

A review of host major-gene resistance to potato viruses X, Y, A and V in potato: genes, genetics and mapped locations

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In view of modern developments in the technologies available for breeding potatoes for resistance to virus diseases, it is timely to review the host major genes that confer resistance, in *Solanum* species, to potato viruses X, Y, A and V (the viruses for which the resistance genes have been most extensively studied). Over the course of 60 years, many such genes in *Solanum* species have been characterized: a comprehensive list is presented. Inheritance studies are reviewed, including linkage studies and molecular mapping, and the positions of resistance genes mapped so far are listed. It is apparent from recent research that disease resistance genes are often clustered in particular regions of the chromosomes; the significance of these resistance gene clusters is discussed. The information presented will be useful for potato breeding, and for genetic and mapping studies and gene cloning.

Keywords: gene clusters, genetics, host gene, molecular mapping, potato virus, resistance.

The viruses

Potato virus Y (PVY), Potato virus A (PVA) and Potato virus V (PVV) are species in the genus *Potyvirus*, and Potato virus X (PVX) is a species in the genus *Potexvirus*. Symptoms caused by these viruses are described in Jeffries (1998), or for a fuller description of the viruses, see Adams *et al.* (1998). The importance of these and other potato viruses, and the need for resistance, are discussed in Solomon-Blackburn & Barker (2001).

The main strains of PVY are PVY^O (common strain), PVY^N and PVY^C. PVY^N causes necrosis in tobacco (*Nicotiana tabacum*) (De Bokx & Huttinga, 1981). More recently, the strain PVY^{NTN} has been described (Beczner *et al.*, 1984; Le Romancer *et al.*, 1994); it causes necrotic ring blemishes on tubers. The main strain groups of PVX are groups 1–4, defined by Cockerham (1955) in terms of resistance genes in potato, and the resistance-breaking strain PVX^{HB} (Moreira *et al.*, 1980). Group 2 is commonly called B. Group 3 is the ‘common strain’.

The host and its genetics

The cultivated potato *Solanum tuberosum* ssp. *tuberosum* (or Tuberosum) is a self-compatible outbreeding tetraploid, derived from another tetraploid subspecies,

S. tuberosum ssp. *andigena* (or Andigena), which probably evolved from diploid species (Bradshaw & Mackay, 1994). *S. tuberosum* is generally considered to be more or less an autotetraploid whose genes are inherited tetrasomically (Cadman, 1942; Howard, 1970). However, it may be a segmental allotetraploid rather than a true autotetraploid, with consequent occasional deviations from the expected tetrasomic segregation ratios (Bradshaw, 1994). Genes have been introduced into Tuberosum (by crossing) from various wild *Solanum* species (Davidson, 1980; Ross, 1986; Bradshaw & Mackay, 1994), of which most are diploids or allopolyploids in which inheritance is disomic (Cockerham, 1970; Ross, 1986).

In potato breeding programmes, initial hybridization with these wild species has been followed by several generations of backcrossing to establish euploidy and climatic adaptation, and to eliminate unwanted wild characteristics; Ross (1986) considered that this can be achieved within four to six generations. Cockerham (1970) reported that progeny of a sixth backcross generation from hybrids with the allotetraploid *S. acaule* behaved as autotetraploids with tetrasomic inheritance, with very occasional double reduction (and hence random chromatid association) indicated by unexpected homozygous recessive seedlings. *S. stoloniferum* (4x), *S. demissum* (6x) and *S. hougasii* (6x) showed disomic inheritance (Cockerham, 1970), but in Tuberosum breeding lines descended from hybrids with *S. stoloniferum* or

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S. hougasii, segregation ratios indicative of tetrasomic inheritance have been seen (Solomon-Blackburn & Mackay, unpubl. obs.). Ross (1958) found that hybrids between *S. stoloniferum* and *Tuberosum* up to the first *Tuberosum* backcross generation appeared to segregate disomically.

Disomic and tetrasomic segregation ratios

When a parent with dominant major-gene resistance at a single locus is crossed with a susceptible (homozygous recessive) parent, disomic inheritance would result in a segregation ratio of 1:1 (if the parent is simplex) or ∞ :0 (duplex) resistant:susceptible seedlings (as in a diploid). Tetrasomic inheritance will result in a ratio of 1:1 (if the parent is simplex), 5:1 (duplex) or ∞ :0 (triplex or quadruplex) if the gene is close to the centromere so that there is random chromosome association. Otherwise, chromatid segregation or double reduction (Bradshaw, 1994) causes an excess of recessive segregants, giving ratios down to 0.86:1 (simplex), 3.67:1 (duplex) and 27:1 (triplex) (Ross, 1986; Bradshaw & Mackay, 1994; Mendoza *et al.*, 1996).

Resistance

Natural virus resistance in potato was reviewed by Valkonen (1994), and in Ross (1986). A comprehensive list of host genes identified for resistance to the potyviruses and PVX in potato is given in Table 1. The nomenclature of the genes is explained below. The relative utility of these genes for breeding purposes is discussed by Solomon-Blackburn & Barker (2001). Further lists of resistances to these viruses in or from various wild *Solanum* species, without genes identified, were published by Webb & Schultz (1961), Horváth, (1968), Bagnall (1972), Tozzini *et al.* (1991) and Valkonen (1997). For examples of potato cultivars with specified virus resistance genes, see Cockerham (1943b), Ross (1986) and Jones (1990). The nomenclature for types of host response to viruses in plants was reviewed by Cooper & Jones (1983) and, for virus resistance in potato, by Valkonen (1994) and Valkonen *et al.* (1996).

Plants with extreme resistance (ER) to a virus show no symptoms, or limited necrosis (e.g. pinpoint lesions, flecks, or localized stem necrosis), when inoculated with virus. Only extremely low amounts of virus, if any, can be detected by sensitive techniques. ER can be comprehensive, conferring resistance to several strains (e.g. *Rx* genes) or even two or three viruses, e.g. *Ry_{sto}* confers resistance to PVY, PVA and PVV (Table 1), unless this represents two or three genes in a very tight linkage group (Barker, 1996). Recently, however, ER genes

specific to PVA have also been discovered, e.g. *Ra_{sto}*, *Ra_{adg}* (Barker, 1996; Hämäläinen *et al.*, 1998).

Plants with hypersensitive resistance (HR) show either local necrotic lesions, which prevent the infection from spreading further, or systemic necrosis. Virus can almost always be detected in affected leaves. HR is often strain-specific. It can also be affected by environmental conditions or by the physiology of the host plant (e.g. maturity). ER and HR to PVX and potyviruses can be determined by sap-inoculation or graft-inoculation (De Bokx, 1972), observing the response (Cockerham, 1970), and testing for infection.

A connection between ER and HR has been suggested, because necrosis can sometimes occur in plants with ER genes (Ross, 1958; Cockerham, 1970; Delhey, 1974). Hinrichs *et al.* (1998) reported that PVY replicated in initially infected leaf cells of inoculated plants of cultivars with the ER gene *Ry_{sto}*, and was transported into neighbouring cells, prior to a limited necrotic reaction after which the infection ceased. The ER gene *Rx_{adg}* in cv. Cara has now been found to control separate virus resistance and cell death responses (Bendahmane *et al.*, 1999); cell death does not normally occur when plants carrying *Rx_{adg}* are inoculated with PVX because the ER is epistatic over the HR. When studying *S. stoloniferum* genes conferring resistance to PVY & PVA, Cockerham (1970) found genes for ER to be dominant or epistatic over genes for HR. Valkonen *et al.* (1994) also found the ER gene *Ry_{adg}* to be epistatic to the HR gene *Ny_{adg}* in an *Andigena*-derived genotype.

Resistance to virus movement occurs where some kind of movement of virus through the plant is impeded, for example where a lower percentage of the tuber progeny plants of an infected plant are infected. HR could be regarded as a kind of resistance to virus movement, because movement is arrested or impeded by cell death. Other types of resistance are described in Solomon-Blackburn & Barker (2001) but do not apply to known major genes for resistance to these four viruses.

Nomenclature of major resistance genes

This paper follows selected proposals of Valkonen *et al.* (1996). The initial letter, a capital to denote a dominant resistance gene, indicates the type of resistance (usually N for HR and R for extreme or other resistance). A second, lower case letter, indicates the virus or strain resisted, and then the species in which the resistance is found or originated is indicated in lower case subscript. In a few cases, the virus letter is followed by the virus strain in upper case subscript: hence *Rx_{HBscr}* is a gene in *S. sucrense* conferring ER to

Table 1 Host genes for virus resistance in potato

Virus	Type of resistance	Gene = synonym	From species	Reference
Potyviruses				
a,bPVY } PVA PVV	ER	$Ry_{sto} = R^1 = Ry$	<i>S. stoloniferum</i>	Cockerham (1970); Ross (1961); Barker (1997);
a,bPVY } PVA PVV	ER(Y) HR(A) ER(V)/ HR(V)	$Ry_{sto}^{na} = R^2$	<i>S. stoloniferum</i>	Cockerham (1970); Barker (1997); Jones (1990)
PVY PVA PVY	ER(Y) HR(A) HR	$Ry_{sto}^{rna} = R^3$	<i>S. stoloniferum</i>	Cockerham (1970)
PVY PVA	HR ER	$Ry_{sto}^{n1} = Rym [= Ny_{sto}^1]$ $Ry_{sto}^{n2} = R^5 [= Ny_{sto}^2]$	"	Cockerham (1970); Ross (1961)
PVA PVA a,bPVY	ER E/HR ER	$Na_{sto} = R^6 = Rym$ $Ra [= Ra_{sto}]$ Ra_{adg} Ry_{adg}	<i>S. stoloniferum?</i> <i>S.t. ssp. andigena</i> "	Cockerham (1970); Ross (1961) Barker (1996) Hämäläinen <i>et al.</i> (1998) Munoz <i>et al.</i> (1975); Valkonen <i>et al.</i> (1994)
PVY° PVY } PVA }	HR HR	Ny_{adg} $Ny_{dms} (= N^y)$	" <i>S. demissum</i>	Valkonen <i>et al.</i> (1994) Cockerham (1970) (1958)
PVA PVY } PVA }	HR ER	$Ry_{dms}^a = Na_{dms} (= N^a)$ Ry_{hou}	" <i>S. hougassii</i>	Cockerham (1970) (1958) Cockerham (1970)
PVY } PVA }	HR	Ny_{chc}	<i>S. chacoense</i> <i>S. microdontum</i>	Cockerham (1970)
PVY	HR	$Ny = Ny_{tbr}$	<i>S. tuberosum</i>	Hutton (1951); Davidson (1980); Jones (1990)
PVA	HR	$Na_{tbr} (= Na)$	"	Cockerham (1970); Cadman (1942)
PVA strain A ¹ PVY strain C PVV	HR HR HR	$Na_{KE} [= Na_{KEtbr}]$ $Nc_{tbr} (= Nc)$ $Nv [= Nv_{tbr}]$	" " "	Valkonen <i>et al.</i> (1995b) Cockerham (1970) (1943a) Jones (1990); Fribourg & Nakashima (1984)
PVX				
°PVX(1,2,3,4) PVX(1,2,3,4)	ER ER	Rx_{adg} $Rx = Rx_{tub} [= Rx_{tbr}]$ ($= Rx_{adg}?$)	<i>S.t. ssp. andigena</i> <i>S.t. ssp. tuberosum</i>	Cockerham (1970, 1955) Ross (1986); Fernandez-Northcote (1990); Mills (1965); Cockerham (1970)
°PVX(1,2,3,4)	ER	Rx_{acl}	<i>S. acaule</i>	Ross (1954); Cockerham (1970);
PVX(1,2,3,4) PVX(1,2,3,4)	ER HR	X^i $Rx_{acl}^n = X^{no} [= Nx_{acl}]$	" <i>S. acaule</i> <i>S.t. ssp. andigena</i>	Cockerham (1958, 1970) Cockerham (1970) (1958); Swieżyński (1994)
PVX(1,2,3,4) PVX(1,3)	HR HR	Nx_{chc} Nx_{tbr}^{spl}	<i>S. chacoense</i> <i>S. sparsipilum</i>	Cockerham (1970) Cockerham (1970)
PVX(1,3)	HR	$Nx_{tbr} = Nx$	<i>S. tuberosum</i>	Cockerham (1970); Cadman (1942)
PVX(2)	HR	$Nb_{tbr} = Nb$	"	Cockerham (1970, 1943a)

Table 1 (Continued)

Virus	Type of resistance	Gene = synonym	From species	Reference
PVX	HR	<i>Nx_{phu}</i>	<i>S. phureja</i>	Tommiska <i>et al.</i> (1998); Valkonen <i>et al.</i> (1995a)
^d PVX(HB)	ER	<i>Rx_{HB}</i> [= <i>Rx_{HB scr}</i>]	<i>S. sucrense</i>	Brown <i>et al.</i> (1984)
^d PVX(2)	ER	<i>Rx_c</i> [= <i>Rx_{CP scr}</i>]	"	Brown <i>et al.</i> (1984)

^aCultivars containing these genes showed ER or at least good resistance to PVY^{NTN} (Barker, 1996; Le Romancer & Nedellec, 1997).

^bIncluding PVY^N (*Ry_{sto}*; Barker, 1996; *Ry_{adg}*; Hämäläinen *et al.*, 1998); cv. Corine containing *Ry_{sto}^{na}* showed ER to PVY^N (Jones, 1990). *Ry_{adg}* does not confer resistance to PVA (Ross, 1986; Hämäläinen *et al.*, 1998).

^cIncluding PVX group 4 according to Cockerham (1955, 1970) but not according to Valkonen (1994) (no data or reference given).

^dStrains 1, 3 and 4 were not mentioned in reference.

Gene synonyms in square brackets are suggested renamings in accordance with selected proposals of Valkonen *et al.* (1996) on gene nomenclature.

Numbers 1–4 and HB in brackets after PVX are strains.

S.t. = *Solanum tuberosum*; Ident = identical.

Table 2 Host gene relationships deduced from phenotypic data

Relationship	Genes	Reference
alleles	<i>Nx_{tbr}</i> , <i>Nx_{tbr}^{sp1}</i> (probably identical)	Cockerham (1970)
alleles	<i>Rx_{acl}</i> , <i>Rx_{acl}ⁿ</i>	
alleles/identical	<i>Rx_{adg}</i> , <i>Rx_(tbr)</i>	
alleles	<i>Ny_{dms}</i> , <i>Na_{dms}</i>	
alleles	<i>Ry_{sto}^{na}</i> , <i>Ry_{sto}^{na}</i> , <i>Ry_{sto}ⁿ²</i>	
alleles	<i>Ry_{sto}</i> , <i>Ry_{sto}</i>	Ross (1958); Cockerham (1970)
linked	<i>Ry_{adg}</i> , <i>Ra_{adg}</i>	Hämäläinen <i>et al.</i> (1998)
linked	<i>Ny_{che}</i> , <i>Nx_{che}</i>	Cockerham (1970)
linked	<i>Nx_{che}</i> , <i>Nx_{tbr}^{sp1}</i>	
linked	<i>Na_{tbr}</i> , <i>Nx_{tbr}</i> (∴ also to <i>Nx_{che}</i> , <i>Ny_{che}</i> loci)	Cadman (1942); Cockerham (1970)
linked in repulsion	<i>Na_{tbr}</i> , <i>Nx_{tbr}</i> in cv. Southesk only	Howard & Fuller (1965)
linked in repulsion	<i>Nx_{tbr}</i> , <i>Nc_{tbr}</i> in cv. Southesk	
independent	" " in cv. Ulster Knight	Solomon (1985)
independent	^a <i>Xⁱ</i> , <i>Nb_{tbr}</i>	
independent	<i>Nx_{tbr}</i> , <i>Nb_{tbr}</i>	Cockerham (1970)
independent	<i>Rx_{adg}</i> , <i>Rx_{acl}</i> , <i>Nx_{tbr}</i>	
independent or homeologous	^b <i>Ry_{sto}</i> locus, <i>Ry_{sto}^{na}</i> locus, <i>Na_{sto}</i>	
independent	^b <i>Ry_{hou}</i> , <i>Ny_{dms}</i>	
independent	^c <i>Na_{tbr}</i> , <i>Nc_{tbr}</i>	
independent	<i>Ry_{sto}</i> , <i>Ra_{sto}</i>	Barker (1996)
independent or not tightly linked	<i>Ny_{adg}</i> , <i>Ry_{adg}</i>	Valkonen <i>et al.</i> (1994)

^aCockerham (1970) suggested that *Xⁱ* was probably *Rx_{acl}* (P344) but see Table 3.

^bCockerham (1970) reported that *Ry_{sto}^{na}* occasionally appeared allelic with *Ry_{sto}*. He suggested the *Ry_{sto}* and *Ry_{sto}^{na}* loci might be homeologous in corresponding genomes of an allotetraploid that occasionally behaves as an autotetraploid. It also seems possible (though there is no evidence) that the *Ry_{hou}* and *Ny_{dms}* loci could be homeologous, because the segregation ratios would be the same as for independence in allohexaploid *S. hougasii* × *S. demissum* hybrids.

^cCockerham (1970) reported conflicting evidence that *Nc* was, and was not, linked to the *NaNx* group, but the former (from his data) was due to χ^2 mistakes on P.311. Howard & Fuller (1965) did find evidence that it was linked (in repulsion) in cv. Southesk but independent in cv. Ulster Knight.

the HB strain of PVX. In Table 2, we adhere to the nomenclature of Cockerham (1970) to avoid confusion in comparisons with literature cited. [*Ry_{sto}ⁿ¹*, *Ry_{sto}ⁿ²* and *Rx_{acl}ⁿ* might be renamed *Ny_{sto}¹*, *Ny_{sto}²* and *Nx_{acl}* otherwise.] All gene names are italicized.

Inheritance

Where the inheritance of ER or HR to these viruses has been investigated in potato, it is monogenic, with dominance for resistance, a situation which might be

expected to evolve in the wild for genes conferring fitness. Earlier models for the inheritance of ER to PVX in USDA 41956, for two dominant complementary genes (Stevenson *et al.*, 1939) and for a recessive allele to a gene for HR (Hutton & Wark, 1952), were tested by Mills (1965) and Cockerham (1970), whose data did not fit these models; both concluded that a single dominant gene was responsible (Rx_{tbr} in Table 1).

Gene relationships deduced from phenotypic segregation data (as opposed to molecular mapping) are listed in Table 2. Some of this research was performed on diploids (e.g. *S. chacoense*, *S. sparsipilum* and dihaploids of *S. tuberosum*) or allopolyploid species (e.g. *S. stoloniferum*, *S. demissum* and *S. hougasii*) with disomic inheritance. In other cases (e.g. autotetraploids *S. tuberosum* ssp. *tuberosum* and ssp. *andigena*, some with genes introgressed from *S. acaule*) inheritance was tetrasomic, involving segregation ratios as explained above (Cockerham, 1970).

Molecular mapping

The chromosomal locations of resistance genes can be mapped by examining segregations in relation to linked molecular markers. Virus-resistance genes mapped so far in potato are summarized in Table 3. Advances in

molecular marker technology, and an expanding map of markers, have improved the prospects for mapping and cloning genes in potato, as well as for marker-assisted selection (Milbourne *et al.*, 1997, 1998; summarized in Solomon-Blackburn & Barker 2001). In the longer term, large-scale sequencing may lead to the development of a complete gene map in potato (W de Jong, pers. comm., discussed in Solomon-Blackburn & Barker, 2001).

Further to the linked virus-resistance gene loci in Tables 2 and 3, disease resistance gene clusters (covering a diverse range of pathogens) have been found in many plant species, including potato (Leister *et al.*, 1996; De Jong *et al.*, 1997; Hämäläinen *et al.*, 1998; Van Der Voort *et al.*, 1999), sometimes at the same chromosomal positions in different plant genera. These linkage groups would facilitate efficient selection for several disease resistances at once, in nature as well as in plant breeding, and would therefore be at a selective advantage over independent genes.

Once mapped, a gene can be cloned, by transposon mutagenesis or by positional cloning. The genes Rx_{adg} (from cv. Cara) and $Rx2$ have been cloned (Bendahmane *et al.*, 1999; Bendahmane & Baulcombe, pers. comm.). Attempts are also being made to clone Nb_{tbr} (De Jong *et al.*, 1997) and Ry_{sto} (Brigneti *et al.*, 1997). Gene cloning has applications in research on resistance

Table 3 Virus resistance genes mapped in potato by molecular methods

Gene	= gene	Source	Chromosome	Position	Reference
Rx1		diploid P18	XII	distal end of 'upper arm'	Ritter <i>et al.</i> (1991)
Rx	Rx_{adg}	tbr cv. Cara	XII	^a different position from $Rx1$	Bendahmane <i>et al.</i> (1997); van der Voort <i>et al.</i> (1999)
^b $Rx2$	$Rx_{acl}?$ (probably not X^i)	diploid P34	V	intermediate 'upper arm'	Ritter <i>et al.</i> (1991)
Nb_{tbr}		tbr cv. Pentland Ivory	V	intermediate 'upper arm'	de Jong <i>et al.</i> (1997)
Nx_{phu}		phu IvP35	IX	long arm	Tommiska <i>et al.</i> (1998)
Ry_{sto}		I-1039	XI	between markers GP125 & CT182	Brigneti <i>et al.</i> (1997)
^c Ry_{adg}		diploid 2x (v-2)7 with adg in pedigree	XI	between markers GP125 & CT182	Hämäläinen <i>et al.</i> (1997, 1998)
Ra_{adg}		as Ry_{adg}	XI	6.8 cM distal to Ry_{adg}	Hämäläinen <i>et al.</i> (1998)

^aThis could be the result of a chromosomal inversion, or of Rx (Cara) and $Rx1$ being different genes (Bendahmane *et al.*, 1997). Rx in Cara is tightly linked to the nematode resistance gene $Gpa2$ on a segment introgressed from the resistant accession CPC1673 (adg) (van der Voort *et al.*, 1999). The source of $Rx1$ also has CPC1673 in its pedigree.

^bThis suggests X^i is not $Rx2$ because X^i and Nb_{tbr} were found independent (Solomon, 1985), although the sources of X^i and $Rx2$ both have the resistant clone MPI 44.1016/10 in their pedigrees. De Jong *et al.* (1997) suggested X^i might be $Rx1$ or a third gene (neither $Rx1$ nor $Rx2$).

^c Ny_{adg} was not linked to Ry_{adg} (Hämäläinen *et al.*, 1997).

tbr, *Solanum tuberosum* ssp. *tuberosum*; adg, *S. tuberosum* ssp. *andigena*; phu, *S. phureja*.

mechanisms and evolutionary studies (Gebhardt, 1997). Several common sequence motifs have been found in genes for resistance to a diverse range of pathogens in a diverse range of plant species. Gebhardt (1997) reported that six or seven classes of resistance genes (with different common sequence motifs) had been isolated, and that there were probably more to be discovered. Possible functions and cellular locations for the proteins encoded have been inferred from these common motifs. For example, a leucine-rich repeat (LRR) of approximately 25 amino acids is frequently found in (predicted proteins encoded by) genes for resistance to viruses, bacteria, fungi or nematodes. Proteins with LRR domains tend to be involved in protein–protein interactions, so a role as receptors was suggested (Gebhardt, 1997). Analysis of resistance and susceptibility alleles of genes isolated from different plant species may help to identify structural features that determine pathogen specificity, which could be manipulated to produce resistance genes tailored for specific crop needs (Leister *et al.*, 1996).

The *Rx_{adg}* gene in cv. Cara has been found to be very similar to the tightly linked gene *Gpa2* for resistance to potato cyst nematode (PCN) (Bendahmane *et al.*, 1999; van der Voort *et al.*, 1999; Van Der Vossen *et al.*, 2000). Clusters of genes resembling resistance genes in sequence motif have also been found around known resistance gene loci. Hämäläinen *et al.* (1998) found three of these resistance-gene-like (RGL) sequences (of the LRR type), two of which were closely linked to (or possibly part of) *Ry_{adg}* on chromosome XI, in Andigena; Leister *et al.* (1996) had found three RGL sequences homologous to those three, in the same region of chromosome XI in Tuberosum (using the same PCR primers designed from sequence motifs common to resistance genes in *Nicotiana tabacum* and *Arabidopsis thaliana*). This region of chromosome XI carries several disease resistance genes in solanaceous species (Leister *et al.*, 1996; Brigneti *et al.*, 1997; Hämäläinen *et al.*, 1997, 1998), including the gene *N* for HR to Tobacco mosaic virus in *N. tabacum* which contains sequences homologous with these RGL sequences in potato (Leister *et al.*, 1996). Common sequence motifs may facilitate the discovery and isolation of unknown resistance genes (Leister *et al.*, 1996). These could include genes for ‘nonhost’ resistance (i.e. from plant species not infected by the pathogen) which could be used to transform plants of other species (Leister *et al.*, 1996; Gebhardt, 1997).

Concluding remarks

From the 1930s to the present, much work has been carried out on characterizing host resistance genes and

phenotypes (Table 1), providing a sound basis for further research and applications to potato breeding. It is inevitable that there are more of these genes yet to be discovered, in view of recently discovered genes and evidence on gene clusters.

Molecular mapping provides more precise information on gene locations than phenotypic linkage studies, although the information from phenotypic linkage studies is also useful in relation to mapping data. Once a gene is mapped, its locus relative to those of other mapped genes is revealed and leads to a more useful map, particularly as shared marker libraries develop.

Cloned genes are used for research on resistance mechanisms and provide insight into the evolutionary processes involved in disease resistance (discussed above). Gene clusters also raise the question of the conceptual difference between a comprehensive resistance gene and two or more adjacent specific resistance genes, as does the dual ER/cell death mechanism found in *Rx_{adg}* (Bendahmane *et al.*, 1999), and genes such as *Ry_{sto}^{na}*, which confers ER to PVY and HR to PVA (Cockerham, 1970). It is possible that the comprehensive *Ry* genes could, in fact, be tightly linked groups of specific resistance genes (Barker, 1996).

At one time, genes of identical phenotype from different sources that segregated as alleles were considered identical, because there was no evidence to suggest otherwise, e.g. *Rx_{adg}* from accession CPC 1673 and *Rx_{ibr}* from USDA 41956 (Cockerham, 1970). However, in the light of recent findings on resistance gene clusters, this may not have been correct. Also, *Ry_{sto}* and *Ry_{adg}* have been mapped to the same, or very similar, position as each other (Table 3; Brigneti *et al.*, 1997; Hämäläinen *et al.*, 1997); these two genes confer the same phenotype with respect to PVY but not PVA. Cockerham (1970) also reported two loci with two or three different PVY resistance alleles in *S. stoloniferum* (Table 2). Allelism or repulsion linkage of dominant major genes for resistance to the same pathogen would confer a selective advantage in nature, in a similar way to multiplex-resistant parents in potato breeding (Wastie *et al.*, 1992; Bradshaw & Mackay, 1994): more of the progeny are resistant when an autotetraploid resistant parent is duplex or triplex than when it is simplex at two or three independent loci (Solomon-Blackburn & Mackay, 1993). In an allopolyploid such as *S. stoloniferum*, all the progeny (except recombinants) will be resistant if a resistant parent is effectively homozygous in one genome (through allelism or repulsion linkage), whereas, if it is heterozygous at two independent loci, one quarter of the progeny will be susceptible in a cross with a susceptible parent. On the other hand, coupling linkage of genes for resistance to different pathogens would be advantageous, as discussed above.

The following paper (Solomon-Blackburn & Barker, 2001) discusses the use of host genes and these technologies in potato breeding for virus resistance, in relation to other emerging technologies and conventional methods. The applications of cloned genes, mapped locations and linked markers in potato breeding, the use of host gene-mediated resistance by conventional breeding methods, and the use and potential of pathogen-derived and other transgenic resistance are also examined.

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