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Comparative performance of FDR and SDR progenies from reciprocal 4x-2x crosses in potato

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Abstract Numerically unreduced (2n) gametes from first division restitution (FDR) are considered to be superior to 2n-gametes from second division restitution (SDR) because they transfer a larger proportion of the total parental heterozygosity and epistasis intact to the tetraploid progeny. This supposed superiority was investigated by comparing 12 sets of reciprocal 4x-2x crosses. Each diploid parent used in a reciprocal set produced 2n-pollen by FDR and 2n-eggs by SDR. Six agronomic characters were investigated. FDR progenies (from 4x.2x) were found to have higher mean yields due to more and bigger tubers. With respect to underwater weight, the overall progeny mean of FDR progenies was significantly higher than that of SDR progenies (from 2x.4x). However, the absolute difference found between both overall progeny means was too small to be of practical significance. No differences between FDR and SDR progeny means were found for vine maturity and chip colour. In addition to the progeny mean, within-progeny variation is important in potato breeding. For vine maturity a higher within-progeny variation was detected in SDR progenies, whereas within-progeny variations for yield, underwater weight and chip colour were not different in FDR and SDR progenies. With regard to vine maturity, we conclude that SDR 2n-gametes are superior to FDR 2n-gametes because, with the same progeny means of FDR and SDR progenies, the within-progeny variation was higher in SDR progenies. Therefore the assumed superiority of FDR 2n-gametes was confirmed for yield but was not observed for vine maturity, underwater weight and chip colour.

Key words First division restitution · Second division restitution · Reciprocal 4x-2x crosses · Solanum

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Introduction

The final step in a potato breeding programme via the diploid level is recovery of the tetraploid level (Chase 1963; Hermsen et al. 1987). A widely advocated method for returning to the tetraploid level is sexual polyploidization by means of 2n-gametes, which result from meiotic nuclear restitution mechanisms. Nuclear restitution may occur either during the first or during the second meiotic division, and the resulting 2n-gametes are called first division restitution (FDR) and second division restitution (SDR) 2n-gametes, respectively. The genetic implications of these two types of 2n-gametes are very different. All of the parental heterozygous loci from centromere to first crossover and 50% of those that are present distally will be heterozygous in FDR 2n-gametes. On the other hand, in SDR 2n-gametes all parental heterozygous loci from centromere to first crossover will be homozygous, and all those that are present distally will be heterozygous. If a random distribution of heterozygous loci along the parental chromosomes is assumed, the retention of heterozygosity in 2n-gametes of synaptic diploids is expected to be about 80% in FDR 2n-gametes and nearly 40% in SDR 2n-gametes (Hermsen 1984). Experimental data on retained heterozygosity come very close to these theoretically estimated percentages (Douches and Quiros 1988a, b; Jongedijk et al. 1991a). In addition to heterozygosity, epistatic gene interactions are also largely maintained in FDR 2n-gametes and can be transmitted to tetraploid progenies via 2x.2x or 4x.2x crosses. As heterozygosity and epistatic interactions may greatly contribute to a good performance of potato, FDR 2n-gametes are considered to be superior to SDR 2n-gametes. For yield, this superiority of FDR 2n-gametes in 4x.2x crosses has been demonstrated by Mok and Peloquin (1975). Analogous investigations involving other agronomic characters have not been reported, as far as the authors are aware.

In comparing the effects of FDR and SDR Mok and Peloquin (1975) used different parents. Consequently, genotypic differences between parents may have influenced their results. Because 2n-pollen in synaptic diploids mostly result from FDR (Watanabe and Peloquin 1992) and 2n-eggs almost exclusively from SDR (Jongedijk 1985; Stelly and Peloquin 1986; Werner and Peloquin 1987; Douches and Quiros 1988b; Jongedijk et al. 1991b; Werner and Peloquin 1991), a better way of testing the assumed superiority of FDR 2n-gametes is to compare the performance of reciprocal 4x-2x crosses. However, such a comparison is only feasible when cytoplasmic effects on agronomic characters and sex differences in genetic recombination are absent.

For yield, differences between progenies from reciprocal potato crosses have been observed and may even be large. These reciprocal differences seem to result from divergent parental maturity rather than from differences between the cytoplasms involved (Sanford and Hanneman 1982; Staub et al. 1982), although results by Maris (1989) do not point to such conclusion. In addition, investigations on SDR progenies from reciprocal 4x-2x crosses involving tetraploid parents with the cytoplasm of *Solanum tuberosum* L. and diploid parents with the cytoplasm of *Solanum phureja* Juz. et Buk. did not reveal any reciprocal differences for yield (Kidane-Mariam and Peloquin 1974, 1975). In reciprocal cross progenies between long-day adapted parents no consistent reciprocal differences were found for maturity (Engel 1956; Tarn and Tai 1977; Maris 1989) and specific gravity (Engel 1956; Hoopes et al. 1980; Maris 1989). Therefore, cytoplasmic effects are not expected to interfere with the comparative research of FDR and SDR by means of reciprocal 4x-2x crosses.

As sex differences in chiasma and bivalent frequencies (Jongedijk and Ramanna 1989), and in genetic recombination (Douches and Quiros 1988b; Jongedijk et al. 1991a) have not been observed in diploid potato clones, the comparison of reciprocal 4x-2x progenies to estimate differences between FDR and SDR 2n-gametes is considered to be a correct approach. Results on reciprocal 4x-2x progenies have been reported (Kidane-Mariam and Peloquin 1974, 1975, Mendiburu and Peloquin 1977). The 4x.2x (FDR) progenies were higher yielding than their reciprocals. The authors did not link these reciprocal differences with different restitution mechanisms in micro- and megasporogenesis because at that time it was not known that 2n-egg formation in synaptic diploid potatoes is almost exclusively through SDR.

The present investigation was carried out to compare the performance of tetraploid progenies from sets of reciprocal 4x-2x crosses involving FDR and SDR 2n-gametes from the diploid parent in each set. Comparisons between FDR and SDR progenies were made for the agronomic characters yield, yield components, vine maturity, chip colour, and underwater weight. The results will indicate whether the superior contribution to yield of FDR 2n-gametes compared to SDR 2n-gametes also applies for other agronomic characters. A good comparison between FDR and SDR progenies for more than yield alone may answer the question of whether it is justified to select only for FDR 2n-gametes in a diploid potato breeding programme.

Materials and methods

In order to obtain equivalent tetraploid progenies from FDR and SDR 2n-gametes, reciprocal 4x-2x crosses were made. Diploid parents were selected among F_1 hybrids of the clones USW 5295.7 (B), USW 5337.3 (C), USW 7589.2 (D) and 77.2102.37 (E). The pedigrees of these clones have been summarized by Jongedijk and Ramanna (1988). Meiosis was studied in the diploid F_1 hybrids producing high frequencies of 2n-pollen. Synaptic clones producing 2n-pollen predominantly through the fusion of metaphase-II spindles, which leads to FDR (Ramanna 1979), were selected. For meiotic studies, flower buds were fixed in a solution of formalin, proponic acid (saturated with ferric acetate) and ethanol (1:3:6). Small portions of the anthers were squashed in 1% aceto-carmine. The diploid F_1 hybrids were then screened for 2n-egg production using seed set in 2x.4x testcrosses as a criterion. Nine F_1 hybrids were found to set berries with seeds in the testcrosses.

These nine selected diploids were reciprocally crossed with vars 'Alcmaria', 'Certa', 'Escort' and 'Hertha'. All 36 reciprocal sets of 4x-2x crosses were successful. Seed set in all 36 4x.2x crosses was comparable to seed set in 4x.4x crosses, whereas seed set was limited in several 2x.4x cross combinations. Total numbers of seeds and numbers of seeds per berry obtained from 2x.4x crosses are presented in Table 1. The frequency of triploid plants in such progenies is expected to be very low due to the 'triploid block' (Marks 1966). However, in 2x.4x cross combinations with a low seed set per berry these few triploid plants may form a rather large proportion of the progeny. Therefore, we decided to restrict this investigation to the

Table 1 Total number of seeds (S) and number of seeds per berry (S/B) from 2x.4x crosses

	Alcmaria		Certa		Escort		Hertha	
	S	S/B	S	S/B	S	S/B	S	S/B
BC1082	4	0.3	16	0.8	7	0.2	21	0.7
BC1083	30	2.5	45	5.0	55	3.2	30	3.3
BE1050	345	34.5	400	21.1	345	19.2	581	29.1
BE1060	71	4.7	109	4.4	78	3.0	96	3.6
CD1015	137	15.2	320	18.8	587	16.3	790	21.9
CD1042	82	3.7	23	3.8	26	3.7	67	5.6
CD1045	201	20.1	671	23.1	529	20.3	1404	34.2
CD1047	43	2.7	12	1.2	29	1.8	81	3.9
CE69	20	1.7	27	2.3	67	3.4	46	2.6

reciprocal progenies involving the diploid clones BE1050, CD1015 and CD1045, which gave a relatively high seed set in both directions of the 4x-2x crosses. In all 2x.4x cross combinations these three diploids gave more than 15 seeds per berry (Table 1).

A maximum of 150 seeds per cross was sown and maximally 100 seedlings were grown in 11- × 11-cm pots in a screenhouse. All seedlings which formed two reasonably sized seed tubers were included in the field trial. The actual number of clones per progeny included in the field trial is shown in Table 2. The field trial consisted of two randomized blocks. Each block contained a random half of the progenies. All measurements were made on a 2 plant per clone basis. The field trial was conducted in 1991 near Wageningen on clay soil. Plant distances were 40 cm within and 75 cm between ridges. The two seed tubers of each clone were placed in the same ridge. Seed tubers were planted on April18th, and foliage was destroyed by spraying 'Reglone' on September 18th.

The characters estimated were:
1. yield in grams of all tubers with a diameter of more than 2 cm;
2. number of tubers more than 2 cm in diameter;
3. tuber size on a 1–9 scale (1 = very small);
4. vine maturity on a 1–9 scale (1 = very late);
5. underwater weight converted to the underwater weight of 5000 g potatoes;
6. chip colour on a 1–9 scale (1 = very dark).

Clones were stored at about 9 °C until they were chipped in the second week of February. To estimate chip colour of a clone, three 1.5-mm-thick slices from each of 3 tubers were chipped and fried in 180 °C peanut oil until bubbling stopped.

Results

The means of FDR (4x.2x) and SDR (2x.4x) progenies for yield, tuber number and tuber size are presented in Table 3. All FDR progenies were higher yielding than their SDR reciprocals, although the differences are significant in 4 sets of reciprocals only. The overall mean yield showed a highly significant superiority of the FDR progenies. Overall means for tuber number and tuber size showed that these higher yields of FDR progenies were due to a combination of more and bigger tubers.

Progeny means for vine maturity, underwater weight and chip colour are presented in Table 4. For these three agronomic characters no significant differences were found within individual sets of reciprocal progenies. A

Table 2 Total number of clones used in the field trial of FDR and SDR progenies obtained from reciprocal 4x-2x crosses.

Parents		Total number of clones	
4x	2x	FDR progeny from 4x.2x	SDR progeny from 2x.4x
Alcmaria	BE1050	66	48
Alcmaria	CD1015	76	70
Alcmaria	CD1045	72	52
Certa	BE1050	49	55
Certa	CD1015	61	48
Certa	CD1045	56	46
Escort	BE1050	41	44
Escort	CD1015	65	53
Escort	CD1045	69	53
Hertha	BE1050	51	54
Hertha	CD1015	70	47
Hertha	CD1045	65	60
Grand total of clones		741	630

Table 3 Mean yield (g), tuber number, and tuber size (1–9 scale, 1 = very small) of 2 clonal plants in FDR (4x.2x) and SDR (2x.4x) progenies

Parents		Yield		Tuber number		Tuber size	
4x	2x	FDR	SDR	FDR	SDR	FDR	SDR
Alcmaria	BE1050	2158	1791	25.5	21.2	6.97	6.77
Alcmaria	CD1015	2404	1995*	43.3	39.6	6.66	6.30
Alcmaria	CD1045	2321	2031	35.4	34.4	6.60	6.21
Certa	BE1050	2060	1787	29.9	29.3	6.39	6.31
Certa	CD1015	1980	1614	45.6	40.0	5.69	5.31
Certa	CD1045	1921	1517*	44.6	43.0	5.39	4.89
Escort	BE1050	2442	2317	26.4	24.4	7.02	7.11
Escort	CD1015	2470	2118	33.0	34.3	6.94	6.70
Escort	CD1045	2720	2142**	44.1	41.3	6.32	5.94
Hertha	BE1050	2598	2216	28.1	27.6	6.90	6.59
Hertha	CD1015	2530	1768**	44.8	38.1*	6.41	5.70*
Hertha	CD1045	2279	2266	43.8	44.1	5.98	6.00
Overall mean		2332	1973**	37.7	35.1*	6.43	6.16**

* and ** indicate significant differences between FDR and SDR progenies at $P < 0.05$ and $P < 0.01$, respectively

Table 4 Mean vine maturity (1–9 scale, 1 = very late), underwater weight (converted to the underwater weight of 5000 g potatoes) and chip colour (1–9 scale, 1 = very dark) in FDR (4x.2x) and SDR (2x.4x) progenies

Parents		Vine maturity		Underwater weight		Chip colour	
4x	2x	FDR	SDR	FDR	SDR	FDR	SDR
Alcmaria	BE1050	6.33	6.29	388	379	4.66	4.85
Alcmaria	CD1015	5.95	5.79	416	395	5.07	4.94
Alcmaria	CD1045	5.56	5.62	425	411	4.99	5.10
Certa	BE1050	4.80	5.05	449	441	5.06	5.30
Certa	CD1015	4.07	4.06	420	410	4.56	4.81
Certa	CD1045	4.11	4.07	441	451	4.11	4.51
Escort	BE1050	5.07	5.16	380	379	5.45	4.98
Escort	CD1015	4.72	4.72	386	368	4.73	4.94
Escort	CD1045	4.49	4.64	392	405	4.48	4.98
Hertha	BE1050	5.20	5.24	444	422	5.45	5.41
Hertha	CD1015	4.31	4.57	436	421	4.94	5.15
Hertha	CD1045	4.38	4.50	444	437	4.40	4.78
Overall Mean		4.94	5.00	418	410*	4.81	4.98

* and ** indicate significant differences between FDR and SDR progenies at $P < 0.05$ and $P < 0.01$, respectively

Table 5 Mean variances for yield, vine maturity, underwater weight and chip colour in FDR (4x.2x) and SDR (2x.4x) progenies

	Mean variance	
Character	FDR progenies	SDR progenies
Yield	542947	432382
Vine maturity	1.19	1.71*
Underwater weight	2047	2222
Chip colour	1.42	1.38

* indicates significant differences ($P < 0.05$) between FDR and SDR progenies

significant difference between overall means was found for underwater weight only.

Besides the progeny mean, within-progeny variation is important in plant breeding. Mean variances for yield, vine maturity, underwater weight and chip colour of FDR and SDR progenies are presented in Table 5. Mean variances of FDR and SDR progenies differed significantly for vine maturity only.

Discussion

The mean yield of the FDR (4x.2x) progenies was higher than the mean yield of the SDR (2x.4x) progenies in all 12 sets of reciprocal 4x-2x crosses. This higher yield of FDR progenies was significant in 4 sets. In addition, the difference between the overall mean yield of the FDR progenies and that of the SDR progenies was highly significant (Table 3). These results confirm those of Mok and Peloquin (1975), that FDR 2n-gametes are superior to SDR 2n-gametes with respect to yield, and are similar to results reported for reciprocal 4x-2x crosses wherein the diploid parents produced FDR 2n-pollen (Kidane-Mariam and Peloquin 1974, 1975; Mendiburu and Peloquin 1977). The higher yield of progenies obtained with FDR 2n-gametes was due to both more and larger tubers. This is of interest because the larger tuber size in FDR progenies indicates that higher yields coincide with a good marketability.

For underwater weight a significant difference between the reciprocal progenies was found only for the overall mean. However, the absolute difference between the overall means was very small. In fact, it is too small to be of practical significance in a breeding programme. For vine maturity and chip colour no significant differences between the reciprocal 4x-2x progenies were found. When for underwater weight, vine maturity and chip colour differences between progenies derived from FDR and SDR 2n-gametes were absent or of no practical significance; FDR 2n-gametes are not superior for these characters. The results for vine maturity are important in connection with the results for yield. They show that the higher yield of FDR progenies is not due to a later maturity of these progenies.

Because the FDR and SDR progenies were only slightly different for mean vine maturity, mean underwater weight and mean chip colour, a higher within-progeny variation for these characters may favour the use of SDR 2n-gametes. SDR 2n-gametes retain nearly 40% of the parental heterozygosity, whereas FDR 2n-gametes retain about 80%. Therefore, SDR 2n-gametes may be genetically dissimilar from the parent and among each other, whereas FDR 2n-gametes are expected to be genetically more similar to the parent and each other. Consequently, FDR 2n-gametes contribute greatly to the uniformity of the progeny, and lower within-progeny variations are expected. No experimental data on within-progeny variation have been reported. There is only one reference (Mendiburu and Peloquin 1977) reporting a remarkable higher degree of within-family uniformity in 4x.2x progenies than in 2x.4x progenies for vegetative characters in the field. As shown in Table 5 for yield, underwater weight and chip colour, no significant differences in within-progeny variation between FDR and SDR progenies were found. For vine maturity the within-progeny variation of SDR progenies was significantly higher than that of FDR progenies. Therefore, for vine maturity SDR 2n-gametes are more desirable than FDR 2n-gametes.

The different amounts of heterozygosity retained in FDR and SDR 2n-gametes created the expectation that FDR and SDR progenies would differ both in progeny mean and within-progeny variation for all of the investigated characters. However, this investigation revealed a different progeny mean only for yield and a different within-progeny variation only for vine maturity. These findings require further discussion.

A difference in progeny mean was found only for yield. Within equivalent progenies, a higher mean yield generally accompanies a greater within-progeny variation. The higher mean yield of the FDR progenies and the higher uniformity of FDR 2n-gametes thereby have opposite effects on the within-progeny variation. This may be the reason why no difference in within-progeny variation for yield between FDR and SDR progenies was observed.

For vine maturity a higher within-progeny variation was found in SDR progenies, whereas the progeny means of FDR and SDR progenies were similar. These results may be explained by assuming an additive inheritance of most of the genes involved in the expression of this character.

For underwater weight and chip colour no differences were found between FDR and SDR progenies for progeny mean or for the within-progeny variance. A tentative explanation might be that all of the clones are homozygous for most of the genes involved in the expression of these characters. Alternatively, it is likely that most of these genes are not located at very distal or proximal positions on the chromosome arms. Genes on these chromosomal positions are not affected very differently by SDR and FDR. Mendiburu and Peloquin (1979) explained that the genetic consequences of FDR and SDR are equal for loci at a genetic distance where 66.7% of the arms show a single chromatid exchange.

Conclusions

The superiority of FDR 2n-gametes with respect to SDR 2n-gametes was confirmed for yield. The higher yields of FDR progenies were not associated with a reduced marketability or a later vine maturity. For other important agronomic characters such as vine maturity, underwater weight and chip colour no considerable differences between the means of FDR and SDR progenies were found. However, for vine maturity the within-progeny variation of SDR progenies was significantly larger than that of FDR progenies. This indicates that for this character SDR 2n-gametes are more desirable than FDR 2n-gametes, perhaps due to the additivity of the genes involved.

For a potato breeding programme, the positive effect of FDR 2n-gametes on yield is of more importance than the positive effect of SDR 2n-gametes on vine maturity. Consequently, FDR 2n-gametes are the preferred type of 2n-gametes for recovery of the tetraploid level in the final step of a potato breeding programme via the diploid level.

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