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Producing commercially attractive, uniform true potato seed progenies: the influence of breeding scheme and parental genotype

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Abstract The production of attractive, uniform true potato seed (TPS) progenies was investigated. Four breeding schemes were compared: intercrossing tetraploid cultivars (cv × cv); doubled dihaploids × cultivars (ddh × cv); cultivars × diploid unreduced-gamete producers (cv × FDR) and doubled dihaploids × diploid unreduced-gamete producers (ddh × FDR). Fifty three progenies and five clones were grown in a glasshouse in a randomised complete block design with three replicates of 25 plants per progeny and clone. Each plant's tubers were counted and the colour, shape, quality of skin finish, flesh colour, and commerical attractiveness (which includes yield) recorded. The most uniform progenies were also selected by visual comparison with the clones. For mean attractiveness, differences ($P < 0.001$) between breeding schemes and between progenies within breeding schemes were detected. The cv × cv and cv × FDR progenies were more attractive than clonal controls. There were significant additive and non-additive effects for attractiveness in all breeding schemes except cv × FDR. There were between-progeny differences ($P < 0.001$) for uniformity for all characters. Progenies uniform for one character could be variable for other traits. Breeding schemes gave different levels of uniformity ($P < 0.001$) for all characters except shape and flesh colour, but none gave low levels of variation for all traits. Doubled-dihaploid parents increased the variation in progenies. There were uniformity differences ($P < 0.001$) between progenies within breeding schemes for all characters. Evidence of additive and non-additive genetic variation for uniformity in all traits was detected. In each breeding scheme, parents with good general combining ability (GCA) for uniformity in several characters were identified. Visually selected uniform progenies had parents with good GCAs for uniformity in a range of traits and high specific combining abilities (SCAs) for several traits. A desynaptic first-division restitution (FDR) clone and a male-sterile doubled-dihaploid clone had the best GCAs for tuber uniformity in TPS progenies. Achieving multitrait uniformity in TPS is problematic but may be aided by the selection of parents with GCAs for uniformity coupled with progeny testing to allow for non-additive effects.

Key words True potato seed · Commerical attractiveness · Uniformity · General combining ability · Desynapsis

Introduction

True potato seed (TPS) is widely used to produce potatoes for human consumption in many countries (Anon 1983; Ross 1986). The use of TPS has a number of advantages over conventional clonal production (Anon 1983; Ross 1986; Clulow and Bradshaw 1994); however, the tuber crops produced from TPS can be very variable. This heterogeneity has limited the uptake of TPS in Europe.

The work of Atlin (1985) and Kidane-Mariam et al. (1985) indicated that inbred individuals were less fertile and less vigorous than those resulting from cross pollination; thus inbred lines may not be useful as TPS parents (Hermsen 1983). However, vigorous, slightly inbred tetraploid clones can be produced from potato dihaploids by somatic chromosome doubling during callus culture (Jacobsen 1978). Doubled dihaploids are more homozygous than their tetraploid parents (De Maine and Jervis 1989) and, although the genotypes produced to-date are male sterile, they have a high female fertility. These clones are potentially useful parents for the production of hydrid TPS.

Diploid clones that produce unreduced gametes by mechanisms akin to first-division restitution (FDR) and second-division restitution (SDR) have been used to

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produce TPS by interploidy (4x-2x) crosses. Progenies produced from FDR gametes exhibit high levels of heterosis, with higher yields and greater uniformity than those derived from SDR gametes (Mok and Peloquin 1975; Peloquin et al. 1989). Researchers have reported that progenies from 4x-2x FDR crosses were more vigorous, higher yielding, and more uniform in a range of environments than open pollinated and 4x-4x hybrid progenies (Mascaso-Khwaja and Peloquin 1983; Kidane-Mariam et al. 1985; Concilio and Peloquin 1987; Buso and Peloquin 1988; Peloquin et al. 1989). The superior breeding value of FDR gametes has been attributed to their ability to transfer intact 80% of the diploid genome to the tetraploid progeny, thereby transferring a large amount of the intra- and inter-locus interactions from parent to offspring (Mok and Peloquin 1975; Peloquin et al. 1989). While being highly heterozygous, FDR gametes are also highly homogeneous, therefore they may confer a high degree of uniformity to TPS progenies (Mok and Peloquin 1975; Peloquin 1979; Iwanaga 1984; Peloquin et al. 1989). Desynapsis genes reduce chiasma frequencies and minimise genetic reassortment during meiosis (Jongedijk and Ramanna 1989; Jongedijk et al. 1991); thus combining desynapsis and FDR gamete production may further increase the uniformity of TPS progenies from 4x-2x crosses.

This study investigates whether cross combinations of tetraploid cultivars, doubled dihaploids, and synaptic and desynaptic-FDR gamete producers can produce commercially attractive TPS progenies where uniformity approaches that of clonally reproduced cultivars. Previous investigations of uniformity in TPS progenies have presented data for phenotypic variation in single traits (Peloquin 1979; Jakubiec 1987; Peloquin et al. 1989) or traits grouped together in a general uniformity index (Thompson 1982; Kidane-Mariam et al. 1985; Rowell et al. 1986; Concilio and Peloquin 1987). In the present study the level of variation in six important tuber characteristics is described. The experimental work was conducted in a glasshouse; previous studies indicate that there is a good relationship between glasshouse and field data (Brown et al. 1987, 1988; Clulow and Bradshaw 1994; Clulow et al. submitted).

Materials and methods

In 1990 and 1991 a total of 53 TPS progenies were produced in a glasshouse by cross-fertilization. Four types of crosses were made: (1) five tetraploid cultivars were intercrossed in a half diallel and selfed (cv × cv); (2) four doubled dihaploids were pollinated with five cultivars (ddh × cv); (3) three cultivars were pollinated with three diploid FDR clones (cv × FDR); and (4) three doubled dihaploids were pollinated with three diploid FDR clones (ddh × FDR). The same parental genotypes were used throughout, although not all of the parents were used in each group of crosses. The doubled dihaploids were produced from the cv Pentland Crown (ddh1) and the breeding clones 8318-4 (ddh 2), 8318-6 (ddh 3) and HAT 35-7 (ddh 4). The diploid FDR clones were derived from *Solanum phureja* material and were selected for unreduced-gamete production and commercially attractive tubers (De Maine, personal communication). The berries were stored and the seed extracted as described by Clulow and Bradshaw (1994).

In 1992, a glasshouse experiment was conducted to investigate the degree of variation in the TPS progenies. This experiment was arranged as a randomised complete block design with three replicates. Each replicate was grown on a separate bench in a glasshouse. In each replicate there was one plot of 25 plants of each of the 53 TPS progenies and each of the five cultivar controls (cvs Cara, Desiree, Katahdin, Maris Piper and Pentland Ivory). Seeds were sown in pans of compost (Fisons Levington) on a mist bench in the glasshouse. Three weeks after germination the seedlings were transplanted to pots of compost. To provide control material that was physiologically similar to the true-seed-derived plants, micropropagated plantlets of five cultivars were prepared as described by Clulow and Bradshaw (1994) and transplanted into pots of compost in the glasshouse on the same day as the seedlings. Seedlings and plantlets were grown in 12.5-cm-square pots of compost, one plant per pot.

The tubers produced by each plant were assessed for six traits. The tubers were counted and tuber colour was recorded on a 1–3 scale where 1 = white, 2 = red, 3 = partly coloured white/red. Tuber shape was recorded on a 1–3 scale where 1 = round, 2 = oval, 3 = long oval. The quality of the skin finish was recorded on a 1–9 scale. Tubers that had growth cracks and cracked, split or rough skins were given low scores. The commerical attractiveness (which includes yield) of the tubers, termed breeder's preference, was recorded on a 1–9 scale of increasing attractiveness. The tubers were cut longitudinally and the tuber flesh colour was recorded as a discrete variable on a 1–4 scale where 1 = white, 2 = cream, 3 = partly coloured white/red, 4 = partly coloured cream/red. The most uniform progenies were visually selected by comparison with the tubers of the cultivars.

Analysis of variance of plot means and variances, with progenies and cultivars as fixed effects, was performed using Genstat V (Lawes Agricultural Trust). Spearman's rank correlations were calculated using the method of Daniel (1978). The diallel analysis used was experimental method 2 of Griffing (1956) for a diallel including the parents selfed and one set of F_1s, and model I in which the genotypes are assumed to be a fixed sample.

Pollen formation in the FDR clones was examined. Flower buds were removed from the plants and fixed in Carnoy's solution (3 ethanol:1 glacial acetic acid) for 24 h. Whole anthers were hydrolysed in 5 N HCl for 50–60 min at room temperature, stained in Schiffs reagent (Sigma) and squashed in 45% acetic acid or squashed directly in 2% aceto-orcein.

Results

A summary of the data is shown in Table 1. The mean breeder's preference score was used as a measure of the commercial attractiveness of each progeny and the progeny variances were used as a measure of uniformity.

As the variances were not expected to be normally distributed, the residuals from the analysis of variance were carefully inspected, and for tuber number variance a log transformation was made. Analysis of variance demonstrated that there were significant differences between the mean breeder's preference scores ($P < 0.001$) and between progeny/cultivar variances for all characters ($P < 0.001$). When the data for the cultivar controls were excluded and the analysis repeated, there were significant differences between TPS progenies for mean breeder's preference scores ($P < 0.001$) and for the variances for all six characters ($P < 0.001$).

Commercial attractiveness of progenies

Progenies were grouped according to the breeding scheme from which they were derived (cv × cv, ddh × cv,

Table 1 Data summary for cultivar controls and TPS progenies: breeder's preference means and mean ranges; mean variance and variance ranges for six tuber characteristics

Item	Cultivar controls		TPS progenies	
	Mean	Range	Mean	Range
Mean breeder's preference	4.94	4.05–5.36	5.13	4.11–6.18
Tuber number variance[a]	3.00	1.35–4.97	5.82	1.73–15.30
Tuber colour variance	0.06	0.00–0.20	0.56	0.00–1.39
Tuber shape variance	0.10	0.03–0.15	0.16	0.05–0.29
Tuber skin finish variance	0.31	0.17–0.47	0.46	0.13–1.95
Tuber flesh colour variance	0.47	0.08–0.38	0.48	0.07–2.14
Breeder's preference variance	1.18	0.46–2.02	0.83	0.30–1.96

[a] Untransformed data

cv × FDR, ddh × FDR) and the clonal controls placed in a fifth group. The data were analysed to identify any inter- and intra-group differences for mean breeder's preference score. There were significant differences between breeding schemes ($P < 0.001$) and between progenies within breeding schemes ($P < 0.001$). The cv × FDR and cv × cv crosses gave progenies that were significantly more attractive than the clonal controls (overall attractiveness: cv × FDR = 5.645, SE = 0.0587; cv × cv = 5.419, SE = 0.0454; clones = 4.943; SE = 0.0787). The other groups were not significantly different from the clonal controls.

The within-group general and specific combining abilities for commercial attractiveness were investigated (Table 2). Although there were differences in general combining ability (GCA) between the parents of the cv × cv crosses ($P < 0.001$), there were also significant differences in specific combining ability (SCA) ($P < 0.001$). In ddh × cv crosses there were significant differences in GCA between cultivars ($P < 0.001$) and between doubled dihaploids ($0.05 < P < 0.01$) and differences in SCA ($P < 0.001$). There were no detectable differences in GCA or SCA for commercial attractiveness in the cv × FDR crosses. In ddh × FDR crosses, differences ($P < 0.001$) in the GCA of the ddh parents and differences in SCA ($0.05 < P < 0.01$) were detected. The GCA of each parent was different in each breeding scheme; however, cv 4 (Maris Piper) had a large positive GCA for commercial attractiveness (cv × cv crosses: GCA = 0.310, SE = 0.0584; ddh × cv crosses: GCA = 0.596, SE = 0.0639).

Table 2 Commercial attractiveness of TPS progenies: mean squares from the analysis of parental combining abilities

Breeding scheme	Source	*df*	ms
cv × cv	GCA	4	0.932***
	SCA	10	0.421***
	Error	28	0.089
ddh × cv	cv GCA	4	1.468***
	ddh GCA	3	0.198*
	SCA	12	0.260***
	Error	34	0.049
cv × FDR	FDR GCA	2	0.117
	cv GCA	2	0.279
	SCA	4	0.024
	Error	16	0.119
ddh × FDR	FDR GCA	2	0.159
	ddh GCA	2	2.103***
	SCA	4	0.490*
	Error	14	0.113

* $P = 0.05–0.01$; *** $P < 0.001$

Uniformity of progenies

Inspection of the data summary shows that, for each trait, some TPS progenies were as uniform as the clonal controls (Table 1).

Rank correlations of progeny variances for different tuber traits

In order to determine whether progenies that were uniform for one character were uniform for other traits, the progeny variances were ranked and rank correlations calculated. The only statistically significant correlation was between flesh colour and skin finish, and the magnitude of this correlation was not high ($r_s = 0.42$). Therefore, in general, progenies that were relatively uniform for one character were variable for other traits.

The effect of the breeding scheme on uniformity

To determine whether the origin of the progenies influenced uniformity, they were grouped by breeding scheme (cv × cv, ddh × cv, cv × FDR, ddh × FDR) and the clones placed in a fifth group. There were differences ($P < 0.001$) between the groups for the level of variation in all characters, except tuber flesh colour ($P > 0.05$), and differences between progenies within breeding schemes for variation in all characters ($P < 0.001$). When the clonal control group was excluded from the analysis, there were differences between breeding schemes for the level of variation in each character ($P < 0.001$) except tuber shape and tuber flesh colour ($P > 0.05$). There were significant differences between progenies within breeding schemes for all characters ($P < 0.001$).

Table 3 Variances for six tuber characters for TPS progenies and cultivars grouped according to breeding scheme and clonal reproduction

Character	Breeding scheme					Residual MS
	cv × cv	ddh × cv	cv × FDR	ddh × FDR	Clones	
Tuber number[a]	0.666	0.787	0.550	0.607	0.421	0.045
Tuber colour	0.448	0.501	0.749	0.666	0.061	0.042
Tuber shape	0.178	0.160	0.165	0.147	0.098	0.004
Skin finish	0.281	0.735	0.350	0.276	0.310	0.045
Flesh colour[b]	0.481	0.464	0.553	0.467	0.471	0.093
Breeder's preference	0.826	0.966	0.687	0.658	1.176	0.198
r (replication)	45	60	27	27	15	

[a] log of variance

[b] No significant differences between groups in ANOVA

$SE = \left(\frac{\text{residual MS}}{r}\right)^{1/2}$

The overall variances for all traits for each breeding scheme are shown in Table 3. For tuber number, colour and shape, the clones were less variable than all TPS breeding schemes. The uniformity of tuber skin finish was similar to the clonal controls for all breeding schemes, except for ddh × cv crosses which were significantly more variable (Table 3).

General and specific combining abilities for uniformity

The general and specific combining abilities of the parents for tuber trait variances were investigated (Table 4). For cv × cv crosses there were significant differences between parental GCAs for variation in tuber number, colour, skin finish, flesh colour and breeder's preference. Cultivar 3 (Katahdin) had large negative GCAs for tuber number and tuber colour variance and moderate or small negative GCAs for variation in all other traits. Cultivar 4 (Maris Piper) had large negative GCAs for tuber colour and flesh colour variances and a small negative GCA for skin finish variance. Within the cv × cv crosses there was evidence of SCA for variation in tuber colour and breeder's preference (Table 4).

In ddh × cv crosses there were differences in GCA between cultivars for variation in all traits, except tuber shape and breeder's preference, and between doubled haploids for all traits except tuber number (Table 4). The only parent that had negative GCA values for all traits where significant differences were detected was ddh 4 (the doubled dihaploid PDH727x2). Although negative, the GCA effects for this parent were small (Table 4). Significant SCA effects were detected for all character variances except for tuber number and breeder's preference (Table 4).

For cv × FDR crosses there were significant differences between cultivar GCAs for tuber colour, shape, skin finish and flesh colour variances (Table 4). Differences between the GCAs of the FDR parents for tuber colour, shape and flesh colour variation were also detected. Where significant GCA effects were detected, only one parent, FDR3 (the clone M6), had negative GCAs for all traits. Differences in SCA for tuber colour and flesh colour variances were detected in the cv × FDR crosses (Table 4).

In the ddh × FDR crosses there were significant differences between ddh parental GCAs for variation in tuber number and flesh colour (Table 4). Significant GCA effects were detected for FDR parents for all traits except tuber number and shape. Only one parent (FDR 3) had negative GCAs for all of the traits where significant differences were detected. There were differences in SCA in the ddh × FDR crosses for tuber number, colour and flesh colour (Table 4).

Visual selection of progeny

Nine progenies visually selected for uniformity, or selected on paper for low variances over a range of traits, had cv 3, cv 4, ddh 4 or FDR3 as one or both parents (Table 5), and high SCAs for several tuber traits.

Pollen formation in FDR clones

All stages of meiosis and sporad formation were studied. Examination of metaphase-1 configurations in pollen mother cells (PMCs) revealed that the clone FDR3 displayed a high degree of desynapsis, whereas clones FDR1 and FDR2 exhibited normal synapsis. During metaphase-II, PMCs either underwent normal meiotic division (two metaphase plates and two sets of spindle fibres) or underwent a restitution division (one metaphase plate and one set of spindle fibres). In the genotypes studied, between 47 and 65% of PMCs had fused metaphase-plates. High frequencies of dyads (57 to 79%) were observed at the sporad stage in all clones. The relative contribution of FDR gametes to the pool of 2n pollen in the FDR parental clones was 60.1%, FDR1; 89.9%, FDR2; and 91.2%, FDR3.

Discussion

The cv × cv and cv × FDR crosses produced TPS progenies that were more commercially attractive than clonally reproduced cultivars and progenies from

Table 4 Mean squares from the analysis of parental combining abilities, and estimates of parental general combining ability effects for TPS progeny variances for six tuber traits

Source	*df*	Parent	Tuber number[a]	Tuber colour	Tuber shape	Skin finish	Flesh colour	Breeder's preference
cv × cv								
GCA	4		0.2594***	1.298***	0.010ns	0.066*	1.849***	0.343**
SCA	10		0.0366ns	0.123**	0.007ns	0.015ns	0.107ns	0.611***
Error	28		0.0351	0.027	0.005	0.024	0.118	0.074
		cv1	0.076	0.431	−0.005	−0.059	−0.162	0.086
		cv2	−0.049	−0.001	0.006	0.081	0.521	−0.205
		cv3	−0.093	−0.152	−0.036	−0.004	−0.035	−0.009
		cv4	0.156	−0.147	0.017	−0.044	−0.183	0.001
		cv5	−0.090	−0.131	0.018	0.026	−0.141	0.127
		SE	0.0365	0.0320	0.0130	0.0311	0.0670	0.0530
ddh × cv								
cv GCA	4		0.1888**	0.910***	0.003ns	0.929***	0.749***	0.417ns
ddh GCA	3		0.0808ns	1.453***	0.062***	4.934***	0.563***	0.927*
SCA	12		0.0348ns	0.140***	0.007*	0.326***	0.231**	0.224ns
Error	34		0.0457	0.027	0.003	0.084	0.073	0.302
		ddh 1	−0.029	−0.117	0.053	−0.430	−0.241	0.061
		ddh 2	−0.071	0.465	0.053	0.631	0.186	0.327
		ddh 3	−0.001	−0.181	−0.079	0.338	0.124	−0.197
		ddh 4	0.101	−0.167	−0.027	−0.538	−0.068	−0.190
		SE	0.0552	0.0425	0.0141	0.0750	0.0697	0.1418
		cv1	0.196	0.474	−0.015	0.124	0.004	0.040
		cv2	−0.053	−0.016	−0.008	0.178	0.312	0.096
		cv3	0.026	−0.082	0.025	0.048	0.175	0.222
		cv4	−0.027	−0.159	−0.004	−0.490	−0.228	−0.266
		cv5	−0.143	−0.216	0.002	0.142	−0.264	−0.091
		SE	0.0617	0.0475	0.0517	0.0839	0.0780	0.1585
cv × FDR								
FDR GCA	2		0.1721ns	0.624***	0.031***	0.004ns	0.545**	0.001ns
cv GCA	2		0.0540ns	0.270*	0.025**	0.138*	2.955***	0.030ns
SCA	4		0.0508ns	0.458***	0.001ns	0.014ns	0.721***	0.336ns
Error	16		0.0722	0.055	0.003	0.025	0.056	0.199
		cv1	0.080	0.153	−0.059	0.020	−0.353	0.028
		cv2	−0.075	0.035	0.016	0.113	0.662	−0.066
		cv5	−0.005	−0.188	0.043	−0.133	−0.307	0.039
		SE	0.0895	0.0780	0.0172	0.0522	0.0790	0.1487
		FDR 1	0.032	0.245	0.039	0.018	−0.186	−0.008
		FDR 2	−0.151	0.034	0.029	0.007	0.279	−0.001
		FDR 3	0.120	−0.279	−0.067	−0.025	−0.092	0.010
		SE	0.0895	0.078	0.0172	0.0522	0.0790	0.1487
ddh × FDR								
FDR GCA	2		0.1238ns	0.404*	0.012ns	0.070*	0.333*	0.430*
ddh GCA	2		0.5919***	0.120ns	0.000ns	0.019ns	1.936***	0.229ns
SCA	4		0.1483*	0.586**	0.006ns	0.007ns	0.426**	0.191ns
Error	14		0.0452	0.071	0.005	0.015	0.078	0.115
		ddh 1	−0.001	0.005	−0.004	−0.044	−0.276	−0.060
		ddh 2	−0.256	0.113	0.000	−0.005	0.536	0.181
		ddh 4	0.257	−0.118	0.004	0.048	−0.259	−0.121
		SE	0.0708	0.0890	0.0232	0.0401	0.0930	0.1129
		FDR 1	0.099	0.209	0.031	0.048	0.145	−0.182
		FDR 2	−0.130	0.006	0.010	0.054	0.074	0.243
		FDR 3	0.031	−0.215	−0.041	−0.102	−0.218	−0.059
		SE	0.0708	0.0890	0.0232	0.0401	0.0930	0.1129

* $P = 0.05$–0.01; ** $P = 0.01$–0.001; *** $P < 0.001$

[a] log of variance

ddh × cv and ddh × FDR crosses. Since the same cultivars were used in cv × cv and ddh × cv crosses, and the same FDR clones were used in the cv × FDR and ddh × FDR crosses, the results indicate that the ddh parents decreased the attractiveness of the progenies. The cv × FDR progenies had high mean breeder's preference scores demonstrating that attractive *S. phureja*-derived FDR clones can transmit desirable genes to their offspring. However, this work confirms that careful selection of FDR clones and tetraploid parents is essen-

Table 5 Progeny variances for eight TPS progenies visually selected for uniformity

Progeny	Tuber number	Tuber colour	Tuber shape	Skin finish	Flesh colour	Breeder's preference
cv3 × cv3	3.33	0.000	0.124	0.252	0.211	0.988
cv3 × cv4	6.09	0.000	0.101	0.167	0.350	0.853
cv4 × cv4	7.12	0.028	0.208	0.251	0.165	0.546
ddh3 × cv4	9.84	0.013	0.058	0.396	0.329	0.459
ddh4 × cv4	5.90	0.013	0.109	0.126	0.194	0.339
ddh4 × cv5	6.73	0.000	0.185	0.182	0.128	0.735
cv5 × FDR3	6.18	0.053	0.154	0.170	0.301	0.736
ddh1 × FDR3	5.80	0.064	0.119	0.178	0.131	0.557
ddh4 × FDR3	7.00	0.035	0.120	0.200	0.318	0.730

tial for the production of superior progenies in 4x-2x crosses (Ortiz et al. 1988). Cultivar 4 (Maris Piper) had a high GCA for attractiveness and is likely to make a good parent for conferring this characteristic to TPS progenies.

For individual traits, TPS progenies can be as uniform as clonally maintained cultivars (Table 1); however, rank correlations demonstrated that progenies which were uniform for one trait were not necessarily uniform for others. This result is in agreement with the work of Thompson and Mendoza (1984) who found a poor correlation between uniformity for tuber colour and tuber shape in a TPS population. Furthermore, none of the breeding schemes tested in our study gave TPS progenies with low levels of variation for all tuber characteristics, and there were significant differences in uniformity between progenies within breeding schemes for most of the tuber traits. These results suggest that achieving multitrait uniformity in TPS progenies will require considerable breeding effort.

Comparing the results of the GCA/SCA analysis and the visual selection provides useful information on the production of TPS progenies with multitrait uniformity. A number of parental genotypes with good GCAs for reducing variation in tuber colour, skin finish, flesh colour and, to a lesser extent, tuber shape, were identified (Table 4). Additive genetic variation has been shown to be important for tuber shape uniformity in TPS progenies from 4x-4x and 4x-2x crosses (Rowell et al. 1986; Ortiz et al. 1988), although it was not detected in cv × cv crosses in the present study (Table 4). Visually-selected progenies, and those with small variances, had parents with negative GCAs for variation in a number of tuber traits (e.g., cv 3, cv 4, ddh 4, FDR3; Tables 4 and 5). These results suggest that selecting parents with appropriate GCAs could produce attractive TPS progenies that are uniform for certain traits; in particular – tuber colour, skin finish, shape and flesh colour.

From the literature, the use of 4x-2x FDR crosses can appear to be the panacea for TPS production (e.g., Peloquin et al. 1989). However, our results support the findings of Ortiz et al. (1988) that careful selection of FDR parents is necessary for the production of superior progenies.

The clone FDR3 had negative GCAs for variation in all the tuber traits where significant effects were detected (Table 4), and was therefore superior to the other two FDR clones. FDR3 is the only clone that is desynaptic and the reduced meiotic recombination in this clone may have contributed to its favourable GCAs for uniformity. This is the first practical demonstration that desynpsis can assist the production of phenotypically uniform TPS progenies and supports the theoretical work of Jogedijk et al. (1991). Although only a limited number of FDR clones were used, our data also suggest that synaptic FDR clones may not be able to produce TPS progenies with high levels of multitrait uniformity (cf. Peloquin et al. 1989). Further work is needed to determine if this is the case.

Diploid clones can produce unreduced gametes by FDR and SDR simultaneously (Ramanna 1979), which would generate variability in TPS progenies. In the present study the clone FDR1 produced approximately 40% of its 2n pollen by mechanisms akin to SDR. Thus, to produce uniform TPS progenies it would be essential to screen parental clones to eliminate those that produce a high proportion of SDR gametes.

The doubled-haploid clone ddh 4 appears to be a good parent for hybrid TPS production. It had consistently negative GCAs for a number of important tuber-trait variances (Table 4), produced some of the most uniform progenies in visual selection tests (Table 5), and is male sterile.

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