	0.87	0.54	0.77	0.91	0.88	0.82
Elvira	0.91	0.75	0.81	0.86	0.87	0.83	0.88	0.83	0.86	0.73	0.83
Means	0.88	0.77	0.82	0.82	0.85	0.82	0.80	0.77	0.88	0.79	0.82

Table 5 Means of tuber number/hill of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen-producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	21.2	12.7	13.5	13.2	13.0	10.7	21.5	17.5	15.3	16.0	15.5
Aracy	14.0	9.7	15.0	17.0	14.8	9.2	10.3	19.0	15.5	9.8	13.4
Spunta	14.8	13.3	11.0	14.8	13.8	12.3	11.8	15.2	16.7	14.3	13.8
Elvira	13.8	16.0	18.7	15.8	15.3	17.0	14.7	18.2	13.3	19.5	16.2
Means	16.0	13.0	15.0	15.2	14.2	12.3	14.6	17.5	15.2	14.9	14.7

was 91.4 and 89.2 days for the FDR-CO and FDR-NCO family groups, respectively. The contrast between FDR-CO vs. FDR-NCO was not significant. The overall HM mean values are presented in Table 9.

Combining ability analysis

When the 4x-2x families were analyzed as a single group, the sources of variation due to males (2x males GCA) and females (4x females GCA) were simultaneously significant for TTY, CY and HM (Table 1). The level of significance for 4x female GCA was higher than that of male GCA (1% vs. 5%, respectively) for TTY and CY. An opposite trend was observed for HM. A significant (at 5% level) source of variation due to males × females (SCA) was observed for ED, PV and HM (Table 1).

The subdivision of the 4x-2x families into two groups (i.e., FDR-CO and FDR-NCO) showed an overall lack of correspondence between the results of both family groups. When the families from the 2x FDR-CO parents were analyzed separately, the sources of variation due to females (GCA females) were significant for TTY and CY. In this group of families the source of variation due to males (GCA males) was significant only for CY

Table 6 Means of eye depth scores[a] of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	3.5	2.5	2.0	3.5	3.0	3.0	3.0	4.0	5.0	2.0	3.2
Aracy	1.0	3.0	1.0	3.5	3.5	2.5	3.0	4.5	1.0	2.5	2.6
Spunta	2.5	1.5	1.5	1.0	3.5	1.0	1.5	4.5	2.0	1.0	2.0
Elvira	1.5	2.0	1.5	2.5	2.5	1.5	2.5	4.0	3.0	4.0	2.5
Means[b]	2.1	2.3	1.5	2.6	3.1	2.0	2.5	4.2	2.8	2.4	2.5

[a] Eye depth based on a scale of 1 = shallow to 5 = very deep
[b] $LSD_{0.05}$ for family means = 1.9

Table 7 Means of plant vigor scores[a] of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen-producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	3.5	3.5	3.0	3.5	3.5	4.0	3.5	3.0	3.5	3.0	3.4
Aracy	3.5	3.5	4.0	4.5	3.0	3.5	4.0	4.0	4.5	2.0	3.7
Spunta	5.0	3.5	3.5	4.5	4.0	4.0	4.0	3.0	4.0	4.0	4.0
Elvira	4.5	3.0	5.0	4.0	3.5	4.5	4.0	5.0	3.0	4.5	4.1
Means[b]	4.1	3.4	3.9	4.1	3.5	4.0	3.9	3.8	3.8	3.4	3.8

[a] Plant vigor based on a scale of 1 = poor to 5 = very good vigor
[b] $LSD_{0.05}$ for family means = 1.3

Table 8 Means of plant uniformity scores[a] of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen-producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	2.5	2.0	2.5	2.5	2.5	2.5	2.0	3.0	3.0	3.5	2.6
Aracy	2.0	3.0	1.5	3.0	3.0	3.5	2.0	2.5	2.0	2.0	2.5
Spunta	2.0	3.0	2.5	3.5	2.5	2.5	2.5	4.5	2.0	2.5	2.8
Elvira	3.0	3.0	3.0	3.5	2.5	2.5	3.0	2.0	3.0	2.5	2.8
Means	2.4	2.8	2.4	3.1	2.6	2.8	2.4	3.0	2.5	2.6	2.7

[a] Plant uniformity score is based on a scale of 1 = uniform to 5 = non-uniform

(at 10% level) and HM (1% level). On the other hand, when families from 2x FDR-NCO parents were analyzed separately, the source of variation due to female GCA was not significant for all eight traits. In this group of families, a significant male GCA was observed only for TTY (at 10% level). For the FDR-NCO family group, the source of variation due to males × females (SCA) was the predominant one, being significant for CY, PV, and ED. However, for the FDR-CO family group, the source of variation due to males × females (SCA) was significant only for HM.

Discussion

The 2n-gametes formed by a mechanism equivalent to the first-division restitution without crossover (FDR-NCO) can transmit almost 100% of the parental heterozygosity and epistatic interactions to the progeny without disruption by recombination. For this reason, FDR-NCO gametes are considered to be genetically superior to those formed by FDR-CO, which can pass on to the progenies approximately 80% of the

Table 9 Means of haulm maturity (days from planting to date of 50% of plants senesced in the plot) of 4x-2x progenies from crosses between tetraploid (4x) cultivars and diploid (2x) Phureja-haploid Tuberosum clones evaluated at Brasilia-DF, Brazil. The 2x clones were 2n-pollen producers by either first division restitution with crossing over (FDR-CO) or first division restitution without crossing over (FDR-NCO)

4x parents	2x FDR-CO						2x FDR-NCO				Half-sib means
	L-10	L-11	H-3	H-4	H-5	M-5	SY-8	SY-11	SY-12	M-6	
Chiquita	82.5	94.0	88.0	104.0	96.0	104.0	86.0	104.0	84.0	104.0	94.7
Aracy	84.0	104.0	86.0	104.0	86.0	104.0	86.0	86.0	84.0	86.0	91.0
Spunta	86.0	94.0	84.0	96.0	84.5	86.0	86.0	96.0	84.0	86.0	88.3
Elvira	86.0	86.0	84.0	86.0	88.0	96.0	86.0	96.0	88.0	86.0	88.2
Means[a]	84.6	94.5	85.5	97.5	88.6	97.5	86.0	95.5	85.0	90.5	90.5

[a] $LSD_{0.05}$ for family means = 11.2

heterozygosity present in the 2n pollen-producer parent. In the present work, a comparison of 4x-2x families obtained from crosses using both FDR-CO and FDR-NCO clones indicated that the higher level of heterozygosity and epistasis transmitted by the 2x FDR-NCO was apparently not enough to produce significant differences in most of the traits under consideration. In fact, significant differences between FDR-NCO vs. FDR-CO families were observed (at 5% level) only for CY but not for the other seven other traits: TTY, HM, PV, PU, ED, NTH, and CTI. **However, it is important to highlight that no differences were found among treatment means for PU, NTH, and CTI.**

Our results for TTY, indicating a lack of superiority of FDR-NCO over FDR-CO, are agreement with previous studies with progenies from 4x-2x crosses (Masson 1985; Buso 1986). In the first study (Masson 1985), a comparison was carried out with 4x families derived from complete factorial crosses between European cultivars and 2x FDR-CO and FDR-NCO clones selected for tuber production under long-day conditions in Wisconsin (USA). The second study employed a set of unadapted 4x parents of European and Brazilian origin (Buso 1986). Our results, which were obtained using 4x parents of Brazilian and European origin selected for good adaptation under tropical conditions, indicate a similar trend (i.e., no significant contrast between FDR-CO and FDR-NCO family groups). Therefore, in all experiments conducted so far there is no evidence supporting the fact that progenies derived from FDR-NCO mechanism are genetically superior over FDR-CO for TTY.

The lack of superiority of FDR-NCO over FDR-CO gametes for TTY has some practical implications for potato breeding programs. Pyramiding both meiotic mutants (*ps* and *sy-3*) in the same genetic background is obviously a more difficult task than incorporating only the *ps* allele. In addition, the incorporation of both recessive genes in the same clone always involves some risk of inbreeding depression. In fact, a possible explanation for the absence of superiority may be already the manifestation of some degree of inbreeding depression affecting the potentially superior genetic performance of the FDR-NCO clones. An additional explanation may be due to sampling bias within the 2x parents. However, these clones are derived from an interspecific cross (see Materials and methods), and the selection of closely related clones would be a very unlikely event.

Another plausible interpretation for this phenomenon is that the physical site of the genes and/or linkats (DeMarly 1979) controlling quantitative trait loci (QTL) for TTY might be predominantly located between the centromeres and the chromosomal sites of the first crossover. This notion is derived from the genetic expectations associated with the FDR-CO and FDR-NCO gametes, including their equivalency for traits controlled by genes located in these particular chromosomal regions as concluded from cytological observations (Peloquin et al. 1989b). This peculiar set of cytogenetic features of these 2n-gametes can be employed as a tool to infer the physical location of QTL (Tai 1994). In fact, the absence of superiority among 4x progenies for QTL predominantly located from the centromere to the first crossover will be the expected outcome regardless of the FDR mechanism (Peloquin et al. 1989a). Therefore, the phenotypic equivalency for quantitative traits observed in a large number of progenies derived from complete factorial crosses is strong evidence that genetic factors controlling a given QTL expression may be physically located in genomic regions where both types of FDR gametes are of similar genetic value.

In this scenario, our results can be interpreted as additional evidence for Tai and De Jong's (1997) hypothesis that the majority of the genetic factors and/or major effect quantitative trait loci for TTY might have a physical location somewhere between the centromeres and the chromosomal regions where the proximal recombination events take place. It is interesting to note that Tai and De Jong (1997) reached the identical conclusion regarding the physical location of major effect TTY loci by evaluating progenies derived from a genetically distinct type of crosses [4x progenies

produced by diploid and their vegetatively doubled-(tetraploid) counterpart parents]. Our results similarly suggest a predominant physical location of the genetic factors controlling the phenotypic expression of HM, PV and ED but apparently not for CY. However, it is important to highlight that this superior effect of FDR-NCO pollen on CY can still be considered as controversial. Indeed, more experiments are necessary to verify the genetic superiority of FDR-NCO gametes for CY, since no differences between FDR-CO vs. FDR-NCO families were observed for this trait in previous experiments conducted in France and USA (Masson 1985). Furthermore, in the field assays also carried out in Wisconsin (Buso 1986), although the CY was not evaluated, the TTY assessment was done only with tubers equal to or more than 25 mm in diameter. This cut-off point, which is less than the criterion used in our present experiment (i.e., more than 33 mm in diameter), can still be considered as a partial evaluation of CY. For instance, in the set of experiments conducted in Wisconsin, once more, no differences were observed between FDR-CO and FDR-NCO family groups for TTY (Buso 1986).

Mok and Peloquin (1975) reported that the mode of 2n-gamete formation (in that case FDR vs. SDR) was implicated with differences in combining ability estimates among 2x haploid-species hybrids in 4x-2x crosses. Their experimental data with diploid hybrids producing 2n pollen with FDR as male parents indicated that only SCA was significant for tuber yield (Mok and Peloquin 1975). However, apart from a few exceptions (e.g., Neele et al. 1991), if one takes into consideration all subsequent reports from 4x-2x crosses, GCA variance has been found to play a more significant role for TTY than SCA (for review see, Ortiz and Peloquin 1994; Tai 1994). This latest trend was observed in our experiment. The sources of variation due to males GCA and females GCA were both significant for TTY, CY and HM (Table 1). The source of variation due to males × females (SCA) was significant for ED and HM. In addition, there was an apparent influence of the mode of 2n pollen formation on the combining ability for some traits. For instance, when families from 2x FDR-CO parents were analyzed separately, the sources of variation due to males (GCA males) and/or females (GCA females) were significant for TTY, CY and HM. Likewise, for families from 2x FDR-NCO the source of variation due to males × females was significant for CY and ED. However, for 2x FDR-NCO families, only the sources of variation due to males and/or females were significant. This significance occurred for TTY and NTH. These results are in disagreement with that obtained with a set of crosses using basically the same group of 2x clones but with a different group of 4x parents (Buso 1986). In this case, the source of variation due to males × females (SCA) was found to be the only one significant for TTY in two field assays (Buso 1986). On the other hand, our results are agreement with that obtained by Masson (1985) where the importance of GCA variance was clearly demonstrated with a set of FDR-CO vs. FDR-NCO families. The importance for potato breeding associated with significant GCA effects is the predictive value, regardless of the mode of 2n-pollen formation by first-meiotic division restitution, of the parental effects for some important traits in individual crosses using these groups of diploid and tetraploid clones and cultivars.

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