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

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Abstract A diallel set of crosses, including selfs and some reciprocal crosses, was made between 15 parents chosen for their male fertility from those included in a tetraploid potato (*Solanum tuberosum* subsp. *tuberosum*) breeding programme at the Scottish Crop Research Institute. Seedling progeny tests were used to evaluate the progenies for non-race-specific resistance to late blight (*Phytophthora infestans*) in both foliage and tubers, quantitative resistance to the white potato cyst-nematode (PCN) (*Globodera pallida*) and the commercial worth of their tubers as judged by breeders' visual preference. No reciprocal differences were found. Comparisons of the selfs and crosses revealed inbreeding depression for breeders' preference, which varied among the parents from negligible to severe, whilst there were also statistically significant differences for foliage and tuber blight, but not for PCN. When the selfs were omitted from the combining ability analyses, large differences in general combining ability (GCA) were found for all four traits, and smaller differences in specific combining ability for tuber blight and breeders' preference. The only statistically significant correlation between GCAs for different traits was a favourable one of $r = 0.56$ between foliage and tuber resistance to late blight. It was concluded that prospects were good for simultaneously improving all four traits by multitrait genotypic recurrent selection.

Key words Potato breeding · Combining ability analysis · Late blight · White potato cyst nematode · Breeders' visual preference · Genotypic recurrent selection

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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). Such information can help breeders decide their hybridization strategy, but this is usually specific to the particular population of genotypes under investigation and, hence, must be sought afresh when new material is introduced into a breeding programme. The seedling progeny tests which have been developed and validated in recent years (see Bradshaw and Mackay 1994) are, therefore, of great value for genetical studies because they can be done within a year of making crosses as part of a breeding programme. When GCA proves significant, parents with good GCA can be used again in future crosses, and continued progress can be sought over a number of generations of multitrait genotypic recurrent selection. When SCA is also present, the progeny tests can be used to identify the best crosses for clonal evaluation and cultivar production.

Seedling progeny tests were, therefore, used in genetical studies at the start of a new breeding programme at the Scottish Crop Research Institute. The main aim of the programme is to combine quantitative resistances to late blight [*Phytophthora infestans* (Mont.) de Bary] and the white potato cyst nematode [*Globodera pallida* (Stone)] with commerically acceptable tuber yields and quality, and to do so as quickly as possible. In breeding for late blight resistance, quantitative field resistance is considered preferable to major gene (*R* gene) resistance, which the fungus can readily overcome, and breeders have now largely abandoned the use of the latter (Colon and Budding 1988; Wastie 1991). Furthermore, it is important to select for blight resistance in the tubers as

well as in the foliage because tubers can be infected by spores from the slowly spreading sporulating lesions of a partially leaf-resistant cultivar ('Toxopeus 1958'). Whilst the common UK pathotype (Ro1) of the golden potato cyst nematode (*G. rostochiensis*) can be completely controlled by the dominant gene *H1* from *S. tuberosum* subsp. *andigena* (Cole and Howard 1957), current sources of resistance to the common UK pathotype (Pa 2/3) of *G. pallida* are controlled by a number of genes (Dale and Phillips 1982). Cultivars with some field resistance to late blight and others with partial resistance to the white potato cyst nematode (PCN) are now available in Europe, but none with high levels of resistance to both.

Whilst it was also thought desirable to include, in the breeding programme, parents with virus resistance, particularly to Potato Leaf Roll Luteovirus (PLRV) and Potato Y Potyvirus (PVY), the inheritance of their resistance is either already known to be under major gene control or is being pursued in separate genetical studies (Barker et al. 1994; and see 'Multiplex Parents' in Bradshaw and Mackay 1994).

Materials and methods

Parents and crossing programme

Parents known to be male fertile were chosen so that all could be selfed. Five were chosen for their resistance to late blight, namely clones 8204a4 and 14897ad17 and cvs 'Shelagh', 'Stirling' and 'Teena'. A further 5 parents were chosen for their resistance to the white potato cyst-nematode. Clones 12288af23 and 15119ac5 had resistance derived from *S. vernei*, whereas clones 12601ab1 and 12674ab1, and cv 'Eden', had resistance derived from *S. tuberosum* subsp. *andigena*. Finally, clone G8107 (1) was chosen for its resistance to PLRV and clones G8830 (1), G8866 (11), G8884 (2) and 15144a3 for their resistance to PVY, together with varying degrees of resistance to PLRV. The parents were checked for their foliage resistance to blight in a field test (Stewart et al. 1983a), for their tuber resistance to blight using a laboratory test on freshly dug tubers (Stewart et al. 1983b) and for their resistance to PCN using a closed container test (Phillips et al. 1980). An equal mixture of two isolates of *Phytophthora infestans* was used for the blight tests for reasons explained in the next section.

During the week beginning 18 May 1992, tubers of all parents were planted on bricks in a glasshouse and covered with compost. Once the plants were established, the compost was washed away from the mother tubers, and daughter tubers were removed as they formed in order to encourage flowering. A half-diallel set of crosses plus selfs were made over 2 months from 24 June to 26 August. Some reciprocal crosses were also made. Berries were harvested and stored at 4 °C, and the seed was extracted, counted and packeted by 26 January 1993. Sufficient quantities of seed were secured to assess all families for the commercial worth (breeders' preference) of their tubers, and most families for resistance to late blight and PCN.

Foliage blight progeny test

Four batches of 25 seeds of each of 137 progenies (100 out of 105 crosses, plus 14 out of 15 selfs, plus 23 reciprocal crosses) were sown in 10-cm pots in the glasshouse in April 1993 in an RCB design, as described by Stewart et al. (1983c), and inoculated 36 days later with a mixture of two isolates of *P. infestans* in equal proportions, each at a concentration of 5×10^4 zoospores ml^{-1}. Virulence tests carried out using whole plants of the major gene (*R* gene) differential series (Black et al. 1953) when they were in bud showed that 1 isolate possessed virulence genes overcoming *R* genes 1, 4, 10 and 11, and the other overcame *R* genes 1, 2, 3, 4 and 7. (The mixture used to test the parents had the same virulence genes but in combinations 1, 3, 4, 7, 10, 11 and 1, 2, 3, 4, 7). It was not possible to test for compatibility with R_6 or R_9 because those differentials were unavailable. In the absence of a fully complex isolate, the use of a mixture to overcome any *R* genes likely to be present in the material was the best possible compromise and ensured as far as possible that any resistance expressed was non-race-specific. The proportion of diseased leaf area in each pot of 25 seedlings was assessed after 7 days on the 1–4 scale of increasing resistance described by Stewart et al. (1983c), where 1 represents more than 50% of the leaf area destroyed and 4, less than 10%.

Tuber blight progeny test

Two additional batches of 25 seeds of 123 progenies (89 out of 105 crosses, plus 13 out of 15 selfs, plus 21 reciprocal crosses, from which seed was still available) were similarly sown in mid-July 1993, transplanted after 22 days into 10-cm pots containing a peat-based compost and grown in the glasshouse for a further 72 days. The method of assessing tuber blight was based on that described by Wastie et al. (1987): the contents of each pot were carefully removed, the largest undamaged tuber selected and placed, together with a tuber from each of the other members of the progeny, in an empty 12.5-cm plastic pot. Two replicate bulks of each progeny were thus obtained, which were inoculated by dipping in a mixed suspension of 2×10^4 zoospores ml^{-1} of the 2 isolates described above. After 2 weeks' incubation the number of infected tubers in each sample was recorded, ignoring any infections that had entered via a wound or the stolon scar. The percentage of infected tubers in each sample was calculated and converted to degrees by the variance-stabilising angular transformation before doing more detailed statistical analyses.

White potato cyst-nematode progeny test

Four batches of 25 seeds of each of 127 progenies (96 out of 105 crosses, plus 14 out of 15 selfs, plus 17 reciprocal crosses) were sown in 10.5-cm diameter clay pots in the glasshouse in mid-June 1993 in an RCB design, as described by Phillips and Dale (1982). The pots contained John Innes No. 2 compost that had been inoculated with a population of *Globodera pallida* Pa 2/3 (Lindley) to a concentration of 20 eggs g^{-1}. Eleven weeks after sowing, the rootballs were examined by eye and the cysts counted. The variance-stabilizing square root transformation was performed before doing more detailed statistical analyses.

Commercial worth of tubers (breeders' preference) progeny test

Four batches of 25 seeds of each of 143 progenies (105 crosses, plus 15 selfs, plus 23 reciprocal crosses) were sown in 10-cm pots at the beginning of April 1993 and placed under a mist unit in an RCB design. After 4 weeks, 18 randomly chosen seedlings from each pot were transplanted into 10-cm square pots that were arranged in two rows of nine on a glasshouse bench in the same RCB design. Fisons Levington F2 peat/sand compost was used for both seed and seedlings. The seedlings were grown to maturity and the senesced foliage removed at the end of August. The pots were covered with polythene to prevent surface tubers greening while the compost dried out. By mid-September the compost had been removed from each pot and the tubers returned to the empty pots. Between 16 and 23 September the tubers in each pot were independently assessed by two breeders on a 1–9 scale of increasing preference, as described by Brown et al. (1988). 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 a correlation for the means of 18 seedlings of $r = 0.77$ with the selfs included and $r = 0.67$ without them.

Statistical methods

A preliminary analysis of variance of progeny means tested for differences between progenies and also 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 are assumed to be a random sample and the GCA item is tested for significance against SCA. The analyses, including the estimation of GCAs and their standard errors, were done by multiple linear regression because some crosses were missing in some progeny tests, whereas others were present in duplicate where reciprocal crosses had been made. 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 time 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. For reasons to be explained later, the GCAs presented in this paper are those estimated from the method 4 analysis in which the selfs are omitted and the model 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.

Results

Blight and PCN data for the parents are shown in Table 1. There were insufficient tubers of clones 12601ab1 and G8107(1) available for their inclusion in the blight tests, but previous tests had shown them to be susceptible in both foliage and tubers. The tests confirmed that parents chosen for their resistance to late blight or PCN did indeed have degrees of resistance and also revealed that clones 12674ab1 and 15144a3 possessed resistance to blight in their tubers.

The results of the analyses of variance for the diallel are shown in Table 2. In the analysis with selfs there were statistically significant differences in GCA for all four traits, and in SCA for foliage blight (item 1), tuber blight (items 2 and 3) and breeders' preference (items 1,2 and 3), but not for PCN. Overall inbreeding depression was large for breeders' preference (mean of 105 crosses minus mean of 15 selfs = 0.675) but varied over parents from negligible for cv 'Stirling' (−0.125) to severe for clone 15119ac5 (1.47). For foliage blight and tuber blight, SCA items 1 and 2, respectively, were only significant at the 5% level. In the analysis without selfs there were again statistically significant differences in GCA for all four traits and, as indicated above, in SCA for tuber blight and breeders' preference but not for foliage blight and PCN. No reciprocal differences were detected. Accurate estimates of the GCA and SCA components of variance were not sought for reasons to be explained later, but an indication of their relative magnitudes was obtained from the ratio:

(GCA mean square minus SCA mean square) ÷ 13 versus SCA minus residual MS.

From the analysis without selfs, for tuber blight and breeders' preference, this ratio was 4.2 and 2.5, respectively.

The GCAs estimated from the F_1 generation (i.e. excluding selfs) are shown in Table 3. They have differing standard errors and do not sum to zero because some parents were involved in more crosses than others. The scales of measurement were such that parents with good GCAs for foliage blight resistance and breeders' preference have high positive values, whereas those with good GCAs for tuber blight and PCN resistance have high negative values. The 5 parents chosen for their blight resistance and the 5 chosen for their PCN resistance had the highest positive and negative GCAs for foliage blight and PCN, respectively. Furthermore, the 5 blight resisters all had negative GCAs for tuber blight, but so did 2 of the PCN resisters. Clone 8204a4 and cv 'Stirling' had the best GCAs for both foliage and tuber blight resistance, and clone 12601ab1 the best GCA for PCN resistance. Although none of the virus-resistant parents conferred blight or PCN resistance on their offspring, they did differ in their GCAs, i.e. some conferred more susceptibility than others on their offspring. At least one parent in each group of 5 had a high GCA for breeders' preference.

The only statistically significant correlation between GCAs for different traits was between foliage and tuber blight ($r = -0.56$, $P = 0.05 - 0.02$), the correlation being negative because foliage resistance was expressed on an increasing scale whereas tuber resistance was on a decreasing scale. The correlations between parental scores (Table 1) and their GCAs (Table 3) for foliage blight, tuber blight and PCN were $r = 0.87$, 0.76 and 0.90 ($P < 0.01$), respectively.

Table 1 Blight and PCN data for the parents

	Foliage blight 1 sus – 9 res	Tuber blight (% tb)	PCN (% of cv Desiree)
8204a4	8.0	0.0	42.5
Stirling	7.5	2.0	65.7
14897ad17	7.5	0.0	55.6
Teena	6.0	27.9	65.7
Shelagh	5.5	62.7	60.9
12601ab1	–	–	6.5
15119ac5	3.5	96.3	15.3
12674ab1	4.5	3.3	6.7
12288af23	1.5	100.0	25.0
Eden	3.0	86.5	16.6
G8107(1)	–	–	63.3
G8830(1)	3.5	62.5	64.7
G8866(11)	4.0	90.0	68.6
G8884(2)	3.5	94.7	91.0
15144a3	4.5	4.1	67.4
S.E.	0.54	5.23	8.01

Discussion

The combining ability analyses were used to partition the genetical variation between the means of seedling progenies into components due to GCA and SCA. Such

Table 2 Analyses of variance of data from progeny tests – mean squares divided by numbers of reps and significance

	Foliage blight 1 sus – 4 res		Tuber blight ang (% tb)		PCN sq rt (no. cysts)		Breeders' preference 1 poor – 9 good	
	df	MS	*df*	MS	*df*	MS	*df*	MS
With selfs								
Rep	3	0.836***	1	2176***	3	13.29***	3	0.209***
Progeny	136	0.310***	122	206***	126	3.28***	142	0.166***
GCA	14	2.055***	14	1424***	14	26.57***	14	0.794***
SCA	99	0.120*	87	50***	95	0.37^{NS}	105	0.111***
1	1	0.460*	1	78^{NS}	1	0.01^{NS}	1	6.024***
2	13	0.152^{NS}	12	71*	13	0.55^{NS}	14	0.103***
3	85	0.111^{NS}	74	47**	81	0.35^{NS}	90	0.046**
recips	23	0.063^{NS}	21	39^{NS}	17	0.33^{NS}	23	0.036^{NS}
Residual	398(10)	0.089	117(5)	32	375(3)	0.34	426	0.032
Without selfs								
Rep	3	0.731***	1	2081***	3	11.36***	3	0.228***
Progeny	122	0.285***	109	172***	112	2.96***	127	0.102***
GCA	14	1.701***	14	1037***	14	21.22***	14	0.572***
SCA	85	0.111^{NS}	74	47***	81	0.35^{NS}	90	0.046***
recips	23	0.063^{NS}	21	39^{NS}	17	0.33^{NS}	23	0.036^{NS}
Residual	356(10)	0.091	104(5)	29	333(3)	0.33	381	0.030

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

Table 3 General Combining Abilities estimated from F_1 generation

Parent	Foliage blight 1 sus – 4 res		Tuber blight ang (% tb)		PCN sq rt (no. cysts)		Breeders' preference 1 poor – 9 good	
	GCA	SE	GCA	SE	GCA	SE	GCA	SE
8204a4	0.624	0.071	−11.88	1.55	1.001	0.143	−0.079	0.047
Stirling	0.617	0.084	−9.70	1.99	1.022	0.161	0.123	0.055
14897ad17	0.279	0.079	−8.10	1.67	0.577	0.147	0.286	0.052
Teena	0.228	0.079	−4.61	1.67	0.777	0.156	−0.264	0.051
Shelagh	0.119	0.094	−6.14	2.81	0.660	0.201	0.002	0.057
12601ab1	−0.317	0.073	3.94	1.55	−2.403	0.136	−0.174	0.047
15119ac5	0.019	0.079	5.60	1.67	−1.532	0.147	−0.245	0.051
12674ab1	−0.151	0.090	−9.19	1.99	−1.518	0.168	−0.024	0.055
12288af23	−0.371	0.079	7.05	1.72	−1.299	0.147	−0.115	0.052
Eden	−0.175	0.077	−5.51	1.78	−0.737	0.147	0.259	0.051
G8107(1)	−0.390	0.093	6.07	2.28	0.549	0.181	0.300	0.057
G8830(1)	−0.390	0.077	6.79	1.79	1.264	0.161	−0.161	0.051
G8866(11)	0.055	0.081	10.52	1.90	0.801	0.151	0.008	0.054
G8884(2)	0.056	0.087	16.18	1.90	0.806	0.173	0.032	0.055
15144a3	−0.260	0.075	0.54	1.63	1.407	0.151	0.181	0.049

an approach excludes the possible detection of major genes through their discrete segregation within progenies, but no major genes of interest were anticipated in the material under study. In assessing the commercial worth of tubers through breeders' visual preference, we took yield and regularity of shape into account, but not discrete characteristics such as skin colour. Dale and Phillips (1982) had shown that the distribution of resistance of *G. pallida* in progenies derived from *S. vernei* and from *S. tuberosum* subsp. *andigena* CPC2802 was continuous and different from the discrete partitioning of resistance to *G. rostochiensis* in the progenies from parents with the *H1* gene from CPC1673. Finally, Stewart et al. (1994) found no evidence of major *R* genes segregating among clones from crosses between resistant (including 'Shelagh', 'Stirling' and 14897ad17) and susceptible parents assessed for foliage and tuber resistance with the same two races as used here. It should, however, be pointed out that the presence of an unidentified *R* gene (or genes) in a parent would primarily increase the means of all its progenies and hence its GCA, the extent depending on whether the parent was resistant to one or both races in the mixture.

The parents were chosen for their blight, PCN and virus resistance from larger sets of such parents included in the breeding programme and, hence, can be regarded as a sample from this larger population, about which inferences are to be made. It was, therefore, considered appropriate to use model II of Griffing (1956) and test for the presence of GCA variation against the SCA item in the analysis of variance, and also to exclude the parents selfed when estimating GCAs, as advocated by

Wright (1985). Comparison of the selfs and crosses did, however, provide information about inbreeding depression. As there was no reason to assume that the parents were derived from a random mating population in equilibrium, no attempt was made to estimate additive (σ_A^2) and dominance (σ_D^2) variances from the GCA and SCA variances because covariances occur between A and D in a non-equilibrium population (Bradshaw 1994). Nevertheless, the large amounts of GCA variation found for all traits must be indicative of much additive genetic variance in the population. Furthermore, the only correlation between traits for GCAs was a favourable one between foliage and tuber resistance to late blight. It would, therefore, seem reasonable to anticipate continued progress over a number of generations of multitrait genotypic recurrent selection, even though the expected response cannot be accurately predicted.

Concerning foliage blight, the 14 selfs were, on average, slightly more susceptible than the 100 crosses (1.70 versus 1.93); otherwise all of the variation was due to GCA, with 'Stirling' and 8204a4 the best parents. Similarly, Stewart et al. (1992) found large differences between 10 parents in their GCAs that were consistent over 2 years, together with an SCA × year interaction. Likewise, Wastie et al. (1993) found large differences in the GCAs of a different set of 10 parents, together with some SCA. Again, 'Stirling' was one of the best parents in both studies. In contrast, Killick and Malcolmson (1973) found that the majority of clones they examined showed no differences in GCA and that the major source of genetical variation was SCA. However, in a later study with different material, Malcolmson and Killick (1980) found all GCA and no SCA. One clone in their earlier study, M109-3, was superior to the rest in GCA and features in the pedigrees of some of the Scottish Crop Research Institute's (SCRI's) recently bred cultivars with high levels of foliage and tuber resistance, including cv 'Stirling' (Wastie 1991). This cultivar came from a cross between clones 8204a4 and 8318-6, the latter being a sister seedling of 8318-4 and 8318-10 which, together with 8204a4, were the three clones with the highest GCAs for foliage resistance reported by Malcolmson and Killick (1980). From these results and the lack of evidence of major gene segregation in a cross between 'Stirling' and a susceptible parent (Stewart et al. 1994), one can tentatively conclude that 'Stirling' has a high level of non-major gene resistance that has been built up and maintained over a number of cycles of crossing and selection, starting from the crosses made by Black (1970) in 1954 when he commenced breeding for field resistance from *S. demissum*-derived material. In contrast, the previously reported (Wastie et al. 1993) high foliage resistance of cv 'Shelagh' was probably due, in part, to R_{10}, as its GCA was lower in this study where one isolate was compatible with R_{10}.

Although some variation due to SCA was present, the large differences in GCA for resistance to tuber blight accounted for most to the variation. In the two previous studies already referred to (Stewart et al. 1992, Wastie et al. 1993), SCA and an SCA × year interaction were present in the first, but no SCA was detected in the second. Although 'Stirling' and 'Teena' were the only parents common to all three studies, 'Stirling' had either the best or second-best GCA in all three and is, therefore, still the best parent from the SCRI programme to use for blight resistance. However, it is also clear from Table 3 that judicious choice of PCN- and virus-resistant parents could aid the achievement of resistance to tuber blight.

The moderate correlation ($r = -0.56$) between GCAs for foliage and tuber resistance was similar to that found by Stewart et al. (1992) but lower than that found by Wastie et al. (1993). Clearly, there is an association between resistance in foliage and tubers that can be exploited in a breeding programme, but it is not sufficiently strong to screen progenies for only one aspect of resistance, as discussed by Stewart et al. (1994).

Parental and GCA scores were highly correlated for foliage blight and moderately correlated for tuber blight, as also found by Stewart et al. (1992). Hence, parental phenotypes can be used as a first screen to select blight-resistant parents for use in a breeding programme.

For PCN, all of the variation between progenies could be accounted for by the differences in the GCAs of the parents. Parental and GCA scores were highly correlated, with the 5 parents chosen for their PCN resistance having the best GCAs. Nevertheless, the other parents did differ in their GCAs, with some conferring greater susceptibility on their progenies than others. The two parents (12288af23 and 15119ac5) with resistance derived from *S. vernei* shared a common parent, clone 10300-13. Interestingly, this clone had the third-best GCA out of 24 parents used by Phillips et al. (1979) to study the inheritance of resistance derived from *S. vernei*, although they found SCA to be as important as GCA, and a poor parental phenotype-GCA correlation ($r = 0.46$) as a consequence. In a half-diallel set of crosses involving 11 parents with resistance derived from *S. tuberosum* subsp. *andigena* CPC2802, Phillips and Dale (1982) again found that GCA and SCA were equally important. They attributed the presence of significant SCA effects to a narrowed genetic base as a consequence of selecting only resistant parents. In contrast, when they crossed the 11 resistant parents with 7 susceptible clones in a North Carolina 2 design, no SCA was detected and there were differences between both the resistant and susceptible parents in their GCAs, as found here. Hence, the choice of the susceptible as well as the resistant parent influences the outcome of a cross. Indeed, Dale and Phillips (1985) recommended that plant breeders should capitalize on any additional resistance available by the judicious choice of 'susceptible' parents.

The glasshouse progeny test for breeders' preference has been shown to correlate well with progeny mean preference scores made in the first and second clonal years at both a seed and ware site (Brown et al. 1988). It

therefore seems reasonable to compare our glasshouse results with earlier ones from both the field and glasshouse. Brown and Caligari (1989), Maris (1989) and Wastie et al. (1993) all found large differences in GCA but no SCA, whereas Neele et al. (1991) found SCA as well as GCA, although the GCA variance was larger than the SCA variance, as found in this present study. Maris (1989) made reciprocal crosses and found reciprocal differences, whereas none were found in our diallel for breeders' preference, nor indeed for PCN and blight resistance. Maris, however, included *S. tuberosum* and *S. andigena* parents in his incomplete diallel, and reciprocal differences have often been reported in crosses between these subspecies (Hoopes et al. 1980; Tarn and Miller 1981). So, for breeders' preference, one can conclude that GCA is more important than SCA, but one cannot predict when or how much SCA will occur. The fact that the differences between selfs and crosses varied from a negligible to a large inbreeding effect is interesting because breeders' preference does include a visual assessment of yield as well as quality. *S. tuberosum* is a tetraploid in which individual genotypes are usually highly heterozygous and display inbreeding depression on selfing (Mendoza and Haynes 1974). However, tetraploid potatoes are self-compatible, and the gene pool of modern cultivars is rather limited and inbred (Glendinning 1983), so perhaps potato breeders have unintentionally practised some selection for clones less prone to inbreeding depression.

Finally, it is worth emphasizing the advantages of using seedling progeny tests to provide genetical data within a year of making crosses. Resources do not need to be diverted from a breeding programme in order to gain knowledge of the inheritance of economically important traits, and such information is directly relevant to the programme. Parents with good GCA are rapidly identified for use in further breeding, and prospects for continued progress through multitrait genotypic recurrent selection are also quickly assessed. Lastly, any SCA found can be immediately exploited by selecting the best crosses for clonal evaluation and cultivar production.

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