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Chromosome regions between centromeres and proximal crossovers are the physical sites of major effect loci for yield in potato: Genetic analysis employing meiotic mutants

J. A. BUSO*, L. S. BOITEUX*, G. C. C. TAI†, AND S. J. PELOQUIN‡§

*Centro Nacional de Pesquisa de Hortaliças (CNPH)–Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Caixa Postal 218, 70359-970 Brasilia-DF, Brazil; †Potato Research Centre, Agriculture and Agri-Food Canada, P.O. Box 20280, Fredericton, New Brunswick, Canada, E3B 4Z7; and ‡Department of Horticulture, 1575 Linden Drive, University of Wisconsin, Madison, WI 53706-1590

Contributed by S. J. Peloquin, December 11, 1998

ABSTRACT **Meiotic mutant (2*n*) gametes formed by first-division restitution without crossover (FDR-NCO) are expected to be superior to FDR with crossover (FDR-CO) because they transmit to the progeny, without disruption by recombination, almost 100% of the parental genotype. FDR-CO transfers ≈80% of the parental heterozygosity and a large fraction of the epistatic interactions. Another genetic expectation associated with both FDR gametes is their equivalence for the phenotypic expression of traits controlled by genes residing between centromeres and proximal crossover sites. This set of unique cytogenetic features of FDR mutants was employed here as a tool to infer physical location of quantitative trait loci controlling total tuber yield (TTY) in potato. Two assays were conducted to verify the superiority of FDR-NCO over FDR-CO gametes for TTY by using progenies from 4x–2x factorial crosses. Male clones were 2*n*-pollen producers by either FDR-CO or FDR-NCO mechanisms. Compared with the 4x parents, TTY of the progenies ranged from 41% to 175% (i.e., high-parent heterosis). However, no significant TTY differences were observed between FDR-CO and FDR-NCO families. In addition, the size of variance components of males was smaller than females and near zero. Our results reinforce the hypothesis that genes controlling yielding ability have a predominant physical location between centromeres and proximal chiasmata. Quantitative trait loci in chromosome regions with reduced levels of recombination may provide a partial explanation for the slow progress in increasing TTY through conventional 4x–4x crosses and for the often high degree of heterosis obtained by introgressing genetic diversity via 4x–2x crosses in potato.**

A more effective introgression of the genetic diversity present in diploid (2x) *Solanum* species into the tetraploid (4x) cultivated potato (*Solanum tuberosum* L.) gene pool has been possible by using haploid-species hybrids (1) in 4x–2x crosses with unilateral sexual polyploidization and 2x–2x crosses with bilateral sexual polyploidization (2). The presence of gametes with the sporophytic (2*n*) chromosome number plays a crucial role in both unilateral sexual polyploidization and bilateral sexual polyploidization breeding schemes (3–5). In fact, the identification and genetic characterization of meiotic mutants controlling 2*n* egg (diplogynoid) and 2*n* pollen (diplandroid) formation was the single major factor allowing for a large scale utilization of the unilateral sexual polyploidization and bilateral sexual polyploidization strategies in potato breeding (6).

Several spontaneous mutants disrupting the regular meiotic process during either megasporogenesis or microsporogenesis have been described in diploid potato species (7). Phenotypic expression of some of these mutant genes involves premeiotic, meiotic, and postmeiotic abnormalities that can ultimately result in the formation of 2*n* gametes (7). Six major mechanisms of 2*n* gamete formation have been cytogenetically characterized: premeiotic doubling; first-division restitution (FDR); chromosome replication during the meiotic interphase; second-division restitution (SDR); postmeiotic doubling; and apospory (8). FDR and SDR are the predominant mechanisms of 2*n* gamete formation in potatoes (8, 9). The FDR-generated gametes are considered to be more valuable than those obtained by SDR because a larger amount of the parental heterozygosity and favorable epistatic interactions can be transferred to the progeny without disruption by recombination events (10–12).

Two meiotic mutants with genetic consequences equivalent to FDR have been particularly useful in potato breeding under the unilateral sexual polyploidization scheme: the recessive alleles *ps* (parallel spindles) and *sy-3* (synaptic-3) from *Solanum phureja* × haploid *S. tuberosum* hybrids (13, 14). The genotype *ps*/*ps* results in the formation of 2*n* pollen by a process equivalent to an FDR mechanism with crossover (FDR-CO). The 2*n* FDR-CO gametes are able to transmit to their progenies ≈80% of the heterozygosity and a large (but not intact) fraction of epistasis present in the parental clone (11). The level of heterozygosity transmitted by 2*n* gametes derived from FDR-CO is about twice of that from SDR mechanism, as demonstrated by restriction fragment length polymorphism analysis (15). When *ps* is combined in the same genetic background with **sy-3**, the 2*n* gametes are formed by a process equivalent to FDR without crossover (FDR-NCO) (16). FDR-NCO clones will transmit virtually intact the heterozygosity and epistasis to the progeny because of an almost complete lack of chiasma formation observed in *ps*/*ps*, *sy-3*/*sy-3* plants (6, 10).

A common feature of both FDR-CO and FDR-NCO gametes (assuming that double or higher order crossovers do not occur) is that all heterozygous loci present in the parental genome from the centromere to the first crossover will be undisturbed by meiosis. In these chromosomal regions the 2x parental genotype will be 100% preserved in FDR-NCO and FDR-CO gametes. Therefore, a genetic expectation associated with both FDR gametes is their equivalence for the phenotypic expression of traits controlled by genes residing between centromeres and proximal crossover sites. A characteristic unique to FDR-CO gametes is that one-half of the parental loci between the first and second crossovers will be heterozygous (10, 11). In SDR-derived gametes, all loci from the centromere to the first crossover will be homozygous and all

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Abbreviations: FDR-CO, first-division restitution with crossover; FDR-NCO, FDR without crossover; GCA, general combining ability; GTA, general tuber appearance; HM, haulm maturity; SCA, specific combining ability; SDR, second-division restitution; TTY, total tuber yield.

§To whom reprint requests should be addressed.

loci between the first and second crossovers that are heterozygous in the parent will remain heterozygous (8).

The preponderance of nonadditive genetic variance for important traits such as tuber yield has been reported for potato (4, 17–19). Therefore, intralocus interactions and interlocus interactions are considered to be the major components associated with tuber yield (4). These observations imply that 2x FDR-NCO clones would be the genetic materials of choice for use as parents in the unilateral sexual polyploidization scheme because they can transmit almost 100% of the heterozygosity and epistasis. Comparative studies have been conducted with FDR-CO vs. SDR-derived progenies (12, 13). In both cases, the genetic superiority of FDR-CO over SDR gametes has been demonstrated for total tuber yield (TTY), confirming the theoretical expectations of FDR-CO superior performance because of the ability to transmit higher levels of heterozygosity to the progeny (12, 13). However, for some other important traits (e.g., chip color and underwater tuber weight), the expected FDR-CO superiority over SDR gametes was not observed (12). These results suggest that a trait-specific manifestation of the actual genetic superiority associated with a given mode of 2*n* gamete formation may be the rule in potato. In addition, the merit of 2*n* gametes in potato improvement will depend on the kind of genetic variance available in the breeding population.

The aim of the present work was to compare the performance of 4x–2x families derived from staminate parents with 2*n* pollen production by either FDR-CO or FDR-NCO mechanisms. For this purpose, we analyzed progenies from two sets of factorial crosses involving 4x cultivars and 2x *S. phureja* × haploid *S. tuberosum* hybrids. The unique cytogenetic features of the FDR gametes were employed here as a tool to infer physical location of major effect quantitative trait loci (QTL). Therefore, our results can provide some insights about the relative merit of each type of FDR diplandroid formation; the respective impact of each type of 2*n* pollen formation on three quantitative traits and the predominant physical location of these traits in the potato genome.

MATERIALS AND METHODS

Plant Material, Crosses, and Mating Design. The 4x families were from two different sets of crosses. In experiment 1 (E1), 24 families were obtained from a 3 × 8 factorial mating design with three 4x female cultivars [Spunta (Holland), Elvira (Germany), and Aracy (Brazil)] and eight 2x male parents [four FDR-CO clones (H-3, H-4, H-5, and M-5) and four FDR-NCO clones (M-6, SY-7, SY-8, and SY-11)]. These 2x clones were selected from previous crosses between clone I (*S. phureja* PI 243472 × Katahdin haploid US-W1) and clone J [*S. phureja* PI 225696 × Chippewa haploid US-W 42]. In experiment 2 (E2), 18 families obtained from a 3 × 6 factorial mating design with three 4x cultivars [Atlantic (USA), Chiquita (Brazil), and Claustar (France)] and six 2x male parents [four FDR-CO clones (H-3, H-4, H-5, and M-5) and two FDR-NCO clones (SY-8 and M-6)]. Controlled crosses were made in the greenhouse. Seedlings of the 42 families were transplanted individually to 10-cm pots and were kept under greenhouse. Tubers were harvested 158 days later. Two tubers of 20 plants per combination were used to constitute two family bags, with one tuber per genotype per bag. These tubers were utilized in the field trials.

Field Experiments. The two field assays (one with each set of crosses) were carried out at Hancock, WI in two adjacent fields, and both experiments were treated in a similar manner (i.e., fertilization, cultural management, and planting and harvesting dates). The 4x–2x families were evaluated by using a randomized complete block design with two replications (20 hill-plots). For comparison, the group of 4x and 2x clones (used as parents) also was planted in the same field using a randomized complete block design with two replications (4 hill-plots). The parental tubers were field grown and were, on average, larger than family tubers. Plants were spaced 0.91 m × 0.31 m. The total duration of the experiments was 111 days from planting to harvesting (June–October). The following traits were evaluated: TTY, in which only of tubers over 25 mm diameter were weighed; haulm maturity (HM) score, done 77 days after planting by using a scale ranging from 1 (plant completely senesced) to 5 (plant still upright, green, flowering or pre-blossom); and general tuber appearance (GTA), evaluated at harvesting by using a scale ranging from 1 (poor) to 5 (excellent).

ANOVA and Restricted Maximum Likelihood Analysis. ANOVAs were carried out individually for each of the two experiments. In addition, data (means over two replicates) of the two experiments were also included for a combined analysis of variance. The source of variation in the combined analysis considered effects of 4x female parent (i.e., 4x general combining ability, GCA), 2x male GCA, and female × male interactions (i.e., specific combining ability, SCA). The sum of squares of male parents was further divided into FDR-CO versus FDR-NCO family groups as well as male parents within FDR-CO or FDR-NCO groups. The error mean square in the combined ANOVA was estimated from the error mean squares in the two separate ANOVAs for the two sets of experiments. Significant tests were based on assumption of a random model in which all effects (i.e., male and female parents and their interactions) represent random effects from hypothetical populations. Thus, effects of female and male parents were tested by the interaction term, whereas interactions between female and male parents were tested by the error mean square. The contrast FDR-CO vs. FDR-NCO families was tested by the within-parents mean square, whereas the latter one was tested by the interaction mean square. E2 had six of the eight 2x parents used in the E1 that were, respectively, crossed with a distinct set of three 4x parents. The combined data of E1 and E2 represent an incomplete two-way table (20) with empty cells corresponding to missing crosses between three 4x parents (Spunta, Elvira, and Aracy) and two 2x parents (SY-7 and SY-11) in E2. Estimation of variance components due to female and male parents and their interactions was achieved by using the method of Restricted Maximum Likelihood (21).

RESULTS

Total Tuber Yield. Significant differences among 4x–2x families and female × male interactions (SCA) were observed

Table 1. ANOVA of TTY, HM, and GTA of 4x–2x families in Hancock, WI

Source of variation	df	Mean squares		
		TTY	HM	GTA
Experiment 1				
Blocks	1	0.025	1.778	0.250
Families	17	0.127**	0.797	0.312*
Males, GCA	5	0.087	1.644**	0.528
Females, GCA	2	0.248	1.861*	0.132
M × F, SCA	19	0.117**	0.161	0.240
Error	23	0.013	0.116	0.149
CV, %		11.66	8.09	13.91
Experiment 2				
Blocks	1	0.001	0.333	0.083
Families	23	0.067**	0.996**	0.521**
Males, GCA	7	0.062	1.893**	0.747
Females, GCA	2	0.016	2.521**	0.646
M × F, SCA	14	0.078**	0.330*	0.390*
Error	17	0.016	0.366	0.103
CV, %		15.28	15.56	12.16

* and **, Significant at 0.05 and 0.01 levels, respectively, according to *F* test. CV, coefficient of variation.

Table 2. Combined ANOVA of TTY, HM, and GTA of 4x–2x families evaluated in Hancock, WI

Source of variation	df	Mean squares		
		TTY	HM	GTA
Females	5	0.0921	0.9444**	0.2045
Males, GCA	7	0.0462	1.4454**	0.2845
FDR-CO vs FDR-NCO	1	0.0017	0.2101	0.3070
Males-FDR-CO/FDR-NCO	6	0.0498	1.5012**	0.3092
Female × Male	29	0.0429**	0.1288	0.2036**
Error	40	0.0071	0.1111	0.0647

**, Significant at 0.01 level according to *F* test.

for TTY in both experiments (Table 1). The combined ANOVA confirmed SCA as the only significant source of variation (Table 2). The size of variance components of 4x females and 2x males was smaller than that due to male × female interactions, indicating the importance of SCA for this trait (Table 3). The variance components showed differential responses to the female parents, as revealed by the large component of interaction effects, implying that heterozygous loci for TTY probably are occupied by a set of distinct alleles in each of these genetic materials. In addition, the size of the male variance component was smaller than that of the female parents and near zero (Table 3). The contrast FDR-NCO- vs. FDR-CO-derived family groups was found to be nonsignificant for TTY (Table 2). The family group showed an 8.8% higher yield than the 4x parent group in E1 (Table 4). In addition, 14 families had higher TTY than their 4x parents. The best 4x–2x family for this trait (Spunta × H-4) had similar TTY to the best 4x parent used in E1 (i.e., Aracy). In E2, families as a group had 13% lower TTY than the 4x parent group (Table 4). However, six families outyielded their 4x parents in E2. The adapted 4x parent Atlantic produced 50% of its families over the mean of the 4x group. The means for TTY were similar (0.93 for cultivars vs. 0.91 for 4x–2x families). However, expressed as percentage of the 4x parent, the TTY among families ranged from 41.1% to 175%.

GTA. Significant differences among 4x–2x families and significant SCA interaction for GTA were observed in both experiments (Table 1). The combined ANOVA also indicated that SCA was the only significant source of variation for GTA (Table 2). The size of the variance components of 4x females for this trait was smaller than the 2x males, and the largest component of GTA was due to male × female interactions (Table 3). The small size of variance component due to female parents is an expected outcome because the 4x commercial cultivars are strongly selected for GTA. The contrast FDR-CO vs. FDR-NCO family groups was not significant for GTA (Table 2). The average family GTA (2.75) was lower than that of the 4x parental group (3.75) in E1. However, seven families had GTA scores ≥3 (Table 5). A GTA score of 3 has been considered as the minimum acceptable for selection purposes in potato breeding programs. Two families surpassed the GTA of their respective 4x parents (Table 5). The families as a group had poorer GTA than the 4x parents in E2. Indeed, only one family had a GTA score equal to its 4x parent. However, considering GTA = 3 as the minimum selection limit for market acceptability, four families would be kept for further evaluation from E2.

HM. A significant difference among families was observed only in E2 (Table 1). For HM, the GCA of males and females were significant in both experiments, whereas the SCA was significant in E2 (Table 1). However, the combined ANOVA indicated SCA as the single significant source of variation (Table 2). The largest component of HM is due to males (Table 3), reflecting the strong directional selection against late maturity in the 4x cultivars. The 4x–2x families were later to mature than the parents in both experiments (Table 6). The means of the 4x cultivars and families were 3.17 and 4.05, respectively. However, 8 of 40 families had HM score identical to that of the 4x parent.

Parent-Family Correlation. No significant correlation was found for TTY in both experiments (Table 7). A significant and negative correlation was observed for GTA only when families from FDR-CO group were considered. In E1, there was a significant correlation between the 2x parent and family means for HM. This correlation was observed when all 24 families were analyzed together and also if FDR-CO and FDR-NCO families were analyzed separately. In E2, the 2x-clone group had significant correlation for HM. Only the GTA of the FDR-CO group mean was significantly correlated with the hybrid family mean in E2.

DISCUSSION

The presence of families with high parent heterosis levels of up to 175% for TTY confirms the genetic value of the FDR gametes for this trait. Our results are in agreement with several previous reports in which the superiority of clones derived from 4x × 2x crosses involving *S. phureja*-haploid Tuberosum hybrids has been demonstrated for TTY (9, 19, 22). The comparison of the 4x–2x family means to their respective 4x parents clearly demonstrate that heterotic families can be obtained with both FDR-CO and FDR-NCO clones as staminate parents. In addition, our results indicated that the theoretical higher level of heterozygosity (≈20%) and epistasis transmitted by the FDR-NCO clones as compared with the FDR-CO clones was apparently not enough to produce significant differences among family groups for all three traits.

The results showing no superiority of FDR-NCO over FDR-CO clones for TTY are in agreement with previous experiments comparing families derived from distinct sets of factorial crosses between 4x cultivars and diploid (FDR-CO and FDR-NCO) clones evaluated at Wisconsin (23, 24). A similar trend also was observed by using 80 families derived from crosses between 8 European cultivars and 17 diploid clones evaluated in France (23). In addition, an identical result was obtained for TTY with another distinct set of 40 families evaluated in Brazil (25). Therefore, taking into account the results reported here, a total sample of 320 families (215 FDR-CO vs. 105 FDR-NCO families) has been examined in three continents. However, there is no available evidence that families with FDR-NCO mechanism of 2*n* pollen formation are genetically superior for TTY.

The lack of superiority of FDR-NCO over FDR-CO gametes for TTY is a distinct asset to the 4x–2x breeding scheme. Combining the *ps* and *sy-3* in the same genetic background is obviously more difficult than using *ps* alone. The ease of obtaining *ps* clones (because of the high frequency of this allele

Table 3. Variance components due to female parents, male parents, and interaction effects between female and male parents of TTY, HM, GTA

Variance component	TTY	HM	GTA
Females	0.0105 ± 0.0106	0.1201 ± 0.0881	0.0023 ± 0.0210
Males	0.0018 ± 0.0056	0.2480 ± 0.1470	0.0150 ± 0.0320
Females × Males	0.0420 ± 0.0110	0.1282 ± 0.0337	0.2019 ± 0.0526

Table 4. Means of total yield (kg per hill) of parents and families from 4x–2x crosses evaluated in Hancock, WI

		FDR-CO				FDR-NCO				
4x Parents	Mean	H-3 0.61	H-4 0.42	H-5 0.50	M-5 0.48	SY-7 0.31	SY-8 0.65	SY-11 0.91	M-6 0.84	Half-sibling means
Experiment 1										
Spunta	0.76	1.03	1.33	1.01	0.58	1.24	0.70	1.10	1.06	1.01
Elvira	0.64	1.05	1.11	1.06	1.07	0.98	0.97	0.98	0.91	1.02
Aracy	1.32	1.01	0.93	0.80	1.21	0.89	0.88	1.27	0.67	0.96
Experiment 2										
Chiquita	1.06	0.71	0.51	0.72	1.01	—	0.73	—	0.51	0.70
Atlantic	1.04	0.74	1.15	1.12	0.98	—	0.81	—	1.07	0.98
Claustar	0.73	0.67	1.25	0.30	0.89	—	0.68	—	0.88	0.78
Mean	0.93	0.87	1.05	0.83	0.96	1.04	0.79	1.12	0.85	0.91

$LSD_{0.05}$ for comparing two family means = 0.24.
$LSD_{0.05}$ for comparing FDR-CO vs. FDR-NCO group means = 0.08.

in both cultivated and wild tuber-bearing species) makes the work of obtaining homozygous *ps* clones relatively simple. In addition, the process of incorporating both recessive genes in the same genetic background involves the risk of possible inbreeding depression. In fact, a possible explanation may be already the manifestation of some degree of inbreeding depression in such way that could obscure the inherent genetic superiority of the FDR-NCO clones. However, it is important to note that no controlled backcross or self-cross was performed to obtain any FDR-NCO clones used in our experiment. These clones are full siblings from the FDR-CO clones and were selected in a progeny from interspecific crosses. At this stage, a very low amount of inbreeding is expected to be present. In addition, if present, inbreeding depression would be a random effect (i.e., it would have an overall similar magnitude on both FDR-CO and FDR-NCO clones). Identical results obtained with a large number of families evaluated so far, using distinct sets of 2x clones (23–25), indicate that sampling of the actual genetic variability within 2x clones is also not an adequate explanation for lack of differences between FDR-CO vs. FDR-NCO families. Another possibility is a close linkage between the *sy-3* gene and deleterious genetic factors affecting TTY performance of FDR-NCO families. However, such deleterious linkage would be manifested or perceived not only in the 4x progenies but also immediately at the parental (2x) level. This situation would be characterized by a systematic inferiority for TTY performance of FDR-NCO clones as compared with FDR-CO clones. However, this phenomenon was not observed here and has not been observed in any of the experiments contrasting FDR-NCO vs. FDR-CO clones (23–25). To reinforce this view, it is important to highlight that in our experiment, the two 2x clones with highest TTY were FDR-NCO clones.

A plausible explanation for our results is that TTY genes and/or linkats (26) could be predominantly located between the centromeres and proximal chiasmata. Therefore, the contrast between FDR-CO and FDR-NCO clones will not be significant because both types of 2*n* gametes are expected to be genetically equivalent for loci present in these regions (1, 6). All heterozygous loci between the centromere and the first crossover are maintained in the gametes and transmitted to the 4x progeny regardless of whether they are the result of either FDR-CO or FDR-NCO mechanism (6). In addition, the sizes of variance components for TTY indicated that the 2x male fraction is smaller than the 4x female fraction and near zero. These results suggest again that heterozygous loci for high yielding ability of 2x parents have a physical location proximal to the centromeres (or less likely in another genomic region with suppressed levels of recombination). In fact, transmission of intact heterozygosity is expected in all types of 2*n* gametes for loci encompassing the centromeres. Molecular mapping studies have shown that regions in a close vicinity of these sites are apparently "cold spots" for recombination in the plant genomes such as wheat (27) and potato (28). On the other hand, regions very close to the centromeres are strongly heterochromatic and potentially poor in ORFs, and they are likely to be devoid of important QTL for tuber yield. Therefore, the chromosomal regions carrying tuber yield QTL are proximal to the potato centromeres but probably do not encompass the heterochromatic region. It is interesting to note that genomic regions with reduced frequency of genetic recombination were found to be sites of a substantial amount of potential genes in potato and tomato genomes as estimated by restriction fragment length polymorphism mapping using cDNA probes (28).

Tai and De Jong (29) hypothesized that the predominant physical location of genetic factors controlling the phenotypic expression of TTY is somewhere between the centromere and the site of the first crossover. They reached this conclusion after comparing the performance of progenies derived from a

Table 5. Means of GTA of parents and families from 4x–2x crosses evaluated in Hancock, WI

		FDR-CO				FDR-NCO				
4x Parents	Mean	H-3 2.75	H-4 3.00	H-5 2.25	M-5 2.75	SY-7 2.25	SY-8 3.25	SY-11 2.75	M-6 2.50	Half-sibling means
Experiment 1										
Spunta	3.75	2.50	2.25	2.75	3.00	4.00	4.25	2.75	2.50	3.00
Elvira	3.50	2.50	2.50	3.00	2.50	2.25	3.00	2.50	2.75	2.63
Aracy	4.00	3.00	2.25	2.50	2.75	2.75	3.25	2.00	2.50	2.63
Experiment 2										
Chiquita	3.75	3.50	2.75	1.75	2.50	—	2.25	—	2.50	2.54
Atlantic	3.25	3.25	3.00	2.25	2.75	—	2.50	—	2.75	2.75
Claustar	4.00	2.50	2.50	2.50	2.75	—	3.00	—	2.50	2.63
Mean	3.71	2.88	2.54	2.46	2.71	3.00	3.04	2.42	2.58	2.70

$LSD_{0.05}$ for comparing two family means = 0.73.
GTA based on a scale from 1 (poor) to 5 (excellent).

Table 6. Means of HM of parents and families from 4x–2x crosses evaluated in Hancock, WI

		FDR-CO				FDR-NCO				
4x Parents	Mean	H-3 3.00	H-4 4.50	H-5 3.00	H-5 4.00	SY-7 3.50	SY-8 3.00	SY-11 4.50	M-6 3.00	Half-sibling means
Experiment 1										
Spunta	3.00[z]	3.00	4.00	4.00	5.00	3.50	3.00	4.00	3.50	3.75
Elvira	3.00	4.00	4.50	4.00	4.50	5.00	3.50	5.00	5.00	4.44
Aracy	4.00	4.00	5.00	4.00	5.00	5.00	3.00	5.00	4.50	4.44
Experiment 2										
Chiquita	3.50	4.00	4.50	5.00	5.00	—	3.50	—	4.00	4.33
Atlantic	3.00	3.00	4.00	3.50	4.50	—	3.00	—	3.50	3.58
Claustar	2.50	3.50	4.50	4.00	4.00	—	3.00	—	3.50	3.75
Mean	3.17	3.58	4.42	4.08	4.67	4.50	3.17	4.67	4.00	4.05

$LSD_{0.05}$ for comparing two family means = 0.95.
HM based on a scale from 1 (senesced) to 5 (still flowering).

genetically distinct type of crosses (4x progenies produced by diploid FDR-CO clones and their vegetatively doubled counterpart parents) (29). The results obtained with FDR-CO vs. FDR-NCO assays in Wisconsin (23, 24, present study), France (23), and Brazil (25) are in perfect agreement with the notion that major effect TTY factors are predominately located within the first crossover region from the centromere. Also reinforcing this view are the results with comparative studies between FDR-CO vs. SDR-derived families where the genetic superiority of FDR-CO over SDR gametes has been demonstrated for TTY (12, 13). In SDR gametes, all loci from the centromere to the first crossover will be homozygous and all loci between the first and second crossovers, which are heterozygous in the parent, will remain heterozygous in the gametes (8). Thus the superiority of FDR-CO over SDR gametes is also an expected outcome based on the hypothesis of the proximal physical location of major effect loci for tuber yield. Tai and De Jong (29) also suggested a similar physical location for genetic factors controlling expression of several tuber traits such as GTA, eye depth, tuber size, and marketable yield. Results from France (23) indicated a similar trend for marketable yield because nonsignificant differences between FDR-CO vs. FDR-NCO clones were detected. In Brazil (25), a similar trend was observed for another yield component (namely, number of tubers per hill). In addition, our work suggests similar physical location of QTL for GTA and HM. However, more experimental evidence is necessary to ascertain the results obtained with other traits than TTY.

Apart from few exceptions (e.g., refs. 13 and 30), most of the reports from 4x–2x crosses indicated GCA is more significant than SCA (9, 19). This trend was not observed in our experiments. The source of variation dueto SCA was found to be the only one significant for TTY in both assays. Our results are also in disagreement with previous experiments in which both GCA and SCA variances of the 4x and 2x parents were significant for TTY with the SCA being smaller than GCA (23). However, it is important to note that the parents and crosses were different from our experiment. Here we employed 4x parents developed for short- and long-day conditions. The 4x group evaluated in France (23) had probably better overall adaptation to long-day conditions than the group of 4x cultivars we employed. On the other hand, when a set of crosses very similar to ours was evaluated under short-day conditions in Brazil, significant 2x and 4x GCA variances were detected (25). Therefore, our analysis also indicates that broad extrapolation or generalizations from GCA and SCA estimates should be avoided because of a possible genotype × environment interaction that has not been accounted for in most of the studies with 4x–2x crosses in potato.

In closely related clones, the allelic diversity is reduced and variation in additive gene action is almost depleted, whereas epistasis can be magnified (30). In populations with a narrow genetic basis, the SCA effects are likely to be significant (30). Even though our 2x clones are the result of crosses (including different *S. phureja* accessions and *S. tuberosum* clones), they may represent (as discussed) a sampling bias in terms of genetic variability. However, the results from France (23) using a set of 2x clones derived from the same cross indicated GCA is more important than SCA. These results provide indirect evidence that low genetic diversity of the 2x clones is probably not a major factor inflating SCA variance in our experiments.

Somewhat surprising was the overall lack of parent–offspring correlation for all traits with both types of FDR parents. This implies that the estimated GCA variance is probably not composed exclusively of additive variance. In fact, a nonexclusive presence of the additive effects is expected to be true for both FDR-NCO and FDR-CO mechanisms because of the large amount of the heterozygosity transmitted to the progeny. Therefore, both types of FDR 2*n* gametes can transfer not only additive effects but also dominance and epistasis (9). The lack of correlation indicates, as suggested earlier (31, 32), that progeny testing will be a necessary step for selecting the best 2x hybrids.

The genetic inference that major-effect TTY genes in potato are in chromosome regions with putative low levels of meiotic recombination is one of the major points raised by the experiments using meiotic mutants. This hypothetical physical location of tuber yield QTL may provide a partial explanation for the very limited increase in yield and stability obtained for

Table 7. Parent–family correlation coefficients (*r*) of TTY, HM, and GTA of 4x–2x families evaluated in Hancock, WI

	TTY				HM				GTA			
	2x			4x	2x			4x	2x			4x
Parent	All	FDR–CO	FDR–NCO		All	FDR–CO	FDR–NCO		ALL	FDR–CO	FDR–NCO	
Experiment 1												
r	−0.08	−0.12	−0.01	−0.14	0.54**	0.66**	0.46*	0.23	0.14	−0.48*	0.34	0.00
Experiment 2												
r	−0.19	−0.37	0.23	0.09	0.57*	0.45	0.45	0.39	0.34	0.57*	0.00	−0.16

* and **, Significant at 0.05 and 0.01 levels, respectively.

TTY with the conventional 4x(Tub)–4x(Tub) crosses in potato (33, 34). It can also explain the reduced amount of transgressive segregation for TTY in the 4x–4x breeding scheme. Furthermore, it can imply that the often high degree of heterosis for TTY observed in 4x–2x progenies is caused by an increase in the amount of allelic diversity (i.e., enhancing heterozygozity and epistasis) via interspecific crossing with *S. phureja*. In fact, allelic diversity in wild and cultivated diploid species is greater than that observed in the tetraploid potato gene pool (35).

Molecular support for major effect TTY loci between centromeres and first-crossover sites remains to be obtained. Extensive QTL mapping of TTY genes is still incipient in potatoes (36–38). The unique behavior of FDR gametes can be also useful in this regard because it provides a tool to generate informative segregating populations and for subsequent placement of QTL in linkage maps (9). Therefore, molecular mapping in conjunction with genomic *in situ* hybridization analysis is one of the available strategies to determine in which particular chromosomes are located the QTL controlling this set of traits in potato.

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1. Peloquin, S. J., Werner, J. E. & Yerk, G. L. (1990) in *Chromosome Engineering in Plants,* eds. Gupta, P. K. & Tsuchiya, T. (Elsevier, London), Part B, pp. 79–92.
2. Mendiburu, A. O., Peloquin, S. J. & Mok, D. W. S. (1974) in *Haploids in Higher Plants: Advances and Potential,* ed. Kasha, K. J. (Gueph Univ. Press, Gueph), pp. 249–258.
3. Mendiburu, A. O. & Peloquin, S. J. (1976) *Theor. Appl. Genet.* **48,** 137–143.
4. Mendiburu, A. O. & Peloquin, S. J. (1977) *Euphytica* **26,** 573–583.
5. Mendiburu, A. O. & Peloquin, S. J. (1977) *Theor. Appl. Genet.* **54,** 177–180.
6. Peloquin, S. J., Yerk, G. L., Werner, J. E. & Darmo, E. (1989) *Genome* **31,** 1000–1004.
7. Veilleux, R. (1985) *Plant Breed. Rev.* **3,** 253–288.
8. Peloquin, S. J., Yerk, G. L. & Werner, J. E. (1989) in *Chromosomes: Eukaryotic, Prokaryotic, and Viral,* ed. Adolph, K. W. (CRC, Boca Raton, FL), Vol. 2, pp. 167–178.
9. Tai, G. C. C. (1994) in *Potato Genetics,* eds. Bradshaw, J. E. & Mackay, G. R. (CAB International, Wallingford, PA), pp. 109–132.
10. Peloquin, S. J. (1983) in *Pollen: Biology and Implications for Plant Breeding,* eds. Mulcahy, D. L. & Ottaviano, E. (Elsevier, London), pp. 311–316.
11. Hermsen, J. G. Th. (1984) *Iowa State J. Res.* **58,** 421–434.
12. Hutten, R. C. B., Schippers, M. G. M., Hermsen, J. G. Th. & Ramanna, M. S. (1994) *Theor. Appl. Genet.* **89,** 545–550.
13. Mok, D. W. S. & Peloquin, S. J. (1975) *Theor. Appl. Genet.* **46,** 307–314.
14. Okwuagwu, C. O. & Peloquin, S. J. (1981) *Am. Potato J.* **58,** 512–513.
15. Barone A., Gebhardt, C. & Frusciante, L. (1995) *Theor. Appl. Genet.* **91,** 98–104.
16. Hermundstad, S. A. & Peloquin, S. J. (1987) in *The Production of New Potato Varieties: Technological Advances*, eds. Jellis, G. J. & Richardson, D. R. (Cambridge Univ. Press, Cambridge, U.K.), pp. 197–210.
17. Plaisted, R. L., Sanford, L., Federer, W. T., Kehr, A. E. & Peterson, L. C. (1962) *Am. Potato J.* **39,** 185–197.
18. Mendoza, H. A. & Haynes, F. L. (1974) *Theor. Appl. Genet.* **45,** 21–25.
19. Ortiz, R. & Peloquin, S. J. (1994) in *Potato Genetics,* eds. Bradshaw, J. E. & Mackay, G. R. (CAB International, Wallingford, PA), pp. 133–154.
20. Tai, G. C. C. & De Jong, H. (1991) *Plant Breed.* **107,** 183–189.
21. GENSTAT5 Release 3 (1993) *Reference Manual* (Clarendon, Oxford), pp. 530–584.
22. Clulow, S. A., McNicoll, J. & Bradshaw, J. E. (1995) *Theor. Appl. Genet.* **90,** 519–525.
23. Masson, M. F. (1985) Ph.D. dissertation (University of Wisconsin, Madison, WI).
24. Schroeder, S. H. (1983) Ph.D. dissertation (University of Wisconsin, Madison, WI).
25. Buso, J. A. (1986) Ph.D. dissertation (University of Wisconsin, Madison, WI).
26. DeMarly, Y. (1979) in *Proceedings of Conference Broadening Genetic Base of Crops*, eds. Zeven, A. C. & Van Harten, A. M. [Agricultural Research Department Centre for Agricultural Publishing and Documentation (PUDOC-DLO), Wageningen, The Netherlands], pp. 257–265.
27. Chen, J. M & Gustafson, J. P. (1995) *Heredity* **75,** 225–233.
28. Tanksley, S. D., Ganal, M. W., Prince, J. P., de Vicente, M. C., Bonierbale, M. W., Broun, P., Fulton, T. M., Giovannoni, J. J., Grandillo, S., Martin, G. B., *et al.* (1992) *Genetics* **132,** 1141–1160.
29. Tai, G. C. C. & De Jong, H. (1997) *Theor. Appl. Genet.* **94,** 303–308.
30. Neele, A. E. F., Nab, H. J. & Louwes, K. M. (1991) *Theor. Appl. Genet.* **82,** 264–272.
31. Ortiz, R., Iwanaga, M. & Mendoza, H. A. (1988) *Potato Res.* **31,** 643–650.
32. Ortiz, R., Peloquin, S. J., Freyre, R. & Iwanaga, M. (1991) *Theor. Appl. Genet.* **82,** 602–608.
33. Mendoza, H. M. & Haynes, F. L. (1974) *HortScience* **9,** 328–330.
34. Douches, D. S., Maas, K. R., Jartrzebski, K. R. & Chase, R. W. (1996) *Crop Sci.* **36,** 1544–1552.
35. Peloquin, S. J. & Ortiz, R. (1992) in *Plant Breeding in the 1990s,* eds. Stalker, H. T & Murphy, J. P. (CAB International, Wallingford, PA), pp. 485–507.
36. Bonierbale, M. L., Plaisted, R. L. & Tanksley, S. D. (1993) *Theor. Appl. Genet.* **86,** 481–491.
37. Ortiz, R., Douches, D. S., Kotch, G. P. & Peloquin, S. J. (1993) *J. Genet. Breed.* **47,** 283–288.
38. Kreike, C. M., Kok-Westeneng, A. A., Vinke, J. H. & Stiekema, W. J. (1996) *Theor. Appl. Genet.* **92,** 463–470.