Theor Appl Genet (2000) 100:772–781

J.E. Bradshaw · D. Todd · R.N. Wilson

Use of tuber progeny tests for genetical studies as part of a potato (*Solanum tuberosum* subsp. *tuberosum*) breeding programme

Received: 28 November 1998 / Accepted: 19 December 1998

Abstract A diallel set of crosses, including selfs and some reciprocal crosses, was made between 15 parents, chosen for their fertility, from those included in a tetraploid potato (*Solanum tuberosum* subsp. *tuberosum*) breeding programme at the Scottish Crop Research Institute. The progenies were grown in randomised complete block trials with two replicates at a high-grade seed site from 1994 to 1996 inclusive and at a ware site in 1995 and 1996. The parents were included in the ware trials. Tubers were assessed for visual preference in all trials and for fry colour at both sites in 1996. Emergence and maturity were recorded in the ware trials and the tubers were assessed for yield, dry matter, size, appearance (regularity of shape), scab, uniformity, sprouting in store and keeping quality. There were very few growth cracks and very few internal defects. No reciprocal differences were found. Inbreeding depression was marked for emergence, yield, tuber size and appearance, and visual preference. In contrast, the selfs had a lighter fry colour than the parents and F_1s.

Combining-ability analysis (selfs omitted) identified fry colour, emergence, maturity, yield, dry matter and sprouting resistance as traits for which the GCA (general combining ability) variance and narrow-sense heritability were high enough for good progress from full-sib family selection. Correlations between GCAs for pairs of traits were examined, including those from previously published seedling progeny tests. For fry colour, an unfavourable correlation with low yield (r = 0.596) was compensated by a favourable one with high dry matter content (r = 0.652), whereas unfavourable ones between foliage and tuber blight resistance and sprouting susceptibility (r = 0.578 and 0.596) were identified for monitoring. Clones with high GCAs were identified for use as parents in future breeding and the extent to which GCAs could be predicted from the parents, and the offspring means from the midparent means, was determined by regression and correlation analysis. The offspring-midparent regression was highest for fry colour, followed by dry matter, emergence and sprouting. Values were lower for scab due to environmental variation; for maturity, yield and tuber size due to SCA (specific combining ability); and for visual preference due to both factors. The implications for a breeding strategy are discussed.

Key words Potato breeding · Combining-ability analysis · Parent-offspring analysis · Yield · Fry colour · Common scab · Genotypic recurrent selection

Communicated by G. Wenzel

J.E. Bradshaw (✉), D. Todd, R.N. Wilson
Scottish Crop Research Institute, Invergowrie,
Dundee DD2 5DA, UK

Introduction

The principal cultivated potato (*Solanum tuberosum* subsp. *tuberosum*) is a tetraploid that displays tetrasomic inheritance. As a consequence, genetical analysis has proved difficult, particularly for traits that display continuous variation. For many economically important traits, it has only been possible to partition genetical variation into components due to general combining ability (GCA) and specific combining ability (SCA) (see Bradshaw and Mackay 1994). Nevertheless, such information is of value to breeders, particularly at the start of a new breeding programme. Hence, Bradshaw et al. (1995) made a diallel set of crosses in 1992 in order to analyse the genetical variation available in a new breeding programme at the Scottish Crop Research Institute (SCRI). This programme was primarily designed to combine quantitative resistances to late blight [*Phytophthora infestans* (Mont.) de Bary] and the white potato cyst nematode (PCN) [*Globodera pallida* (Stone)] with commerically acceptable tuber yield and quality, but included parents with resistance to Potato Leaf Roll Luterovirus (PLRV) and Potato Y Potyvirus (PVY). The results of the seedling progeny tests for late blight, PCN and breeders‘ visual preference have already been published (Bradshaw et al. 1995), and so have those for gangrene (*Phoma foveata*) (Bradshaw et al. 1996). For the

assessment of other economically important traits, including yield and fry colour, tuber progenies were required. Therefore, in 1993, the seedling progenies from the glasshouse were kept and assessed as tuber progenies at a high-grade seed site from 1994 to 1996, and in replicated ware trials in 1995 and 1996. The results are used to illustrate the value and limitations for use in a practical potato breeding programme of a diallel analysis which includes the parents and their selfs.

Materials and methods

Parents and crossing programme

The diallel set of crosses had been made in 1992 between 15 male-fertile parents from the breeding programme, of which five were resistant to late blight (clones 8204a4 and 14897ad17 and cvs 'Shelagh', 'Stirling' and 'Teena'), five were resistant to the white potato cyst-nematode (clones 12288af23, 12601ab1, 12674ab1 and 15119ac5 and cv 'Eden'), and five had virus resistance [clones G8107(1), G8830(1), G8866(11), G8884(2) and 15144a3] (Bradshaw et al. 1995). Seed was secured from all 105 crosses and 15 selfs together with 23 reciprocal crosses, making 143 progenies in total.

Tubers were kept from the first two replicates of the seedling progeny test which was grown in a glasshouse in 1993 to assess the commercial worth of tubers. They were stored in the dark at 6°C until mid-April 1994, when they were moved to a glasshouse ready for planting at SCRI's high grade seed site.

Maintenance and assessment of tuber progenies at a high-grade seed site

The 143 progenies were grown at SCRI's high-grade seed site (Blythbank Farm, West Linton, Peeblesshire) from 1994 to 1996 inclusive, in randomised complete block (RCB) designs, keeping the same two replicates as in the glasshouse but with new randomisations of the progenies each year. Each progeny in each replicate comprised a single drill of 18 plants (unique genotypes) at 50-cm spacing, with 75 cm between drills. The trials were planted on 9 May 1994, 4 May 1995 and 13 May 1996. The fertiliser applied, and the use of aphicides, herbicides and fungicides (for late blight control) were standard for seed potatoes in Scotland. The desiccant Reglone was applied at half the recommended rate before harvest to kill sufficient foliage to make it easier to dig the trials by hand on 31 August 1994, 30 August 1995 and 4 September 1996. At harvest, two breeders (J.E.B. and a colleague) independently assessed the produce of all plants on a 1—9 scale of increasing preference. The mean of the 18 seedlings of each progeny in each replicate was calculated for each breeder and then averaged over the two breeders to give the data used for analysis. There was, in fact, reasonable agreement between the two breeders, with correlations for the means of 18 seedlings in the 3 years of $r = 0.632$, 0.738 and 0.752.

Two bulks of tubers (as many as there were plants in a drill) were taken from each progeny in each replicate and kept in a potato store at Blythbank until the following year. One bulk was replanted at Blythbank and the other in a replicated ware trial. In the bulk for the 1996 ware trial, the number of tubers was made up to 18 by taking a second tuber from as many plants as necessary and, at the 1996 Blythbank harvest, a similar bulk was taken for fry colour analysis after storage at ambient but frost-free temperature in a potato store at SCRI, Dundee.

Tuber progeny trials at the ware site

The tuber progenies and their parents were grown at a ware site (Gourdie Farm, Dundee) in 1995 and 1996. Each year the trial had an RCB design with two replicates of each parent and progeny in two-drill plots of up to 18 tubers (2 rows of 9) spaced 45-cm apart within drills and 75-cm between drills. Gaps (2 m) were left at the ends of the drills to allow machine harvesting. In 1995, where there were less than 14 tubers available for a plot, nine were planted in one drill and the other was planted with an infill of nine tubers of cv Maris Piper. Twenty one out of the 286 progeny plots required an infill. At harvest, the yield of the first drill was doubled to give a realistic estimate of plot yield. As already explained, infills were not required in 1996 and a count after establishment revealed at least 14 plants in each plot.

Tubers were brought from the Blythbank potato store in mid-February and then, in mid-March, placed in open, brown paper bags in a glasshouse to chit ready for planting, which took place on 18 April 1995 and 8 May 1996. The drills were covered the same day.

Cultural details

Fertiliser was incorporated into the soil on 4 April 1995 and 27 March 1996 to supply 147, 147 and 220.5 kg ha^{-1} of N, P_2O_5 and K_2O.

Stomp 400 SC (pendimethalin) herbicide at 3.3 l ha^{-1} and Lexone 70 DF (metribuzin) at 0.5 kg ha^{-1} were applied for weed control on 1 May 1995 and 3 June 1996, followed by Gramoxone 100 (paraquat) at 3 l ha^{-1} on 16 May 1995, but not in 1996.

Aphids were controlled by spraying with Aphox (pirimicarb) at 280 g ha^{-1} on seven occasions from 12 June until 23 August 1995 and on four occasions from 25 June until 23 August 1996. In 1996, there was also an application of Decisquick (deltametrin + heptenophos) at 0.3 l ha^{-1} on 24 July.

Late blight (*P. infestans*) was controlled with fungicide sprays: Dithane 945 (mancozeb) at 1.7 kg ha^{-1} on five occasions (with the Aphox) from 12 June until 28 July 1995 and on four occasions (with the Aphox and Decisquick) from 25 June until 7 August 1996, followed by Super-Tin 4L (fentin hydroxide) at 560 ml ha^{-1} on 11 and 23 August 1995 and 23 August 1996.

Scoring and harvesting

Emergence was scored on a 1 (none) to 9 (all plants in a plot well established) scale on 29 May 1995 and 11 June 1996.

Maturity was scored on a 1 (all plants in a plot dead) to 9 (all plants still green) scale on 22 August 1995 and 19 August 1996.

In 1995, the trial was burnt down with one application of sulphuric acid on 25 August, whereas the 1996 trial was pulverised on 22 August.

Harvesting was done on 30 August 1995 and 27 August 1996 with a single-row digger. The tubers from each drill were placed in a box, taken into a potato store, and the contents of the pairs of boxes making up a plot were amalgamated.

The plots were graded (< 45 mm, 45–65 mm, 65–85 mm and > 85 mm) and the fractions weighed separately on 5 September 1995 and 29 August 1996. The weights were recorded automatically by an Avery balance connected to an Epson HX-20 portable computer. The specific gravity, and hence the dry matter content, of a 3.63-kg sample of tubers from each plot was determined using a hydrometer on 24/25 September 1995 and 30 August 1996.

Visual assessments of each plot were made on 6 September 1995 and 10 September 1996 on a 1 (low) to 9 (high) scale for tuber size, regularity of shape (appearance), resistance to growth cracking, resistance to common scab [*Streptomyces scabies* (Thaxt.) Waksman and Henrici] and uniformity of size and appearance. Nine large tubers from each plot were cut open to check for internal defects (incipient hollow heart, hollow heart, internal necrosis and flecking) and the plot given an internal condition score on a 1 (all nine tubers with severe defect such as hollow heart) to 9 (no defects) scale. The plots were then independently given an overall preference score by D.T. and R.N.W. on a 1 to 9 scale of

increasing preference, which took account of yield but not internal condition, so that it was comparable to the Blythbank scores. The mean of the two scorers was used as the most accurate evaluation of the plot available. The correlations between scores (over 316 plots) were in fact moderately large for the 2 years, $r = 0.533$ and 0.676.

The fry colours of the 18 tubers from each plot at the seed site were determined on 10 December 1996, followed by 18 tubers from each plot of the ware trial on 17 December 1996 (first replicate) and 6 January 1997 (second replicate). Each of the 18 tubers was cut in half and a 2 mm-thick slice was taken and fried in vegetable oil at 175°C in a thermostatically-controlled chip fryer until all of the water had boiled off (bubbling ceased). Colour was assessed on a 1–9 scale by comparison with a standardised colour chart (1 = extremely dark to 9 = extremely pale), where 5 and above is an acceptably light colour (Mackay and Dale 1990). The mean of the 18 scores for each plot was determined and used in the subsequent analysis.

Lastly, on 19 February 1996 and 9 January 1997, all of the plots were given a final score for sprouting (1 extensive to 9 none) and keeping quality (1 tubers very soft to 9 tubers still hard).

Statistical analyses

Genstat 5 Release 3 (Genstat 5 Committee 1993) was used for all of the statistical analyses. Preliminary analyses of variance were done to test for differences between years and between parents, F_1s and selfs, as well as for reciprocal differences. As no reciprocal differences were found, more detailed analyses of variance were based on experimental methods 2 (including parents selfed) and 4 (excluding parents selfed) of Griffing (1956), and model II in which genotypes were assumed to be a random sample from a larger population (i.e. all of the parents included in the breeding programme). In model II, the GCA item is tested for significance against the SCA item. However, as years (but not sites for fry colour) were also considered a random sample, this meant that in the presence of both a GCA × years interaction and SCA, there was no unambiguous test for GCA. The analyses were done by multiple linear regression because those crosses where reciprocals had been made were present in duplicate.

This approach also allowed the SCA item in method 2 to be partitioned into three components: (1) the overall difference between selfs and crosses, (2) variation between parents in the differences between selfs and crosses, and (3) a remainder that corresponds to the SCA item in method 4 where the selfs are omitted. This analysis of variance is equivalent to Analysis II of Gardner and Eberhart (1966) for a variety cross diallel in which heterosis (SCA) is partitioned into average, variety and specific components. However, the genetical interpretation is different because their model was a diploid one for random-mating varieties and the crosses between them, whereas here we are dealing with tetraploids and it is the parents selfed that are included in the analysis. The GCAs presented in this paper are those estimated from the method-4 analysis in which the selfs were omitted because, otherwise, the diallel set of crosses would be more inbred than the larger population, about which inferences are to be made. The model for this analysis is as follows:

$$\text{progeny}_{ij} = \mu + \text{GCA}_i + \text{GCA}_j + \text{SCA}_{ij} + \text{residual},$$

where μ is the overall population mean, and the GCA and SCA effects are measured from this overall mean.

The components of variance (σ^2) were then estimated from the mean squares in the parental analysis and from those in the method-4 progeny analysis, having first eliminated at random one reciprocal cross from all such pairs, both for ease of analysis and so that all GCAs had equal precision. The expected mean squares for the parents and for a 15 × 15 half diallel without selfs are as follows:

parents	$\sigma^2_{resp} + [r\,\sigma^2_{PARE}] + nr\,\sigma^2_{PAR}$
parents × environments	$\sigma^2_{resp} + r\,\sigma^2_{PARE}$
residual for plots of parents	σ^2_{resp}
GCA	$\sigma^2_{res} + [r\,\sigma^2_{SCAE}] + nr\,\sigma^2_{SCA} + [13r\,\sigma^2_{GCAE}] + 13\,nr\,\sigma^2_{GCA}$
SCA	$\sigma^2_{resp} + [r\,\sigma^2_{SCAE}] + nr\,\sigma^2_{SCA}$
GCA × environments	$\sigma^2_{res} + r\,\sigma^2_{SCAE} + 13r\,\sigma^2_{GCAE}$
SCA × environments	$\sigma^2_{res} + r\,\sigma^2_{SCAE}$
residual for plots of progenies	$\sigma^2_{res,}$

where r is the number of replicates (two) in each trial and n is the number of environments (two sites or 2 or 3 years), and components in square brackets are included when environments are a random rather than a fixed sample.

The broad-sense heritability of parental means was estimated as:

$$\sigma^2_{PAR}/[\sigma^2_{PAR} + \sigma^2_{PARE}/n + \sigma^2_{resp}/(nr)].$$

The narrow-sense heritability of progeny means was estimated as:

$$2\sigma^2_{GCA}/[2\sigma^2_{GCA} + \sigma^2_{SCA} + (2\sigma^2_{GCAE} + \sigma^2_{SCAE})/n + \sigma^2_{res}/(nr)].$$

The correlations between the GCAs for all pairs of traits and all GCA-parent and offspring-midparent correlations were calculated from the analyses which included the reciprocal crosses, but not the selfs. The offspring-midparent regression coefficients were also calculated as estimates of the narrow-sense heritability of the midparent values. Finally, the offspring-midself correlations were calculated for comparison with the offspring-midparent correlations.

Results

Summary statistics and preliminary analyses

The means over all parents and progenies for the 1995 and 1996 ware trials are given in Table 1, together with the averages over the 2 years of the means of all parents, their F_1s (having first taken the means of any reciprocal crosses) and their selfs. The fry colour means are also given for the progenies at the seed site in 1996 and for the parents and progenies at the ware site in the same year. The mean of all the progenies at the seed site for visual preference was 3.66 in 1994, 3.65 in 1995 and slightly higher at 4.03 in 1996. Averaged over all 3 years, the mean of the F_1s was higher than the mean of the selfs (3.86 v 3.33).

As the differences between environments were compared with the differences between replicates within environments, very few of them (visual preference at seed site, emergence, dry matter, fry colour and sprouting) were statistically significant ($P < 0.05$) because of the low numbers of degrees of freedom involved. Nevertheless, it can be seen that, in 1996, emergence was faster from a later planting, yields were higher, dry matter-content was lower and sprouting resistance and keeping quality had higher values, albeit at an earlier scoring date. Fry colours were slightly lighter at the ware site.

For all traits, except growth cracks, there were significant differences ($P < 0.05$) between the parents, F_1s and selfs when tested against the residual variation within trials, with the scores being in the order parents >F_1s> selfs

Table 1 Summary of data from 1995 and 1996 ware trials and fry colour data from seed and ware site in 1996, on a 1 (undesirable) to 9 (desirable) scale unless stated otherwise

Trait	Mean of parents and progenies		Mean of years			
	1995	1996	Parents	F_1s	Selfs	SED[a]
Emergence	4.17	5.73	5.54	4.93	4.08	0.113
Maturity (9 late)	4.49	4.71	4.81	4.60	4.07	0.124
Yield (kg/plot)						
Total	17.19	22.39	22.61	20.16	14.53	0.433
Saleable (> 45)	13.91	18.47	19.40	16.59	10.73	0.441
Ware (45—85)	13.56	18.34	19.09	16.33	10.66	0.429
Dry matter (%)	23.26	20.29	22.40	21.79	21.08	0.154
Visual size	5.29	4.80	5.48	5.15	3.97	0.131
Visual appearance	4.21	4.16	4.87	4.19	3.62	0.124
Visual growth cracks	8.91	8.91	9.00	8.90	8.87	0.065
Scab	7.15	6.86	7.32	6.99	7.15	0.128
Uniformity	4.57	4.49	5.34	4.48	4.20	0.136
Internal condition	8.47	8.76	8.77	8.58	8.73	0.085
Visual preference	3.69	3.65	4.34	3.70	2.97	0.089
Fry colour						
Seed site (progenies)	–	4.49	–	4.38	4.88	0.103
Ware site	–	5.25	4.97	5.17	5.48	0.131
Sprouting	3.48	5.59	5.29	4.39	4.94	0.150
Keeping quality	4.55	5.35	5.40	4.92	4.90	0.140

[a] Standard error of difference between means of F_1s and parents and F_1s and selfs, based on residual variation within trials. Multiply by 1.34 to obtain SED for parents and selfs

for all traits except scab, internal condition, fry colour (where they were in the reverse order) and sprouting. However, for emergence, maturity and dry matter, the differences were not significant when tested against their interactions with years which were also significant ($P < 0.01$) for these traits and involved a change in ranking of the parents and F_1s for emergence and maturity. The mean of the F_1s was just greater than that of the parents for maturity in 1995 and for emergence in 1996, but was less in the other year.

Detailed analyses of variance on parents

Analyses of variance revealed that there was statistically significant differences ($P < 0.05$) between the parents for all traits except visual appearance, visual growth cracks, uniformity (as expected of clones) and internal condition, and that the differences for maturity and keeping quality were significant ($P < 0.001$ and $P < 0.01$, respectively) when tested against their parent × year interactions, which were also significant ($P = 0.05$–0.01). There was also a significant interaction ($P = 0.05$–0.01) for internal condition.

As there were very few growth cracks and very few internal defects (Table 1), these traits were not analysed further. For the remaining traits, the phenotypic variances of the parental means and their broad-sense heritabilities are shown later in Table 5 for ease of comparison with the parent-offspring statistics.

Detailed analyses of variance on progenies

The results of the analyses of variance on the progenies are summarised in Table 2. GCA was significant ($P < 0.05$) when tested against the larger of SCA and GCA × E for all traits except keeping quality. There were GCA × E interactions for all traits except dry matter, visual appearance, scab and uniformity. The differences between the F_1s and selfs (SCA1) were significant for all traits shown in Table 2, except scab, uniformity and keeping quality (Table 1). There was evidence of these differences varying with parent (SCA2) for maturity, uniformity, visual preference, fry colour and sprouting. There were differences between the F_1s due to specific combining ability (SCA3) for maturity, yield, visual size, uniformity, visual preference and fry colour, but no SCA3 × E interactions.

There were no statistically significant ($P > 0.05$) reciprocal differences, nor any reciprocal difference × environment interactions. Furthermore, there were no overall SCA × E interactions, although for emergence the interaction with SCA2 was significant ($P = 0.01$—0.001) and for uniformity the interaction with SCA1 was significant ($P = 0.05$—0.01).

General combining abilities

The general combining abilities shown in Table 3 were estimated from the method-4 analysis, in which the selfs were omitted. The standard errors vary slightly depending upon the number of reciprocal crosses. The GCAs for saleable and ware yields were highly correlated ($r > 0.90$) with those for total yield and hence are omitted. Visual

Table 2 Analyses of variance on progenies: significance of general (GCA) and specific (SCA) combining abilities and their interactions with environments (E) which were sites for fry colour and years for all other traits

Trait	GCA	SCA1	SCA2	SCA3	GCA × E	SCA × E
Emergence	***	***	NS	NS	**	** (SCA2)
Maturity	***	***	**	***	***	NS
Yield						
Total	***	***	NS	**	*	NS
Saleable	***	***	NS	**	**	NS
Ware	***	***	NS	**	**	NS
Dry matter	***	***	NS	NS	NS	NS
Visual size	**	***	NS	***	**	NS
Visual appearance	**	***	NS	NS	NS	NS
Scab	***	NS	NS	NS	NS	NS
Uniformity	**	NS	*	*	NS	* (SCA1)
Visual preference						
Seed site	***	***	***	***	***	NS
Ware site	*	***	*	*	***	NS
Fry colour	***	***	***	***	*	NS
Sprouting	**	***	*	NS	***	NS
Keeping quality	NS	NS	NS	NS	***	NS

*** $P < 0.001$;
** $P = 0.01$–0.001;
* $P = 0.05$–0.01; NS, not significant

Table 3 General combining abilities estimated from F_1 generation

Parent		Emergence	Maturity	Total yield	Dry matter	Visual size
8204a4		0.285	0.508	0.124	–0.994	0.284
12288af23		0.434	–1.312	3.375	–0.560	0.468
12601ab1		0.204	0.043	–2.547	1.309	–0.672
12674ab1		0.173	0.399	–0.897	0.315	0.049
14897ad17		0.600	0.365	1.163	–0.247	0.013
15119ac5		0.012	–0.636	–1.036	–0.663	–0.417
15144a3		0.353	0.324	–0.172	–0.114	0.106
G8107(1)		–0.264	–0.330	–0.107	0.678	–0.158
G8830(1)		–0.479	0.016	–0.637	–0.188	0.172
G8866(11)		–0.919	–0.563	0.151	–0.110	0.124
G8884(2)		–0.852	0.373	–0.616	0.550	–0.339
Eden		0.096	0.099	0.822	0.543	0.110
Stirling		0.053	0.087	0.422	–0.608	0.333
Shelagh		–0.120	0.365	0.877	–0.274	0.357
Teena		0.090	0.190	–0.250	0.394	–0.279
SE	from	0.086	0.124	0.410	0.145	0.140
	to	0.104	0.151	0.496	0.176	0.170

Parent		Scab	Visual preference		Fry colour	Sprouting
			Seed site	Ware site		
8204a4		–0.048	–0.168	0.086	–0.101	–0.442
12288af23		0.346	–0.388	0.152	–1.301	–0.039
12601ab1		–0.561	–0.239	–0.485	1.537	0.795
12674ab1		–0.032	–0.043	0.004	0.479	–0.264
14897ad17		–0.132	0.343	0.291	–0.142	–1.456
15119ac5		0.158	–0.166	–0.366	–1.063	0.173
15144a3		–0.419	0.092	0.028	–0.138	–0.042
G8107(1)		–0.202	0.470	0.291	–0.153	0.185
G8830(1)		0.028	–0.010	0.107	0.988	0.393
G8866(11)		0.371	0.122	–0.060	–1.181	0.689
G8884(2)		0.403	0.326	0.114	0.130	0.184
Eden		–0.359	0.005	–0.051	0.683	0.703
Stirling		0.195	0.245	0.392	–0.315	–0.485
Shelagh		0.314	–0.166	–0.018	–0.228	–0.253
Teena		0.234	–0.195	–0.256	0.327	–0.313
SE	from	0.115	0.0547	0.0799	0.087	0.137
	to	0.139	0.0662	0.0968	0.105	0.166

Table 4 Components of variance and heritability estimated from the F_1 generation, excluding reciprocals, where E was sites for fry colour and years for all other traits

Trait	Components of variance					Heritability
	GCA	SCA	GCA × E	SCA × E	Residual for plots	
Emergence	0.176	0	0.024	0	0.640	0.657
Maturity	0.220	0.112	0.028	0	0.897	0.547
Yield						
Total	1.529	1.146	0.557	0	9.763	0.425
Saleable	1.786	1.403	0.723	0	10.094	0.435
Ware	1.674	1.269	0.742	0	9.615	0.431
Dry matter	0.363	0.059^{NS}	0	0	1.468	0.630
Visual size	0.051	0.161	0.054	0.080^{NS}	0.925	0.175
Visual appearance	0.037^{NS}	0.007^{NS}	0.008	0	0.905	0.235
Scab	0.082	0.057^{NS}	0.005^{NS}	0	0.839	0.378
Uniformity	0.040	0.071	0	0	1.069	0.193
Visual preference						
Seed site	0.052	0.040	0.006	0	0.150	0.601
Ware site	0.028	0.031	0.032	0	0.424	0.250
Fry colour	0.648	0.045	0.016^{NS}	0	0.396	0.900
Sprouting	0.266	0.070^{NS}	0.133	0	1.189	0.515
Keeping quality	0.031^{NS}	0.028^{NS}	0.067	0.002^{NS}	1.073	0.144

^{NS} Not significant in ANOVA

appearance is not shown because, on omitting the selfs, a statistically significant GCA × year interaction was found and the GCA item was not significant in comparison. Furthermore, there had been no significant differences between the parents for this trait. For uniformity (data not shown), the GCAs ranged from 0.451 ± 0.144 for clone G8884(2) to –0.652 ± 0.132 for clone G8830(1). The progenies of this latter clone looked variable beause they contained white-, red- and purple-skinned tubers. Keeping quality is also omitted because the differences in GCA were not significant when tested against their interactions with years, in contrast to the differences between the parents.

It is worth noting that the four G clones had the highest negative GCAs for emergence (i.e. slow emergence). Clone 12288af23 had the highest GCA for yield and visual size and the lowest for maturity (early maturity), visual preference at the seed site and fry colour. In contrast, clone 12601ab1 had the lowest GCA for yield, visual size, scab and visual preference at the ware site, but the highest for dry matter, fry colour and sprouting resistance. Clone 14897ad17 had the highest GCA for emergence (i.e. rapid emergence) but the lowest for sprouting resistance, and clone 8204a4 had the highest GCA for maturity (i.e. late maturity) but the lowest for dry matter. Clone G8884(2) had the highest GCA for scab resistance. Clone G8107(1) had the highest GCA for visual preference at the seed site and cv Stirling the highest at the ware site.

Components of variance

As years and parents were both considered random samples from a larger set of years and parents, this meant that, in the presence of both a GCA × years interaction and SCA, there was no unambiguous test for GCA. However, an indication of the relative importance of the variation due to GCA can be gained from the components of variance shown in Table 4. Reciprocal crosses were eliminated for ease of estimation. Any components with a negative estimate were set equal to zero and the other components re-calculated, and any non-zero ones that were not statistically significant in the analysis of variance are marked NS.

For fry colour, GCA was the largest component; otherwise, the residual variation for plots was by far the largest component, although it must be remembered that its contribution to the variation in progeny means averaged over *n* trials with r replicates is 1/(*n*r) of the values given in Table 4, where r is two replicates and *n* is two sites for fry colour, 3 years for visual preference at the seed site, and 2 years for all other traits. GCA was the next largest component for all remaining traits except visual size, uniformity, visual preference at the ware site and keeping quality, although there were sizeable SCA contributions to the variation for maturity, yield and visual preference at the seed site. Again, it must be remembered that the contributions of GCA and SCA to the variation in progeny means are $2\sigma^2_{GCA} + \sigma^2_{SCA}$ and to the progeny × environments interaction $(2\sigma^2_{GCAE} + \sigma^2_{SCAE})/n$, and these are reflected in the narrow-sense heritabilities of progeny means $[2\sigma^2_{GCA}/$(phenotypic variance of progeny means)] shown in Table 4. Therefore, the highest heritabilities were for fry colour, emergence and dry matter, and the lowest were for visual size, uniformity and keeping quality.

Table 5 Phenotypic variance and broad-sense heritability of the parental means, and GCA-parent correlation and offspring-midparent correlation and regression (narrow-sense heritability) estimated from all of the F_1s

Trait	Phenotypic variance of parental means	Broad--sense heritability of parental means	GCA--parent correlation	Offspring--midparent correlation	Offspring-midparent regression	
				(*r*)	(b)	SE
Emergence	1.211	0.833	0.866	0.731	0.683	0.057
Maturity	2.348	0.907	0.796	0.636	0.531	0.057
Yield						
Total	19.155	0.841	0.848	0.612	0.518	0.060
Saleable	24.920	0.801	0.935	0.696	0.555	0.051
Ware	22.560	0.803	0.939	0.702	0.569	0.052
Dry matter	2.342	0.910	0.935	0.762	0.762	0.058
Visual size	1.627	0.861	0.919	0.551	0.466	0.063
Visual appearance	0.208	0.301	0.457^{NS}	0.256	0.471	0.159
Scab	0.868	0.687	0.678	0.450	0.455	0.080
Uniformity	0.188	0.000	0.352^{NS}	0.204	0.426	0.182
Visual preference						
Ware site	0.434	0.669	0.777	0.555	0.583	0.078
Fry colour						
Ware site 1996	2.579	0.939	0.942	0.855	0.944	0.051
Sprouting	2.367	0.857	0.816	0.651	0.609	0.063
Keeping quality	1.505	0.732	0.738	0.458	0.359	0.062

^{NS} Not significant

GCA-parent correlation, offspring-midparent correlation and regression (narrow-sense heritability), and offspring-midself correlation

The GCA-parent and offspring-midparent correlations are shown in Table 5, along with the phenotypic variance and broad-sense heritability of the parental means. The GCA-parent correlations were larger than the offspring-midparent ones for all traits. This was because the GCA-parent and offspring-midparent covariances were similar (as expected) and the variance of midparent values was approximately half the variance of the parents (as expected), but the offspring variance was more than twice the GCA variance. The only really small correlations were for visual appearance and uniformity, traits for which there were no statistically significant differences between the parents.

The offspring-midparent regression coefficient (b) is also shown as an estimate of the narrow-sense heritability of midparent values. The standard error of the regression was large for visual appearance and uniformity because of the lack of statistically significant differences between the parents. The highest heritability was for fry colour, followed by dry matter, emergence and sprouting; traits with a high broad-sense heritability and very little, if any, SCA. Heritabilities were lower for traits where either SCA was more important (maturity, yield and visual size) or broad-sense heritability was lower (scab), or where both of these factors applied (visual preference and keeping quality).

The offspring-midself correlations (data not shown) were all slightly less than the offspring-midparent correlations.

Correlations between GCAs

Interest centres on the correlations between the GCAs of traits assessed in the glasshouse progeny tests and at the seed site, and those assessed in the ware trials, because the former traits are the selection criteria used in the breeding programme. There were a number of statistically significant ($P < 0.05$) and moderately sized correlations. They are described so that they are all positive correlations.

Foliage blight resistance was correlated with low dry matter content ($r = 0.518$), sprouting susceptibility (0.578) and poor keeping quality (0.586). Tuber blight resistance was correlated with fast emergence (0.656) and late maturity (0.521), as well as with sprouting susceptibility (0.596) and poor keeping quality (0.629). PCN resistance was correlated with poor visual preference (0.569). Breeders' preference in the glasshouse was correlated with visual appearance (0.609) and visual preference at the seed (0.755) and ware site (0.649), and visual preference at the seed site was also correlated with visual appearance (0.615) and visual preference in the ware trials (0.618).

Of final interest are the fry colour correlations: light colour with late maturity (0.597), low yield (0.596), high dry matter content (0.652) and scab susceptibility (0.606).

Discussion

As the primary aim of the diallel was to analyse the genetical variation available in a new breeding programme at SCRI, the results are strictly speaking, specific to this

programme. However, they will indicate the extent and nature of the variation available in a modern potato breeding programme where disease and pest resistances have been introgressed from *S. tuberosum* subsp. *andigena* and from wild species, in particular *S. demissum* for late blight and PVY resistance and *S. vernei* for PCN resistance. Furthermore, the methodology is of general relevance to potato breeding. In particular, the diallel was much larger than those previously reported in the literature, which typically involved 5–10 parents (e.g. Killick 1977; Brown and Caligari 1989; Maris 1989; Neele et al. 1991). This was achieved by choosing parents known to be male- and female-fertile from those included in the new breeding programme at SCRI and evaluating the offspring as plots of tuber progenies at normal spacing in ware trials without attempting to identify individual clones within progenies. The advantages of a large complete set of crosses (accuracy and no missing values) were thought to outweigh any concerns about the parents not being a strictly random sample from the breeding programme, and loss of information on genetical and environmental variation within full-sib families. Potential difficulties in scoring a large number of variable progeny did not arise in practice, with one exception; it was not possible to steam sufficient tubers to determine after-cooking blackening, whereas it was possible to cop with fry colour.

A major component of the SCRI breeding programme is full-sib family selection on a 3-year cycle (Bradshaw et al. 1994). The best guides to prospects for improving the traits considered in this paper are the GCA variances (σ^2_{GCA}) and heritabilities (h^2) given in Table 4, as the immediate response to selection in an equilibrium population is proportional to the square root of ($2\sigma^2_{GCA}\ h^2$). The immediate response to selection is not the final equilibrium response, but the latter is not required for a clonally propagated crop. However, continued selection will induce a gametic-phase disequilibrium which does reduce the observed GCA variance (Bradshaw 1994). A heritability for any number of replications and environments can, in fact, be estimated from the components of variance in Table 4, as can the optimum allocation of fixed resources. The exact response to selection can not, however, be accurately predicted because the parents were the products of past breeding and, hence, they and their offspring were not a random mating population in equilibrium. (With tetrasomic inheritance, not even the single-locus equilibrium is attained with one generation of random mating.) This was also the reason why it was considered inappropriate to estimate the genetic components of variance suggested by Levings and Dudley (1963) for alfalfa (a tetraploid), and discussed for potatoes by Bradshaw (1994).

Prospects are clearly best for improving fry colour, an important processing trait. Interestingly, of the four best parents for fry colour (GCAs in Table 3), three (12601ab1, 12674ab1 and Eden) are known to have low-temperature sugar-stability, whilst the fourth [G8830(1)] is known to be derived from such a clone. Love et al. (1998) have reported steady progress since about 1960 in North America in improving fry colour (through lower reducing sugar contents), regardless of whether tubers were stored at 4.4°C or 10°C. However, selection for fry colour after storage of 4°C for at least 3 months is the safest method as this ensures that clones can be stored at this temperature to control the development of diseases, weight loss and sprouting in store, with reduced reliance on sprout inhibiting chemicals, but still produce an acceptably light fry colour. Selection at the seed site would be just as effective as at the ware site because there were no genotype × site interactions amongst the F_1s (Table 4), and such selection has already been proved effective in a targeted and accelerated breeding programme at SCRI (Mackay et al. 1997). The GCA variances and the heritabilities (Table 4) for emergence, maturity, yield, dry matter and sprouting resistance were high enough for a reasonable response to selection for any single trait, but the more traits that are selected, the less is the progress that is made for each. Hence, for the immediate future, it is likely that tuber progeny selection for fry colour at the seed site will follow seedling progeny selection for blight and PCN resistance and breeders‘ visual preference, and that the overall scheme will continue to operate on a 3-year cycle (Bradshaw et al. 1994).

Some comparisons between the results given in Table 4 and earlier work can be made. Bradshaw and Mackay (1994) summarised the results of combining-ability analyses done since 1962 on different types of breeding material for a number of taits, including breeders’ visual preference, emergence, maturity, regularity of tuber shape (appearance), specific gravity (dry matter), tuber weight (size), and yield (Plaisted et al. 1962; Tai 1976; Killick 1977; Veilleux and Lauer 1981; Brown and Caligari 1989; Maris 1989; Neele et al. 1991). In addition, the results of combining-ability analysis for scab can be found in Pfeffer and Effmert (1985) GCA was more important than SCA for specific gravity, maturity and scab, whereas SCA was often as important as GCA for yield. For the other traits, no generalisations were possible emphasising the importance of determining the extent and nature of the genetical variation available at the start of a new breeding programme.

A number of moderately sized correlations (r = 0.518–0.755) were found between the GCAs for blight and PCN resistance, breeders‘ visual preference and fry colour, and those for the other traits assessed in the ware trials. They are mentioned at the end of the Results section. The unfavourable ones, which could be a cause for concern in the breeding programme, were those between blight resistance and sprouting susceptibility and poor keeping quality, the one between PCN resistance and poor visual preference, and those between light fry colour and low yield and scab susceptibility. However, for keeping quality, visual preference at the ware site and scab susceptibility, their GCA variances and correlations with the traits being selected were low enough to make large unfavourable correlated responses (proportional to

$r\sqrt{2\sigma^2_{GCA}}$) unlikely, and for fry colour, the unfavourable correlation with yield was compensated by a favourable one with dry matter content. Hence, the only likely unfavourable correlated response is for sprouting susceptibility, so this would be worth monitoring in the potato store at the seed site.

Cultivars and clones with high GCAs were identified for use as parents in future breeding (Table 3), and the extent to which GCAs could be predicted from the parents, and offspring means from the midparent means, were determined and expressed as correlations for comparison with earlier work (Table 5). However, both the GCA-parent and offspring-midparent covariances are estimates of the parent-offspring covariance and, hence, the offspring-midparent regression (Table 5) and twice the GCA-parent regression, are both estimates of narrow-sense heritability for predicting the immediate response to selection of the phenotypically better parents (midparent values) for use in a breeding programme. For one set of F_1s in a diallel with k parents, the offspring-midparent regression does equal twice the GCA-parent regression because the ratio of twice the variance of midparent values to the variance of parental values and the ratio of the offspring-midparent covariance to the GCA-parent covariance are both (k–1)/(k+1). Where low heritabilities were the result of environmental and genotype × environmental interaction variation (e.g. scab), the heritability and response to selection could be increased through increased replication in individual trials and of environments, respectively, if this was thought to be a good use of additional resources. Where low values were due to SCA (e.g. maturity, yield and visual size), the narrow-sense heritability can not be increased and sufficient crosses need to be made and assessed in order to find the best ones for cultivar production. Nevertheless, selection of the better parents for crossing is considered worthwhile for all traits except visual appearance and uniformity for which the offspring-midparent correlations were really low (Table 5). The only really low correlations ($r < 0.4$) found by Brown and Caligari (1989), Maris (1989) and Neele et al. (1991) were for date of emergence and plant height (out of ten traits) by Maris and ware tuber yield (out of 11 traits) by Neele et al., whereas the highest correlation found by Gopal (1998) was 0.42 for tuber shape (out of ten traits). Again, these differences emphasise the importance of determining the extent and nature of the genetical variation available at the start of a new breeding programme, and the value of progeny tests for this purpose (Bradshaw et al. 1995).

For all traits except fry colour, the mean of the parents was higher than the mean of the F_1s, although the differences were not always statistically significant (Table 1). Presumably, on crossing parents which have been selected for desirable characteristics, more favourable combinations of genes are broken down than reassembled in the offspring. An important consequence of the midparent values being greater, on average, than the offspring means is that the number of clones in a cross exceeding the better parent will be less than expected from just considering the midparent values.

For all traits, the offspring-midself correlations were slightly less than the offspring-midparent correlations. Hence, there would be no advantage in selfing the parents and assessing the selfed progenies in order to improve the prediction of offspring means. Neele et al. (1991) also concluded that there was little or no advantage in using the mean of two selfed progenies as a predictor for the ware potato harvest over the use of the midparent value, although the correlations for midselfs were higher for tuber yield, the number of tubers, and underwater weight. In contrast, Brown and Caligari (1989) found midself values to be superior to midparent values for tuber yield and both of its components, mean tuber weight and number of tubers, and Gopal (1998) found the same for most of the traits in his experiment, although all of the correlation coefficients were of low to moderate magnitude. It would, therefore, seem desirable to seek theoretical explanations for these experimental results, if necessary through computer simulations, in order to overcome the complexities of tetrasomic inheritance.

Most traits displayed inbreeding depression, as expected of a highly heterozygous outbreeding crop, with the means of the selfs considerably less than the means of the parents and F_1s (Table 1) for emergence, yield, size and appearance (regularity of shape) of tubers, and visual preference. For visual preference, the magnitude of the difference between the selfs and F_1s varied with the parents (SCA2 in Table 2), as found in the glasshouse by Bradshaw et al. (1995). Again, the difference for cv Stirling was negligible at both the seed and ware site. These results confirm the desirability of minimising inbreeding in a potato breeding programme by avoiding crossing closely related individuals. The one exception to this was fry colour where, on average, the selfs had a desirably lighter colour than the parents and F_1s, although this did vary with parent. Hence, for this trait, positive assortative mating is desirable. Dale and Mackay (1994) reached a similar conclusion for low-temperature sugar-stability and, as already mentioned, the parents identified as best for fry colour are known to be sugar-stable.

In conclusion, it is worth emphasising that the phenotypic and genotypic variances of the parents, the parent-offspring covariance, and the effects of selfing the parents have provided valuable breeding information to complement the combining-ability analysis of the F_1 progenies. Furthermore, the inclusion of the parents and selfs in the same trials as the progenies avoided unwanted problems arising from genotype × environment interactions. It would, therefore, seem worthwhile using computer simulations to explore the possibility of obtaining additional worthwhile information from a genetic-components analysis despite failures of the assumptions in the underlying genetical model.

Acknowledgements Thanks are due to Geoff Swan and Moira Myles for making the crosses, to Finlay Dale (MFBD) for scoring the tuber progeny trials at Blythbank Farm, to Ian Chapman and Malcolm Campbell for help at Blythbank Farm, to Dave Jack for help at Gourdie Farm, to Margaret McInroy for technical assistance, to George Mackay for discussions on potato breeding, and to the Scottish Office Agriculture, Environment and Fisheries Department for funding.

References

Bradshaw JE (1994) Quatitative genetics theory for tetrasomic inheritance. In: Bradshaw JE, Mackay GR (eds) Potato genetics. CAB Int, Wallingford, UK, pp 71–99

Bradshaw JE, Mackay GR (1994) Breeding strategies for clonally propagated potatoes. In: Bradshaw JE, Mackay GR (eds) Potato genetics. CAB Int, Wallinford, UK, pp 467–497

Bradshaw JE, Dale MFB, Mackay GR, Wilkinson MJ (1994) Potato breeding at SCRI: from wild species to finished cultivars. SCRI Annual Report 1994, pp 36–39

Bradshaw JE, Stewart HE, Wastie RL, Dale MFB, Phillips MS (1995) Use of seedling progeny tests for genetical studies as part of a potato (*Solanum tuberosum* subsp. *tuberosum*) breeding programme. Theor Appl Genet 90:899–905

Bradshaw JE, Wastie RL, Stewart HE (1996) Assessing general combining ability for gangrene resistance by means of a glasshouse seedling test. Potato Res 39:179–183

Brown J, Caligari PDS (1989) Cross prediction in a potato breeding programme by evaluation of parental material. Theor Appl Genet 77:246–252

Dale MFB, Mackay GR (1994) Inheritance of table and processing quality. In: Bradshaw JE, Mackay GR (eds) Potato genetics. CAB Int, Wallingford, UK, pp 285–315

Gardner CO, Eberhart SA (1966) Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22: 439–452

Genstat 5 Committee (1993) Genstat 5 release 3 reference manual. Clarendon Press, Oxford

Gopal J (1998) Identification of superior parents and crosses in potato breeding programmes. Theor Appl Genet 96:287–293

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9: 463–493

Killick RJ (1997) Genetic analysis of several traits in potatoes by means of a diallel cross. Ann Appl Biol 86:279–289

Levings CS, Dudley JW (1963) Evaluation of certain mating designs for estimation of genetic variance in autotetraploid alfalfa. Crop Sci 3:532–535

Love SL, Pavek JJ, Thompson-Johns A, Bohl W (1998) Breeding progress for potato chip quality in North American cultivars. Am J Potato Res 75:27–36

Mackay GR, Dale MFB (1990) Quality in potatoes. SCRI Annual Report 1990, pp 9–12

Mackay GR, Todd D, Bradshaw JE, Dale MFB (1997) The targeted and accelerated breeding of potatoes. SCRI Annual Report 1996/97, pp 40–45

Maris B (1989) Analysis of an incomplete diallel cross among three ssp. *tuberosum* varieties and seven long-day adapted ssp. *andigena* clones of the potato (*Solanum tuberosum* L.). Euphytica 41:163–182

Neele AEF, Nab HJ, Louwes KM (1991) Identification of superior parents in a potato breeding programme. Theor Appl Genet 82: 264–272

Pfeffer C, Effmert M (1985) Breeding homozygous parents for resistane to potato scab caused by *Streptomyces scabies* (Thaxt.) Waksman and Henrici. Arch Züchtungsforsch 15:325–333

Plaisted RL, Sanford L, Federer WT, Kehr AE, Peterson LC (1962) Specific and general combining ability for yield in potatoes. Am Potato J 39:185–197

Tai GCC (1976) Estimation of general and specific combining abilities in potato. Can J Genet Cytol 18:463–470

Veilleux RE, Lauer FI (1981) Breeding behaviour of yield components and hollow heart in tetraploid-diploid vs conventionally derived potato hybrids. Euphytica 30:547–561