

G. C. C. Tai · H. De Jong

A comparison of performance of tetraploid progenies produced by diploid and their vegetatively doubled (tetraploid) counterpart parents

Received: 24 April 1996 / Accepted: 26 July 1996

Abstract Two diploid potato parents, W5295.7 and W5337.3, and their colchicine-doubled tetraploids were used as male to cross with three cultivars: 'Raritan', 'Shepody' and 'Superior'. Both diploids produced $2n$ gametes via first division restitution (FDR) during meiosis. Field experiments were carried out on seedlings of the 12 hybrid progenies in 1991 and 1992. Six of the progenies represented the tetraploid-diploid ($4x-2x$) hybrids and the other six tetraploid-tetraploid ($4x-4x$) progenies. The genetic consequence of FDR gametes was examined by comparing the mean and genotypic variance of six tuber traits of $4x-2x$ and $4x-4x$ progenies. Tuber appearance, eye depth, specific gravity and tuber size showed significant differences between the means of $4x-2x$ and $4x-4x$ progenies from either both or one of the diploid parents. The genotypic variances of these traits in $4x-2x$ progenies were reduced in various degrees from those observed in $4x-4x$ progenies. Major genes responsible for the inheritance of these traits are probably located close to the centromere. The two diploid parents may also carry alleles of different size and direction of non-additive genic effects in their $2n$ gametes. The $4x-2x$ progenies also outperformed the $4x-4x$ progenies with respect to the means of total and marketable yield. There were thus heterotic gene loci for high yield located close to the centromere. No marked reduction of genotypic variance, however, was observed. The results suggest that genes for yield would be scattered between the centromere and the site for maximum recombination.

Key words Potato genetics · Tetraploid-diploid hybrids · $2n$ gametes · Heterosis

Introduction

The induction of haploids from the tetraploid ($2n = 4x = 48$) cultivated species *Solanum tuberosum* L. through a parthenogenetic process (Peloquin et al. 1989, 1996) and the subsequent discovery of the formation of $2n$ gametes in the haploid \times diploid species hybrids (see Hermsen 1984; Peloquin et al. 1989; Tai 1994) represent a major advancement in potato genetics and breeding. Many studies compare the genetical consequences and breeding value of $2n$ gametes formed by the first (FDR) and second (SDR) division restitution mechanisms during meiosis (Boudec et al. 1989; Haynes 1990, 1992; David et al. 1995; Ortiz and Peloquin 1994; Tai 1994). Verification of the theoretical expectations requires experimental materials produced by complex mating designs. Hutten et al. (1994) compared the performance of six agronomic traits of FDR and SDR progenies from 12 sets of reciprocal $4x-2x$ crosses. FDR progenies had higher mean yields due to more and bigger tubers and higher underwater weight than those of SDR progenies. No differences were found for vine maturity and chip color. The within-progeny variation of vine maturity of SDR progenies was found to be higher than that of FDR progenies, whereas those for yield, underwater weight and chip color were not different in FDR and SDR progenies. Recently, Barone et al. (1995) have verified that the heterozygosity of restriction fragment length polymorphism (RFLP) markers transmitted via FDR gametes is more than twice that of SDR gametes. The aim of the study presented here was to compare hybrid progenies produced by mating two $2x$ parents and their vegetatively doubled counterparts with another group of three $4x$ parents. The hybrid population does not meet the requirement of an ideal mating design for the genetical analysis of $2n$ gametes. The results do, however, provide some answers on the expected genetical consequences of $2n$ gametes produced by the FDR mechanism.

Communicated by G. Wenzel

G. C. C. Tai (✉) · H. De Jong
Potato Research Centre, Agriculture and Agri-Food Canada,
P.O. Box 20280, Fredericton, N.B., Canada, E3B 4Z7

Theory

Assuming a diploid (2x) parent which produces unreduced gametes by the first division restitution (FDR) mechanism, a heterozygous locus Aa produces 2n gametes of genotypes AA, Aa and aa of frequencies

$$AA:Aa:aa = \beta/4:(2-\beta)/2: \beta/4$$

where β is the frequency of single-exchange tetrads (Mendiburu and Peloquin 1979; Tai 1982). The vegetatively doubled counterpart of such a diploid parent is the duplex AAaa. It produces three types of gametes at frequencies of

$$AA:Aa:aa = (1 + 2\alpha)/6:(2 - 2\alpha)/3:(1 + 2\alpha)/6$$

where α is the coefficient of double reduction. β has a range of $\beta = 0$ to $\beta = 1$, whereas α ranges from $\alpha = 0$ to $\alpha = 1/6$ (Tai 1989b). A locus located close to the centromere has $\beta \approx 0$ and $\alpha \approx 0$. Clearly, the diploid has an excess of heterozygous gametes over the duplex tetraploid in this situation.

Another tetraploid (4x) parent of unknown genotype is used as female to cross with the 2x and 4x parents to produce two types of crosses, 4x-2x and 4x-4x crosses. The above relationship between gametes would yield the following expected results when the performance of 4x progenies from 4x-2x and 4x-4x crosses is compared:

(1) Means of a quantitative trait of 4x-2x and 4x-4x progenies are equal to each other when the genic effect is additive in nature.

(2) For dominance effect, i.e. $Aa > (AA + aa)/2$ (or $Aa < (AA + aa)/2$), the mean of the 4x-2x progenies is expected to be greater (or smaller) than that of the 4x-4x progenies when the locus is close to the centromere ($\alpha \approx 0$ and $\beta \approx 0$). This difference is slowly diminished when the locus concerned is located increasingly further away from the centromere. The reverse trend between 4x-4x and 4x-2x progenies is expected only when the distance between the locus and centromere is close to the theoretical maximum, i.e. $\beta \approx 1$ and $\alpha \approx 1/6$.

(3) The variance among progenies is expected to be reduced for the 4x-2x cross when compared to that of 4x-4x cross when the locus concerned is located close to the centromere. This is the result of the higher concentration of Aa gametes in 4x-2x progenies. Again, the difference gradually decreases as the distance between the concerned locus and the centromere increases. This variance-reduction effect is expected regardless of whether the genic effect is additive or dominant. A large reduction effect is expected when the AA, Aa and aa gametes show large differences between their effects.

The unknown genotype of the other 4x parent would undoubtedly influence the size of the differences in the

mean and variance between 4x-2x and 4x-4x progenies. However, the trend would be maintained.

Materials and methods

Two 2x parents, W5295.7 and W5337.3, kindly provided by Dr. S.J. Peloquin of the University of Wisconsin, were used in this study. Both produce 2n gametes via the FDR mechanism (Mok and Peloquin 1975). Colchicine-doubled tetraploids W5295.7 (4x) and W5337.3 (4x) were developed using the method described by Ross et al. (1967) and used as corresponding 4x parents. These four parents were used as males to cross with three *S. tuberosum* cultivars: 'Raritan', 'Shepody' and 'Superior'. True seed of the 12 progenies were sown in 1989 in the greenhouse. One greenhouse-grown tuber per genotype was used to plant the first field generation. Single-hill plots were used to grow the seed in field. Tubers of 30 randomly selected genotypes of each of the progenies were harvested in 1990 and used as seed for a field experiment in 1991. Tubers harvested from the seedlings in the 1991 experiment were again used as seed for the field experiment in 1992.

The experiments were carried out in 1991 and 1992 at the Agriculture and Agri-Food Canada Benton Ridge Potato Breeding Substation in New Brunswick, Canada. The field plots were divided into three blocks, and each block was used to grow 10 genotypes of each of the 12 progenies. Plots of the same progeny were grouped together in a block. The three female parents were grown in a single plot in each of the three blocks. The male parents W5295.7 and W5295.7(4x) were also grown in a single plot in each of the three blocks. Tubers of W5337.3 and W5337.3(4x) were not available in sufficiently large quantities, and thus these two parents were not used in the field experiments. Each plot contained five hills. The spacing between adjacent hills in a plot was 25 cm and that between adjacent plots was 90 cm. The 1991 experiment was planted on May 26 and harvested on September 27. The 1992 experiment was planted on May 22 and harvested on September 14.

The following traits were recorded and used in the present study: (1) tuber appearance, scale 1 (poor) to 3 (good); (2) eye depth, scale 1 (shallow) to 3 (deep); (3) tuber size, scale 1 (small) to 3 (large); (4) marketable yield: weight of tubers ≥ 56 cm in kilograms per plot; (5) total yield: yield of all tubers in kilograms per plot; and (6) specific gravity as determined by the weight-in-air and weight-in-water method and converted into (specific gravity - 1) * 1000 for statistical analysis.

The focus of this study is a comparison between the performance of progenies of the corresponding 2x and 4x male parents. Data on 4x-2x and 4x-4x progenies of W5295.7 and those of W5337.3 were treated as two hybrid populations and analyzed separately. Two statistical analyses were conducted for each of the two hybrid populations. The analysis of variance was done for each of the quantitative traits to compare the effects due to years (1991 and 1992), female parents ('Raritan', 'Shepody' and 'Superior') and ploidy levels (4x and 2x) of the male parent, and interactions between the three sources of variation. This analysis was specifically aimed at detecting differences between means of the two ploidy levels of the male parents.

The second analysis is a comparison between the genotypic variances of corresponding 4x-4x and 4x-2x progenies. Data of 4x-4x crosses and 4x-2x crosses in a hybrid population were separately analyzed. The analysis of variance was carried out with the following sources of variation: years, seedlings and year * seedling interactions. This analysis pooled together the data of three female parents and was aimed at estimating the genotypic variance due to a specific ploidy level. The genotypic variance due to a ploidy level (4x or 2x) of a male parent (W5295.7 or W5337.3) was estimated by (mean square for seedlings - mean square for seedling * year interactions)/2. A 90% confidence interval for the genotypic variance was established based on the method of Tai (1989a).

Table 1 Analyses of variance of six traits of progenies of the male parents W5295.7 and W5337.3

Source	Degrees of freedom	Appearance	Eye depth	Tuber size	Marketable yield	Total yield	Specific gravity
W5295.7							
Year (Y)	1	0.039	0.122	1.154**	108.63**	146.86**	747.30**
Female pnt (F)	2	0.224*	0.744**	0.291**	17.96**	15.98**	695.53**
Ploidy (P)	1	0.415*	2.303**	0.102	26.21**	25.55**	549.35**
Y * F	2	0.123	0.097	0.006	1.26	1.43	197.90
Y * P	1	0.001	0.041	0.018	0.18	0.11	25.82
F * P	2	0.454**	0.573**	0.027	3.48	3.77	53.35
Y * F * P	2	0.068	0.023	0.010	0.33	0.78	22.09
Residual	344	0.069	0.048	0.027	1.91	1.85	76.32
W5337.3							
Year	1	0.176	1.225**	0.379**	33.49**	70.27**	15131.60**
Female pnt (F)	2	1.092**	0.476**	0.371**	2.38	1.30	375.89**
Ploidy (P)	1	1.063**	0.314**	0.082	10.22*	2.54	62.71
Y * F	2	0.149	0.013	0.118	4.19	3.05	111.36
Y * P	1	0.100	0.020	0.010	0.00	0.35	60.94
F * P	2	0.006	0.036	0.028	0.32	0.81	53.75
Y * F * P	2	0.012	0.016	0.018	1.14	0.76	116.86
Residual	346	0.084	0.027	0.032	1.97	1.84	73.03

***Significant at $P = 0.05$ and 0.01 levels, respectively

Table 2 Means of six traits of 4x-2x and 4x-4x progenies of the male parents W5295.7 and W5337.3 pooled over the three female parents, together with means of the three female parents and the male parents W5295.7 (2x) and W5295.7 (4x)

	Progeny		Female parents	Male parent	
	4x-2x	4x-4x		2x	4x
W5295.7					
Appearance	2.35 ± 0.28	2.42 ± 0.25	2.61 ± 0.15	2.08 ± 0.29	2.23 ± 0.15
Eye depth	2.30 ± 0.17	2.13 ± 0.29	1.89 ± 0.20	2.40 ± 0.13	2.43 ± 0.10
Tuber size	2.07 ± 0.18	2.04 ± 0.17	2.07 ± 0.07	1.68 ± 0.15	1.87 ± 0.10
Marketable yield	4.44 ± 1.52	3.90 ± 1.51	4.15 ± 1.10	1.30 ± 0.71	1.92 ± 0.44
Total yield	5.75 ± 1.49	5.22 ± 1.57	4.79 ± 1.10	3.41 ± 0.60	3.39 ± 0.55
Specific gravity	91.7 ± 10.1	87.4 ± 11.4	96.9 ± 10.1	90.2 ± 5.2	87.7 ± 3.6
W5337.3					
Appearance	2.37 ± 0.28	2.26 ± 0.31	2.61 ± 0.15	–	–
Eye depth	2.20 ± 0.19	2.26 ± 0.17	1.89 ± 0.20	–	–
Tuber size	2.10 ± 0.17	2.07 ± 0.20	2.07 ± 0.07	–	–
Marketable yield	4.46 ± 1.44	4.13 ± 1.43	4.15 ± 1.10	–	–
Total yield	5.80 ± 1.51	5.63 ± 1.32	4.79 ± 1.10	–	–
Specific gravity	82.7 ± 11.0	81.9 ± 12.1	96.9 ± 10.1	–	–

Results

Analyses of variance were carried out for progenies of W5295.7 and W5337.3 (Table 1). Highly significant differences between years were observed for tuber size, marketable and total yield and specific gravity for both hybrid progenies and for eye depth for progenies of W5337.3. A significant difference for tuber appearance and highly significant differences for the other five traits were observed among the female parents ('Raritan', 'Shepody' and 'Superior') of the W5295.7 progenies. Appearance, eye depth, tuber size and specific gravity were highly significantly different among the female parents of the W5337.3 progenies. The difference between the two ploidy (4x vs. 2x) levels was highly significant for eye depth, yield (both total and market-

able), and specific gravity, and was significant for tuber appearance for the W5295.7 progenies. The ploidy levels showed a highly significant difference for tuber appearance and eye depth and a significant difference for marketable yield of the W5337.3 progenies. Tuber size of both progenies and total yield and specific gravity of the W5337.3 progenies showed no significant differences with respect to ploidy levels. The only interaction effects observed were between female parents and ploidy levels for tuber appearance and eye depth of the W5295.7 progenies.

Means of the six traits of the 4x-2x and 4x-4x progenies of the W5295.7 and W5337.3 progenies are presented in Table 2 with those of the parents. The 4x-2x progenies had a lower tuber-appearance and higher eye-depth scores than the 4x-4x progenies in the W5295.7 progenies. The reverse was true when the

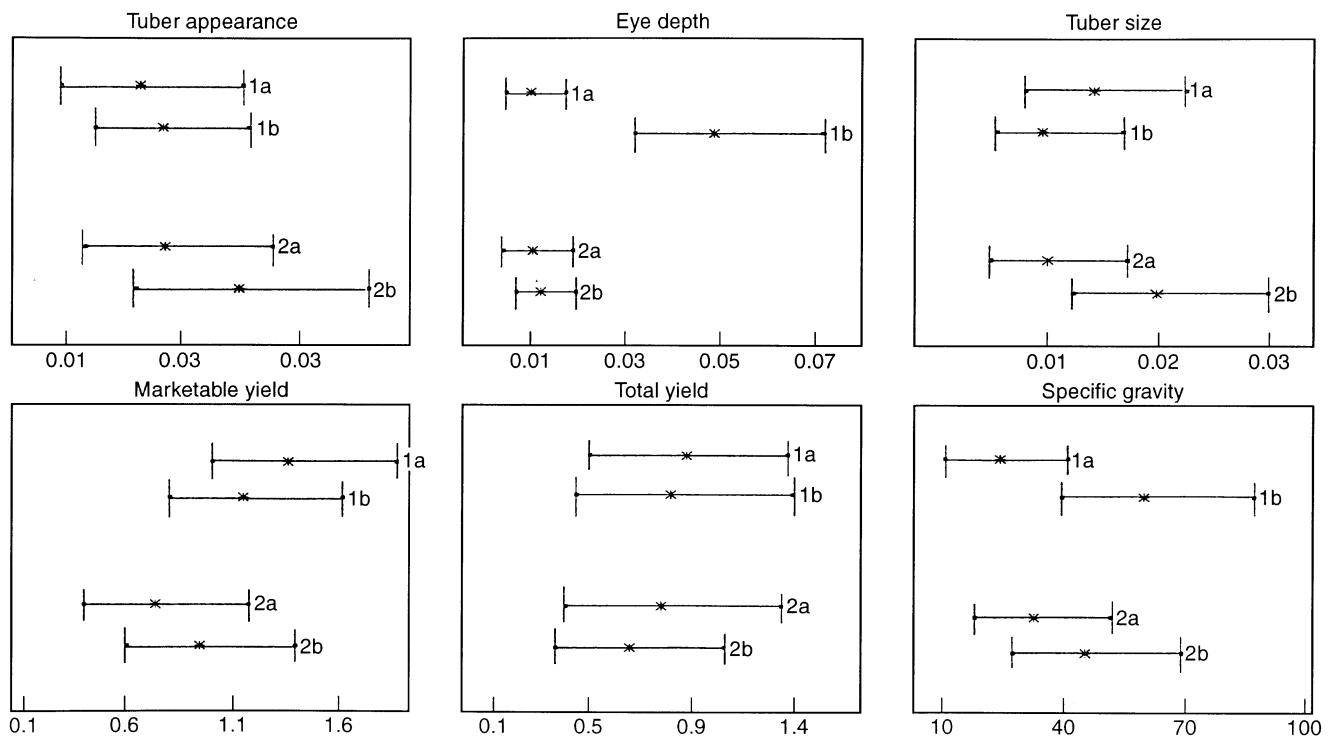
4x-2x and 4x-4x progenies of the W5337.3 progenies were compared, and both had a lower tuber-appearance score and deeper eyes than the means of their female parents. The tuber-appearance score of W5295.7 (4x) was higher than that of W5295.7 (2x), but both scores were lower than that of their progenies. Also, both had the deepest eyes. No difference was observed for tuber size between the means of the 4x-2x and 4x-4x progenies, and all four populations had means close to that of the female parents. All of them had much larger tubers than the two W5295.7 (2x and 4x) parents.

All 4x-2x progenies had a higher total and marketable yield than the corresponding 4x-4x progenies and the parents. The difference between ploidy levels was, however, not significant for total yield of the W5337.3 progenies. While the total yield of all 4x-4x progenies was higher than that of the female parents, their marketable yields were lower but close to those of the female parents. W5295.7 (4x) had higher yields than W5295.7 (2x), and both showed a much lower yielding ability than the hybrid progenies and female parents. The total and marketable yields of the 4x-2x progenies of the two hybrid progenies were 20% and 7% above those of their female parents, respectively. The 4x-2x progenies of W5295.7 had significantly higher mean total and marketable yields than those of their respective 4x-4x progenies.

The specific gravity of the 4x-2x progenies was higher than that of the 4x-4x progenies in the W5295.7 progenies. W5337.3 progenies showed a similar specific gravity for the two ploidy levels. All the hybrids had means lower than those of their female parents. W5295.7(2x) also had a higher specific gravity than W5295.7 (4x).

Four sets of data were formulated from the original data-base. Each represented a set of 4x-2x or 4x-4x progenies derived from the male parents W5295.7 or W5337.3 and pooled over the three female parents. They were subjected to four separate analyses of variance to compare seedlings in each of the four hybrid progenies. Highly significant differences among seedlings were observed for all six traits in all four hybrid progenies. The variance component due to seedlings (i.e. genotypes) was estimated together with the 90% confidence interval (Tai 1989a) for each of the four populations. The sizes of the estimates of variance components were compared between ploidy levels of the same male parent (i.e. W5295.7 or W5337.3). The results are shown in Fig. 1. Out of 12 comparisons, the progenies of the 4x parents showed larger variability than those of the 2x parents in eight cases. The confidence intervals for eye depth and specific gravity for W5295.7 were not overlapping with each other indicating magnitudes that were highly significantly different. The confidence intervals for tuber appearance, tuber size, marketable yield and specific gravity of W5337.3 were partially overlapping with those from the 4x parents, but they covered a range of lower readings than the corresponding ones from the 4x parents (Fig. 1). The intervals of tuber appearance of W5295.7 progenies

Fig. 1 Estimates and 90% confidence intervals of genotypic variances of six traits for corresponding 4x-2x and 4x-4x progenies derived from the male parents W5295.7 and W5337.3. 1 Progenies from W5295.7, 2 progenies from W5337.3, a 4x-2x progenies, b 4x-4x progenies



and eye depth of W5337.3 progenies were largely overlapping with each other. The 4x-2x progenies had higher estimates of the variance component than those of corresponding 4x-4x progenies in tuber size, marketable and total yields in the W5295.7 progenies and total yield in the W5337.3 progenies. The confidence intervals of all comparisons, however, showed much overlapping.

Discussion

Diploid and vegetatively doubled clones of *S. phureja* × haploid *S. tuberosum* hybrids have been compared for their performance by Rowe (1967) and Maris (1990). The 4x families tend to have taller plants, later maturity, fewer tubers and higher mean tuber weight. The value of intense selection at the 2x level, followed by vegetative doubling of the best clones, and the use of *S. tuberosum* haploids in potato breeding were questioned. The value of unreduced 2n gametes from haploid - diploid species hybrids in 4x-2x and 2x-2x crosses, on the other hand, has been confirmed in many genetical and breeding studies (see Ortiz and Peloquin 1994; Tai 1994).

The genetical consequences of 2n gametes produced via FDR and SDR mechanisms are discussed by Peloquin et al. (1989), Hermsen (1984), Veilleux (1985), Boudec et al (1989), Haynes (1990, 1992), Tai (1989b, 1994), Ortiz and Peloquin (1994) and David et al. (1995). Barone et al. (1995) have verified the expected differences between FDR and SDR gametes by comparing frequencies of heterozygous restriction fragment length polymorphism (RFLP) markers in 4x progenies from bilateral sexual polyploidization in a cross between two 2x interspecific hybrids. Experimental verification of the theoretical expectations is hard to achieve with regard to quantitative traits as a complicated mating design is required (e.g. Tai 1989b, 1994; David et al. 1995). The present study represents an attempt to verify the theoretical difference of sizes of means and variances between 4x-2x and 4x-4x hybrids. The experimental data are not able to provide estimates of various genetic parameters in association with tetrasomic inheritance as described in the theoretical papers.

The results of the comparison of means and variances of 4x-2x and 4x-4x progenies generally verify the theoretical expectation of 2n gametes formed by the FDR mechanism. W5337.3 produced 4x-2x progenies with better mean tuber appearance and shallower mean depth of eye than those from 4x-4x progenies. The opposite was true for these two traits when 4x-2x and 4x-4x progenies from W5295.7 were compared. The 4x-2x progenies of W5295.7 had a higher mean specific gravity than that of the 4x-4x progenies, whereas no difference was found between the means of the 4x-2x

and 4x-4x progenies obtained from W5337.3. The variances observed in the 4x-2x progenies of W5295.7 were much reduced for eye depth and specific gravity when compared to those of corresponding 4x-4x progenies. To a lesser extent, the variances of the 4x-2x progenies of W5337.3 were smaller than those of the 4x-4x progenies for tuber appearance and tuber size. The results would support the hypothesis that gene(s) responsible for the inheritance for these traits are probably located close to the centromere. The two male parents may also carry alleles of different size and direction of non-additive genic effects in their 2n gametes. Hutten et al. (1994) found that the underwater weight of FDR progenies was higher than that of SDR progenies. They did not, however, detect difference of within-progeny variations between them.

The yield traits of 4x-2x progenies showed heterotic effects on mean values when compared with the performances of their female parents. The 4x-2x progenies also outperformed corresponding 4x-4x progenies. All the evidence supports the hypothesis of superior FDR gametes. They did not show, however, a marked reduction of genotypic variances from corresponding 4x-4x progenies. Hutten et al. (1994) reported similar results for yield. This suggests that the inheritance of yielding ability would be more complex than that of the other traits studied. Tai (1994) compared the frequencies of homozygous and heterozygous 2n gametes between balanced diallelic (i.e. duplex) 4x- and diallelic 2x-FDR parents. The FDR parent maintains a higher frequency of heterozygous gametes until the distance between the gene and centromere is fairly close to the maximum recombination rate (i.e. 50%). It is likely that genes for yield are scattered between the centromere and the site with $(\alpha, \beta) = (1/6, 1)$. Some highly heterotic loci are located close to the centromere. This situation would produce 4x-2x progenies with a higher mean but closer variance when compared with those of 4x-4x progenies.

The *tuberosum* parents used in the present are superior cultivars. The allelic structure within each of the loci for yield in these cultivars is unknown but expected to be highly heterozygous due to selection pressure for good performance. This would contribute to the complex genetical behavior for the yield that observed in the 4x-2x and 4x-4x progenies.

Acknowledgements The authors thank Dr. S. J. Peloquin, University of Wisconsin, for the generous provision of clones W5295.7 and W5337.3. The technical assistance of R. Brown, V. J. Burns and S. Oborn is much appreciated. The excellent field work by the staff of the Benton Ridge Potato Breeding Substation and other members of the potato breeding team is gratefully acknowledged.

References

- Barone A, Gebhardt C, Frusciant L (1995) Heterozygosity in 2n gametes of potato evaluated by RFLP markers. *Theor Appl Genet* 91:98-104

- Boudec P, Masson M, Dattee Y (1989) A quantitative genetics model for the estimation of variances, covariances between relatives in crosses using 2n gametes, in potatoes. In: Louwes KM, Toussaint HAJM, and Dellaert LMW (eds) Parental line breeding and selection in potato breeding. Centre for Agricultural Publishing and Documentation, PUDOC, Wageningen, The Netherlands, pp 43–48
- David JL, Boudec P, Gallais A (1995) Quantitative genetics of 4x-2x hybrid populations with first-division restitution and second-division restitution 2n gametes produced by diploid parents. *Genetics* 139:1797–1803
- Haynes KG (1990) Covariances between diploid parent and tetraploid offspring in tetraploid × haploid-species hybrid in 4x-2x crosses of *Solanum tuberosum* L. *J Hered* 81:208–210
- Haynes KG (1992) Covariance between haploid-species hybrid and *tuberosum* × haploid-species hybrid in 4x-2x crosses of *Solanum tuberosum* L. *J Hered.* 83:119–122
- Hermesen JG Th (1984) Mechanisms and genetic implications of 2n-gamete formation. *Iowa State J Res* 58:421–434
- Hutten RCB, Schippers MGM, Hermesen JG Th, Ramanna MS (1994) Comparative performance of FDR and SDR progenies from reciprocal 4x-2x crosses in potato. *Theor Appl Genet* 89:545–550
- Maris B (1990) Comparison of diploid and tetraploid potato families derived from *Solanum phurea* × dihaploid *S. tuberosum* hybrids and their vegetatively doubled counterparts. *Euphytica* 46:15–33
- Mendiburu AO, Peloquin SJ (1979) Gene-centromere mapping by 4x-2x matings in potatoes. *Theor Appl Genet* 54:177–180
- Mok DWS, Peloquin SJ (1975) Three mechanisms of 2n pollen formation in diploid potatoes. *Can J Genet Cytol* 17:217–225
- Ortiz R, Peloquin SJ (1994) Use of 24-chromosome potatoes. In: Bradshaw JE, Mackay GR (eds) *Potato genetics*. CAB Int, Wallingford, UK, pp 133–154
- Peloquin SJ, Yerk GL, Werner JE, Darro E (1989) Potato breeding with haploids and 2n gametes. *Genome* 31:1000–1004
- Peloquin SJ, Gabert AC, Ortiz R (1996) Nature of ‘pollinator’ effect in potato (*Solanum tuberosum* L.) haploid production. *Ann Bot* 77:539–542
- Ross RW, Dionne R, Hougas RW (1967) Doubling the chromosome number of selected *Solanum* genotypes. *Eur Potato J* 10:37–52
- Rowe PR (1967) Performance of diploid and vegetatively doubled clones of Phureja-haploid *Tuberosum* hybrids. *Am Potato J* 44:195–203
- Tai GCC (1982) Estimation of double reduction and genetic parameters of autotetraploids *Heredity* 49:63–70
- Tai GCC (1989a) A new procedure to construct confidence intervals for genotypic variance and expected response to selection. *Genome* 32:307–308
- Tai GCC (1989b) Biometrical methods in investigating 2n gametes in tetraploid-diploid and diploid-diploid crosses. In: Louwes KM, Toussaint HAJM, Dellaert LMW (eds) *Parental line breeding and selection in potato breeding*. Centre for Agricultural Publishing and Documentation, PUDOC, Wageningen, The Netherlands, pp 15–21
- Tai GCC (1994) Use of 2n gametes. In: Bradshaw JE, Mackay GR (eds) *Potato genetics*. CAB Int, Wallingford, UK, pp 109–132
- Veilleux RE (1985) Diploid and polyploid gametes in crop plants: mechanisms of formation and utilization in plant breeding. *Plant Breed Rev* 3:253–288