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Disease resistance in *Solanum phureja* and diploid and tetraploid *S. tuberosum* × *S. phureja* hybrids

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Summary

Diploid *Solanum phureja*, diploid and tetraploid *S. tuberosum* × *S. phureja* hybrid, and tetraploid *S. tuberosum* backcross clones were assessed for resistance to commercially important diseases. There was a reduction in the expression of *S. phureja* characteristics with increasing dosage of *S. tuberosum* genetic material. The generally high resistance of the *S. phureja* group to common scab, potato leafroll virus and potato virus Y decreased, while resistance to gangrene, foliage and tuber blight tended to increase.

Resistance genes were probably well dispersed throughout the *S. phureja* genotype so that many were lost on hybridisation, but *S. phureja* could be a useful source of scab and virus resistance in the production of *S. tuberosum* cultivars.

Introduction

A pool of *Solanum phureja* clones has been developed over more than 20 years at the Scottish Crop Research Institute (SCRI) by a combination of mass selection and pedigree breeding, chiefly to improve yield and other tuber characteristics (Carroll, 1982). The objective in using the species was to hybridise it with *S. tuberosum* and increase the genetic diversity of germplasm available for producing new cultivars. In this way the programme paralleled that using the tetraploid species *S. andigena*, as described by Glendinning (1975). To maximise the fertility of the interspecies crosses, hybridisations were initially carried out using parents of the same ploidy, with *S. tuberosum* being reduced from 4x to 2x by dihaploid induction. However, as tetraploidy is considered to be the optimum ploidy level for *S. tuberosum* (Mendoza & Haynes, 1974), 4x × 2x crosses were also carried out by pollinating *S. tuberosum* cultivars with *S. phureja* to produce 4x offspring from the fertilisation of normal 2x eggs by 2x sperms from unreduced pollen. To recover more of the *S. tuberosum* phenotype and hence increase their agronomic performance, some of these tetraploid hybrids were back-crossed to 4x cultivars.

Carroll & De,Maine (1989), in reporting on the 4x F1 hybrids, concluded that the high tuber number from *S. phureja* and high tuber weight from *S. tuberosum* complemented each other, to produce high-yielding offspring. The emphasis in this work had been primarily on assessing the effect of *S. phureja* germplasm on yield and finding parental clones which, while giving high yields, also gave visually acceptable tubers in their offspring. Work on the disease resistance of the material went on in

parallel but was to remain of secondary importance until the problems of tuber appearance, such as roughness, deep eyes and lack of dormancy, could be overcome. Selection therefore was not based on disease resistance. This means that, assuming no linkage between disease resistance and tuber appearance, the material can be used to illustrate the effects of hybridising the two species, represented by our populations, on disease resistance. It has been possible to identify individual clones resistant to common diseases. Carroll (1982) found moderate resistance to foliage blight (*Phytophthora infestans*) in SCRI *S. phureja* clones in field tests but not in laboratory or glasshouse tests. Carroll (1987) also found there were clones with resistance to potato leafroll virus, potato virus Y, common scab (*Streptomyces scabies*) or gangrene (*Phoma foveata*). The best indication of whether progress is being made by using *S. phureja* in a breeding scheme is to examine the groups of material generated from it. Selection can then be concentrated on the best group in order to increase the efficiency of clonal selection. Also trends in resistance levels can be observed in order to give some idea of the future progress likely to be made as breeding continues. Screening for resistance to a number of fungal and virus diseases was routinely carried out over a period of 10 years on *S. phureja* clones and *S. tuberosum* × *S. phureja* diploid and tetraploid hybrids, previously selected on the basis of high yield and other good tuber characters. A summary of all the results of this screening is presented in this report.

Data based on the screening of material in a breeding scheme are seldom complete, as selection progressively depletes families, making parental comparisons difficult. We have therefore compared four types of hybrids as populations (*S. phureja* × *S. phureja*, *S. tuberosum* (2x) × *S. phureja*, *S. tuberosum* (4x) × *S. phureja*, *S. tuberosum* (4x) × (*S. tuberosum* × *S. phureja* (4x))) ignoring differences between parent clones. This is reasonable because we are dealing with two different species, the differences between which are likely to be greater than those within each species. The same *S. phureja* clones and *S. tuberosum* cultivars were used in each population except for the 2x F1 hybrids which were produced using *S. tuberosum* dihaploids from various tetraploid breeding lines. Comparing these populations therefore is a means of examining the interactions between species and ploidies rather than between parental clones.

Materials and methods

Diploid *S. phureja* clones, selected on the basis of tuber yield, size, shape and dormancy, were used to pollinate *S. tuberosum* dihaploids and tetraploid *S. tuberosum* cultivars. Diploid *S. phureja* × *S. phureja*, diploid and tetraploid *S. tuberosum* × *S. phureja* hybrids and tetraploid *S. tuberosum* × (*S. tuberosum* × *S. phureja*) material was obtained. Root-tip squashes were used to check the somatic chromosome number of seedlings obtained from 4x × 2x crosses and only tetraploid offspring retained. Seedlings which had been selected on the basis of their tuber characters after assessment over two or more years in field plots were screened for disease resistance. The numbers of clones from each type of cross which were subjected to the different disease resistance tests varied (Tables 1 to 3).

The *S. tuberosum* cultivars used to produce the 4x F1 and back-cross hybrids were Record, Pentland Dell, Ulster Concord, Golden Wonder, Arran Consul, Maris Piper, Pentland Squire, Stormont Enterprise and Desiree. Five *S. phureja* clones,

BZ115, 13T8, 13T48, DB152(31) and DB171(11), were the parents or grandparents of most of the hybrid material.

Clones were assessed for resistance to common scab by comparing their reaction with those of control cultivars having a range of resistances in a non-irrigated field trial grown in soil naturally infected with *S. scabies* in East Lothian, Scotland. A three-replicate randomised complete block design was used, each clone being represented by a two-tuber plot once and each control twice in each replicate.

Resistance to gangrene was tested using the method of Wastie et al. (1988) and foliage and tuber blight resistance tested by the methods of Stewart et al. (1983a,b), using complex race 1, 2, 3, 4, 5, 7, 8, 9, 10, 11 of *P. infestans*. Resistances to potato leafroll virus and potato virus Y were tested by exposing tuber-derived plants to infection in the field as described by Davidson (1973).

All the assessments were converted to a score on a 1 (highly susceptible) to 9 (highly resistant) scale. Where tests were carried out on the same clone in more than one year the mean of the scores has been used for analysis.

The cultivar parents were not included in the resistance tests, the objective in producing the hybrids being to assess chiefly their tuber characteristics when compared with standard cultivars chosen for their high tuber yield, good shape and size (see Carroll & De,Maine, 1989). However, for reference, the mean of the *S. tuberosum* cultivar resistance scores (National Institute of Agricultural Botany, 1990) has been given for the 4x F1 and back-cross populations weighted according to the proportion of offspring arising from each cultivar. The weighted mean of the other parent group has also been given for reference, where available. Single factor analyses of variance were carried out for each disease resistance to compare progeny groups. Comparisons between groups within all possible pairs were carried out using *t* tests. Two factor analyses of variance were carried out using the mean scores for common scab and blight resistance by the computer statistics package, GENSTAT (Lawes Agricultural Trust), which allows for missing values.

Results

The mean scores and the number tested in each genotype group are given in Table 1 for each disease resistance. The high common scab resistance of the *S. phureja* group was reduced by over 10% by the introduction of a single *S. tuberosum* genome in the 2x hybrids and this is statistically significant ($P<0.05$). The presence of an additional *S. tuberosum* genome in the 4x hybrids coincided with a further significant reduction ($P<0.001$) in scab resistance. Further dilution of *S. phureja* genetic material also resulted in a further reduction in resistance as shown by the mean score for the 4x *S. tuberosum* backcross group although this was not statistically significant ($P>0.05$).

The mean gangrene resistance of the *S. phureja* group increased by 18% with the introduction of one *S. tuberosum* genome and there was a further increase with the addition of a second. Although each increase in resistance was not statistically significant, there was a significant increase in going from *S. phureja* to 4x hybrids ($P<0.001$). Although gangrene resistance in the *S. phureja* group on average was low, as reported by Carroll (1987), several individual clones had high scores. There was no discernible effect on foliage blight resistance of diluting *S. phureja* by *S. tuberosum* genetic material to produce 2x and 4x F1 hybrids. The backcross hybrids,

Table 1. Mean scores ($\bar{x}$) for resistance to six pathogens, numbers tested (nr) and standard errors (se) of four progeny groups from hybridisations involving *Solanum tubersum* (tbr) and *S. phureja* (phu). The weighted means of the parents are given where available.

Progeny group type	Parent group means	Progeny group	Resistance to					
			Common scab	Gangrene	Tuber blight	Foliage blight	PLRV	PVY
phu (2×)		$\bar{x}$	6.7	3.3	3.0	3.7	3.8	6.1
		nr	160	132	105	153	104	104
		se	0.14	0.18	0.23	0.08	0.35	0.37
tbr × phu	tbr (2×)		5.4	–	5.6	4.4	–	–
(2× F1)	phu		7.7	4.5	4.7	4.0	–	–
		$\bar{x}$	5.9	3.9	2.9	3.6	4.7	5.7
		nr	37	28	54	38	16	17
		se	0.33	0.42	0.33	0.16	0.92	0.92
tbr × phu	tbr (4×)		3.7	6.0	5.9	5.5	3.7	4.1
(4× F1)	phu		8.4	1.9	3.7	3.7	4.4	9.0
		$\bar{x}$	4.6	4.6	3.9	3.7	3.1	3.1
		nr	102	97	108	104	95	96
		se	0.16	0.24	0.21	0.11	0.26	0.33
tbr ×	tbr (4×)		4.1	–	5.8	5.4	–	–
(tbr × phu)	tbr × phu		5.6	–	–	3.8	–	–
(4×)	(4×)	$\bar{x}$	4.3	–	3.6	4.4	–	–
(backcross)		nr	25	–	18	48	–	–
		se	0.28	–	0.58	0.32	–	–

however, were significantly more resistant than *S. phureja* ($P<0.001$). Two *S. tuberosum* genomes in the genotype coincided with a reduction in the level of PLRV and PVY resistance (although this was only significant in the case of PVY ($P<0.001$)) and an increase in the level of tuber blight resistance ($P<0.001$). The mean resistance scores in Table 1 can be used to derive scores for the likeness of material to the *S. phureja* phenotype. Using a 1 – 9 scale where similarity to *S. phureja* scores high, the scab, PLRV and PVY resistance scores can be retained as likeness scores since resistance decreased between *S. phureja* and *S. tuberosum*. The reciprocals (computed as ten minus the resistance score) would be used to obtain likeness scores from gangrene, tuber and foliage blight resistance scores as resistance increased from *S. phureja* to *S. tuberosum*. There was a significant negative correlation between *S. phureja* likeness scores and content of *S. tuberosum* germplasm, from *S. phureja* (zero *S. tuberosum* content) through 4x F1 (average 50%) and 4x back-cross (average 75%) to *S. tuberosum* cultivars (100%) ($r=-0.560$; $P<0.01$). The correlation was improved when the PLRV scores, which showed an unclear trend, are withheld from the analysis ($r=-0.727$; $P<0.001$). Comparing the 2x and 4x F1 hybrids, the addition of a second *S. tuberosum* genome always reduced the likeness of the material to *S. phureja* even though the average proportions of germplasm from both species were the same in each group.

Table 2 gives the mean common scab resistance scores shown by each genotype

Table 2. Mean scores ($\bar{x}$) for resistance to common scab (*Streptomyces scabies*) of four *Solanum phureja* clones and their offspring from hybridisations involving *S. phureja* (phu) and *S. tuberosum* (tbr). Number of clones (nr) tested in each progeny group, standard errors (se) and weighted means of parents are given where available.

Progeny group type	Parent means	Progeny group	BZ115	13T8	13T48	DB152(31)	se (group)
	own score		-	8.3	9.0	6.0	0.46
phu (2×)	phu		-	7.4	8.1	-	
		$\bar{x}$	-	6.6	6.5	-	0.57
		nr	-	12	5.0	-	
tbr × phu	tbr (2×)		5.5	5.4	5.5	-	
(2× F1)		$\bar{x}$	6.0	5.0	6.7	-	0.46
		nr	5.0	5.0	4.0	-	
tbr × phu	tbr (4×)		5.0	3.8	3.6	3.4	
(4× F1)		$\bar{x}$	5.3	4.4	4.8	5.0	0.40
		nr	3.0	33	61	5.0	
tbr ×	tbr (4×)		5.0	4.1	3.9	-	
(tbr × phu)	tbr × phu		6.3	5.7	5.8	-	
(4×)	(4×)						0.46
(backcross)		$\bar{x}$	3.6	4.3	4.5	-	
		nr	8.0	10	10	-	
se (clone)			0.46	0.36	0.36	0.57	

group derived from four *S. phureja* clones. Where known, the resistance score of the *S. phureja* parent is given. For all four parental clones the progeny group mean scab resistance scores decreased from top to bottom down the table, coinciding with an increase in *S. tuberosum* genomes from one to two, followed by further dilution of the *S. phureja* gene complement to an average of about 25% in the backcross material.

One tetraploid clone obtained from the cross between the common scab susceptible cultivar Maris Piper and the *S. phureja* clone 13T8 gave a scab resistance score of 6.7. Two clones obtained from the backcross between this clone and cv. Maris Piper and selected on the basis of tuber characteristics had scab resistance scores of 2.3 and 2.8 respectively. Also, a tetraploid hybrid from the cross cv. Ulster Concord × 13T48, previously selected for good tuber yield, shape and size, scored 6.7. A selected clone from the backcross between the hybrid clone and cv. Maris Piper scored 5.7.

Table 3 gives the mean foliage blight resistance scores shown by each genotype group derived from five *S. phureja* clones and the parent's score where known. Although the trend was less clear than with common scab, there was a rising level of blight resistance as the *S. phureja* parental gene complement was reduced. The resistances of DB152(31) and DB171(11) were increased in the 4x hybrid group and the resistances of the 4x hybrids derived from BZ115, 13T8 and 13T48 increased in the *S. tuberosum* backcross group.

Table 3. Mean scores ($\bar{x}$) for resistance to foliage late blight (*Phytophthora infestans*) of *Solanum phureja* clones and their offspring from hybridisations involving *S. phureja* (phu) and *S. tuberosum* (tbr). Number of clones (nr) tested in each progeny group, standard errors (se) and weighted means of parents are given where available.

Progeny group type	Parent means	Progeny group	BZ115	13T8	13T48	DB152(31)	DB171(11)	se (group)
	own score		-	4.0	-	2.5	3.5	0.25
phu (2×)	phu		-	-	-	-	-	
		$\bar{x}$	-	3.1	-	-	-	0.43
		nr	-	9.0	-	-	-	
tbr × phu	tbr (2×)		4.8	4.7	3.7	-	-	
(2× F1)		$\bar{x}$	3.8	4.5	3.3	-	-	0.25
		nr	4.0	7.0	4.0	-	-	
tbr × phu	tbr (4×)		6.7	5.9	5.4	5.7	6.3	
(4× F1)		$\bar{x}$	3.5	3.7	3.6	3.5	4.4	0.19
		nr	3.0	30	46	3.0	8.0	
tbr ×	tbr (4×)		6.0	6.1	5.1	-	-	
(tbr × phu)	tbr × phu		4.5	4.0	3.5	-	-	
(4×)	(4×)							0.25
(backcross)		$\bar{x}$	4.9	4.3	4.1	-	-	
		nr	13	10	31	-	-	
se (clone)			0.25	0.19	0.25	0.30	0.30	

We found significant differences between *S. phureja* parents using the 4x F1 mean PVY resistance scores ($P<0.05$) but not using the other disease resistances.

Discussion

The resistance or susceptibility of *S. phureja* clones to different diseases was usually reduced when *S. tuberosum* genomes were combined with those of *S. phureja*. Therefore, as the *S. phureja* germplasm became progressively diluted, the level of resistance increasingly resembled that of *S. tuberosum*, as represented by the cultivars used in this experiment. The combination of one *S. tuberosum* genome, from a dihaploid, with one from *S. phureja* resulted in diploid hybrids usually with reduced expression of *S. phureja* characters. The tetraploid hybrids were formed by the combination of two *S. phureja* genomes from 2x pollen with two *S. tuberosum* genomes from 2x eggs. It was assumed by Carroll (1977) from his own observations and the evidence of Quinn et al. (1974) that the unreduced pollen produced by the *S. phureja* parents was produced by First meiotic Division Restitution (FDR). With FDR pollen, much of the original genotype of the pollen parent would be preserved and transferred into the hybrids (Mendiburu et al., 1974). More gene combinations governing *S. phureja* characters would therefore be transferred to the tetraploid than to the diploid hybrids. If diploid pollen from the *S. phureja* parent was produced by Second Division Restitution (SDR), fewer of its gene combinations would be passed

on to 4x offspring but, on average, the dilution by *S. tuberosum* genes would be similar to that occurring in 2x hybrids. Although the proportion of *S. tuberosum* to *S. phureja* genomes in both diploid and tetraploid hybrids is the same (1:1), Table 1 shows that the characteristics of the tetraploids were less like those of *S. phureja* as a group than the diploid hybrids. The addition of a second *S. tuberosum* genome appears to reduce *S. phureja* characteristics further, even though most of its gene combinations have been transferred intact into 4x offspring (Mendiburu et al., 1974).

Common scab, PLRV and PVY resistances were, in the examples given here, reduced from their *S. phureja* levels more in the tetraploid than in the diploid hybrids whereas gangrene and foliage blight resistances were increased. The effect of further diluting these *S. phureja* genes by backcrossing to the *S. tuberosum* cultivars is shown in Tables 1 and 2 for common scab resistance, which was reduced again. It is further illustrated by the specific examples given above of *S. phureja* clones producing less resistant 4x hybrids whose backcross offspring had resistance even further reduced. Foliage blight resistance was increased slightly by the addition of *S. tuberosum* genetic material.

The reduction in the level of expression of *S. phureja* characters with increasing dosage of *S. tuberosum* genetic material is probably due mainly to the loss of the *S. phureja* genes concerned. It is also possible that genes introduced from *S. tuberosum* interfered with the expression of *S. phureja* genes. Reduced expression of characters would also be due to the disruption of gene combinations and interactions. This probably explains why a progeny group mean can be reduced below the level of its lowest parent group.

In a potato genetic improvement programme, making use of *S. phureja* germplasm where there has been prior selection for yield and other tuber characters, it has been possible only to compare the different types of material as genotype groups rather than as progenies with common parents. It has not been possible to identify the effects of differences between parent clones within the groups. Nevertheless, the results indicate that *S. phureja* could be a useful source of resistance to common scab at the tetraploid level, and possibly PLRV and PVY at the 2x level. They show that the level of dilution of *S. phureja* genetic material in the hybrid genome is important, suggesting a wide dispersion of resistance genes and possibly a lack of dominance in the *S. phureja* genes. They also indicate that, conversely, there may be some risk of increasing susceptibility to gangrene and foliage blight by introducing *S. phureja* germplasm into a *S. tuberosum* breeding scheme.

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