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Pest Resistance Traits Controlled by Quantitative Loci and Molecular Breeding Strategies in Tuber-bearing *Solanum*

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I. General introduction

The potato is one of the most valuable food crops in the world. Despite utmost efforts to control biotic stresses, approximately 22% of the yield is lost per year due to diseases and pests (Ross 1986). To reduce the extensive use of pesticides and to facilitate integrated management of pests, conferring resistance to pests in cultivars is of global importance in potato breeding programs.

Generally, quantitatively inherited traits depend on the collective interaction of numerous genes or polygenic system (Stoskopf *et al.* 1993). Therefore, many traits, including the classical example of corolla length of tobacco (East 1915), can be explained quantitatively, in stead of simply dominant or recessive. Such inheritance is common for economically important traits in domesticated animals and cultivated plants, and for traits affecting survival and fertility in wild species (Bradshaw 1994). There are several terms related to quantitative inheritance, including field resistance, infection resistance, horizontal resistance, polygenes, and minor genes, which can be instrumentally regarded as the same entities.

Among pest resistance traits in potatoes, followings are considered to be controlled by quantitative loci in their breeding history: 1) field resistance to late blight (LB) [*Phytophthora infestans* (Mont.) de Bary]; 2) early blight (EB) [*Alternaria solani* (Ellis and Martin) Jones and Grout]; 3) common scab [*Streptomyces scabies* (Thaxt.) Waksman & Henrici]; 4) bacterial wilt (BW) caused by *Pseudomonas solanacearum*, 5) blackleg and bacterial soft rot caused by *Erwinia carotovora*; 6) potato leaf roll virus (PLRV); 7) potato cyst nematodes (PCN) (*Globodera rostochiensis* and *G. pallida*; 8) root-knot nematodes (RKN) (*Meloidogyne* spp.); and 9) potato tuber moth (PTM) [*Phthorimaea opercullella* (Zeller)]. Types A and B glandular trichomes on leaves are also controlled by quantitative loci, and they confer resistance to a broad range of insects and mites (Bonierbale *et al.* 1994).

Here we provide classical examples by literature associated with the quantitative resistance traits (QRTs) and their contemporary uses by molecular breeding. Also, transgenic potatoes are reviewed as an alternative approach.

II. Resistances available in potato genetic resources

II-1. Fungal disease

Late Blight

Phytophthora infestans (Mont.) de Bary (late blight, LB), causing haulm destruction and decay of the tubers, is the most important fungal parasite of the potato (Ross 1986). Probably breeding for resistance to late blight in potatoes was the first attempt at scientifically based resistance breeding on potatoes, and yet no major progress has been made since the great potato famine about 150 years ago (Umaerus and Umaerus 1994). Its importance has ever been the greatest since potato cultivars spread to countries with warm and humid climates, where it is a prime production constraint (Ross 1986). Economists estimate that the overall annual cost of controlling late blight in developing countries is $3.25 billion and this disease costs another $1.8 billion a year, globally, for the expense of purchasing chemicals to fight the blight (Mackin 1998).

Eleven R genes as dominant alleles in *Solanum demissum* were identified and have been transferred to cultivated potatoes (Malcolmson and Black 1966). Simple Mendelian inheritance of these dominant genes was demonstrated (Malcolmson and Black 1966, Mastenbroek 1953). On the other hand, an excess of susceptible progenies has been frequently observed in segregating populations (Black

1970). The problem of potato breeding for LB resistance using R genes is its durability. Elsewhere in the world, many of these new R-gene cultivars were soon being found to be susceptible, as new races were produced by the variable and resourceful fungus pathogen (Niederhauser *et al.* 1996).

The importance of general (horizontal or field) resistance to LB is attributed to the fact that the development of any isolate of the fungus is not limited in the host plant (Umaerus and Umaerus 1994). General resistance is considered to be a quantitative trait resulting from the joint action of polygenes (Black 1970). However, the resistance mechanism is unknown (Colon and Budding 1988).

Sixty tuber-bearing species, listed by Darsow & Hinze (1991), are potential sources of resistance to LB. A number of crosses were attempted to transmit the field resistance found in wild species to cultivars. However, only a small part of the original resistance of the wild species were remained after several generations of backcrosses (Tazelaar 1981, Stagemann and Schnick 1982). Also, the stability of general resistance has most certainly been confounded at times by climatic and other environmental effects (Forbes and Jarvis 1994).

Early Blight

Early blight caused by *Alternaria solani* (Ellis and Martin) Jones and Grout, is found worldwide in the potato-growing regions. (Weingartner 1981). It affects leafy organ, leading to defoliation, as well as tubers of potatoes, especially devastating to susceptible, early-maturing varieties (Pavek and Corsini 1994). Resistance to early blight was found in several species including *S. tuberosum, S. stenotomum* and *S. phureja* (Herriott *et al.* 1986).

Inheritance of resistance to early blight was shown to be controlled by a few genes (Herriott *et al.* 1986, Herriott and Haynes 1990). Other group proposed quantitative inheritance of susceptibility to early blight (Pavek and Corsini 1994). Maturity values and resistance levels were not significantly correlated, indicating existence of true resistance rather than apparent resistance due to late maturity in the study by Herriott and Haynes (1990).

Common scab

Common scab caused by *Streptomyces scabies* (Thaxt.) Waksman & Henrici, produces tuber lesions. These lesions are responsible for disfigurement of potato tuber, decreasing grade quality, total yield and storing ability. Common scab is observed in most area where potatoes are grown (Hooker 1981).

Relative resistance to common scab could be found in both cultivated potatoes (Kranz and Edie 1948, Cipar and Lawrence 1972) and wild species (Hawkes 1990). The inheritance of the relative resistance to common scab has not completely been clarified yet, however, reports by Cipar and Lawrence (1972), Howard (1978) and Pfeffer and Effmert (1985) suggested polygenic inheritance of the resistance. Resistance appears to be associated, at least in part, with the effectiveness of the periderm at isolating an infection and preventing it from spreading more deeply into the cortex (Wastie 1994). However, yet there has been no strong resistance identified among germplasm so far against the common scab.

II-2. Bacterial disease

Bacterial wilt

Bacterial wilt (BW) caused by *Pseudomonas solanacearum* is responsible for severe potato crop loss in tropical and subtropical climates (French 1985). The damage can be increased especially by interaction with other pathogens and pests, such as bacterial soft rot (*Erwinia* spp.) and root-knot nematodes (*Meloidogyne* spp.) (Schmiediche 1988).

Wild diploid potato species including *Solanum raphanifolium, S. microdontum, S. sparsipilum, S. chacoense,* as well as the cultivated diploid species *S. phureja* have been used in breeding for resistance to BW (Schmiediche 1983, CIP 1987). Resistance to BW is a quantitatively inherited trait (Rowe and Sequeira 1970, Schmiediche 1988, Tung *et al.* 1990a), which hampers prompt improvement of resistance at the tetraploid level (Schmiediche 1988). Diploid breeding material lines with a significantly higher level of the quantitative resistance have been generated (Watanabe *et al.* 1992). The resistance to BW is temperature sensitive (Harison 1961, French 1985) and strain specific (Sequeira and Rowe 1969, French and De Lindo 1982). Therefore, the level of the resistance is variable depending on the interaction among host, pathogen and environment (Tung *et al.* 1990b). Changes in the pathogenicity of isolates with temperature can be the major source of variation in resistance (Tung *et al.* 1990b). On the other hand, genes for adaptation to the environment as well as genes for heat tolerance were also involved in the expression of resistance to BW (Tung *et al.* 1990a, b, Watanabe *et al.* 1999a).

Blackleg and bacterial soft rot

Blackleg and bacterial soft rot, principally caused by two varieties of the same species of bacterium, *Erwinia carotovora*, are found wherever potatoes are grown (Harrison and Nielsen 1981). They affect stems, leaves and tubers. There is no principal means available for the chemical control of these diseases. The integrated use of resistant or tolerant varieties, seed certification, improved cropping methods and general on-farm hygiene is currently applied for the control. (French 1988, De-Boer 1990, Murphy 1990).

Resistance to *Erwinia* spp. has been found in wild diploid *Solanum* spp., primitive cultivars, and *S. tuberosum* subsp. *andigena* (Lojkowska and Kelman 1989, Huamán *et al.* 1988). Resistance traits to *Erwinia* spp. are not controlled qualitatively (Van den Plank 1978). Lellbach (1978) proposed that resistance was probably controlled by minor genes, whose additive effects could increase resistance levels. Positive correlation between resistance to blackleg and soft rot was reported in tetraploid cultivars (Dobias 1975, Munzert 1984) and in primitive cultivars (Elphinstone 1990), but the mechanism is unknown.

II-3. Virus

Potato leaf roll virus

Potato leafroll, an aphid-transmitted disease (PLRV), is one of the most serious problems in potatoes and is responsible for high yield loss (Peters and Jones 1981). Resistance is determined by many genes with additive effects (Peters and Jones 1981). Several types of quantitative resistance to PRLV were reported; 1) resistance to multiplication in *S. acaule* (Rodorigues 1987) and in *S. brevidens* (Jones 1979); 2) resistance to infection in *S. brevidens* (Jones 1979), in *S.* x *edinense* (Ross 1979), *S acaule* (Ross 1979), *S. tuberosum*, (Ross 1979, Butkiewicz 1978); and 3) resistance to vector in *S. brevidens* (Jones 1979).

II-4. Nematodes

Potato cyst nematodes

Potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*, PCN) are primarily distributed in cooler areas of tropical and subtropical regions, as well as in the temperate regions. Losses as high as 80% are not uncommon in some potato-growing areas of the tropics where infestation levels are high and continuous potato cultivation is practiced (Jatala 1994).

Inheritance of PCN involves both qualitative and quantitative traits. Qualitative inheritance in PCN resistance relates genes *H1* (Toxopeus and Hujisman 1953), *K1* (Huijisman 1960), *Fa* and *Fb* (Ross 1962) for *Globodera rostochiensis*, and genes *H2* (Dunnett 1957) and *H3* (Horward *et al.* 1970) for *G. pallida*. Quantitative resistance to both types of PCN was found in *S. vernei* (Ellenby 1948, Mai and Peterson 1952, Plaisted *et al.* 1962). Ross reported that there were likely to be four major dominant genes from *S. vernei* inherited in a Mendelian way (Ross 1986). It was confirmed that resistance to PCN was controlled by polygenes (Dale and Phillips 1982, Phillips *et al.* 1979).

Root-knot nematodes

Root-knot nematodes (*Meloidogyne* spp., RKN) are cosmopolitan in distribution, attacking almost all the major crops and many weed species (Jatala 1994). Losses due to these nematodes may reach 25% or more and vary depending on the cultivar resistance, environmental conditions, and nematodes species (Mai *et al.* 1981). These nematodes do not reduce yield only by infecting the roots and limiting plant growth, but also by affecting crop quality (Jatala 1994).

Species of root-knot nematodes that parasitizes potatoes are *M. arenaria, M. incognita, M. hapla, M. javanica, M. thamesi,* and *M. chitwoodii* (Phillips 1994). A large number of tuber-bearing *Solanum* species resistant to RKN were screened, including *S. bulbocastanum, S. gandallasii, S. lignicaule, S. ajamhuiri, S. tuberosum subsp. andigena, S. spegazzinii, S. vernei* (Nirula *et al.* 1967, 1969), *S. capsicibaccatum, S. megistacrolobum, S. microdontum, S. acroscopicum, S. gourlari* and *S. sparsipilum* (Jatala and Rowe, 1976). Gomez *et al.* (1983) concluded that more than one gene is involved in the expression of RKN resistance. However, the details of inheritance in resistance to RKN has not been intensively investigated yet. Cytoplasmic effects on the expression of RKN resistance were reported (Gomez *et al.* 1983, Iwanaga *et al.* 1989, Watanabe *et al.* 1999b).

II-5. Insects and morphological characteristic related to insect resistance

Potato tuber moth

Potato tuber moth [*Phthorimaea opercullella* (Zeller), PTM] is one of the most damaging pests of the potato in storage and the field in warmer climates. Tuber infestation by PTM causes dramatic losses, as damaged tubers are attacked by different secondary pests and diseases (Van Rie *et al.* 1994). There are two types of resistance to PTM: antixenosis (or non-preference) and antibiosis (Painter 1958). Antixenosis involves the tuber unattractiveness to insect pests while the tuber with antibiosis resistance adversely affect the insect feeding (Ortiz *et al.* 1990). Antibiosis was the major mechanism of the resistance (Ortiz *et al.* 1990).

Resistance to PTM has been reported from host *Solanum* species including *S. sparsipilum* (Raman and Palacios 1982), *S. commersonii, S. sucrense,* and *S. tarjense* (Chavez *et al.* 1988).

Resistance to PTM in *S. sparsipilum* was reported to be controlled by a few genes (Raman *et al.* 1981, Ortiz *et al.* 1990). However, cytoplasmic factors also influence the expression of the resistance together with nuclear genes (Ortiz *et al.* 1990, Watanabe *et al.* 1999c). The mechanism of cytoplasmic effects on the expression of PTM resistance is unknown.

Glandular trichomes

Tingey *et al.* (1981) and Ochoa (1980) described several species of potatoes with glandular trichomes. Glandular trichomes immobilize insects on the foliage, leading to cessation of feeding and death (Tingey 1991, Gregory *et al.* 1986) Glandular trichomes are effective in reducing damages caused by PTM, leafminer fly (*Liriomyza huidobrensis*), green peach aphids (*Myzus percicae*), red spider mites (*Tetranychus urticae*), and several other mites and insects (Raman *et al.* 1994). The presence of grandular trichomes has been reported for tuber-bearing species and non-tuber-bearing species (Ochoa 1980). Both types of glandular trichomes, Type A and Type B trichomes, are known to be quantitatively inherited. Details of quantitative trait loci (QTLs) analysis will be discussed later.

III. Breeding strategies for quantitative pest resistance traits

III-1. Genetic resources

Wild relatives of cultivated potatoes provide many variable genes conferring pest resistance which do not exist in cultivated tetraploid potatoes. Germplasm enhancement with diploid tuber-bearing *Solanum species*, including some diploid cultivated taxa, has been conducted widely in many potato breeding programs at tetraploid levels, using; 1) haploid from 4x cultivars, and 2) 2n gametes [reviewed in Watanabe *et al.* (1995)]. Furthermore, the concept of the endosperm balance number (EBN) has greatly assisted prediction of success in interspecific and/or interploidy crosses (Johnson *et al.* 1980). Genetic resources for quantitative resistance to pests are summarized in **Table 1**. Great deal of efforts invested on potato breeding could mainly be attributed to the followings genetic characteristics (Ross 1986, Watanabe 1999a).

First, the majority of common potato cultivars in the world are tetraploid. This makes the potato breeding difficult due to their complicated inheritance, compared to diploids. In diploids, two alleles exist in a locus. In tetraploids, four alleles can be found at maximum in a locus, resulting in far more complicated inheritance patterns. When multiple alleles exist, numerous genotypes are found even on a single locus. Moreover, if a trait is controlled by more than one locus, the expression of the trait could be further complicated. Consequently, a large variation on intra-locus interaction and inter-locus interaction should be considered.

Second, the potato is an outcrossing species, therefore, it does not resemble characteristics in inheritance and breeding of autogamous species. This outcrossing nature of the potato causes difficulties to fix genotypes for making pure breeding lines both in tetraploids, and diploids. Backcrossing can not be made using the same genotypes due to self and cross incompatibilities (Fritz and Hanneman 1989), incongruity by genetic control indicated as Endosperm Balanced Number (EBN) (Ehlenfeldt and Hanneman 1988), and/or inbreeding depression (Kotch *et al.* 1992, Peloquin *et al.* 1989a,b). Even when the hybrids were to be obtained, they could be male-sterility (Iwanaga *et al.* 1991).

Third, most of agronomic and pest resistant traits targeted in breeding programs are quantitatively inherited as described above. The expression of quantitatively inherited traits are outstandingly complicated due to the nature of tetraploids and genotype × environment interaction. Screening procedures for quantitatively inherited traits often require repeated trials to confirm results.

Finally the dicot potato has different cytogenetical characteristics from monocot plants, especially in microsporogenesis. In addition, chromosome manipulation, common in breeding of wheat, is not feasible. Each chromosome of the potato can not be easily distinguished at present. Recombination of chromosomes originated from different genetic background is not simple. Accordingly, addition of extra chromosome(s) and creation of aneuploids could not be easily achieved in potatoes.

Conventional potato breeding methods have taken decades to incorporate variable traits from genetic resources. On the other hand, some progress was made even with the conventional approach to cope with the constraints in some degree (Peloquin *et al.* 1989a, b, Ross 1986). The incorporation of the polyploid genetics knowledge, haploidization techniques from tetraploid potatoes (Kotch *et al.* 1992), breaking interspecific barriers by the concept of EBN (Ehlenfeldt and Hannman 1988) and use of the 2n gametes had made access to the diverse range of wild and cultivated genetic resources which have a

Table 1. Summary of genetic resources to confer quantitatively inherited pest resistance in tuber bearing *Solanum* species based on several references*. Only more important species included.

Resistance	1 EBN	2EBN		4EBN		Others or EBN undetermine
	2x	2x	4x	4x	6x	
Late blight	*bulbocastanum* *circaeifolium* *pinnatisectum* *polyadenium*	*berthaultii* *microdontum* *tarijense* *vernei* *verrucosum*	*fendleri* *stoloniferum*	*andigena*	*demissum* *guerreroense*	
Early blight		*candolleanum* *multiinterruptum* *phureja* *toralapanum* *vernei* *toralapanum*	*colombianum* *tuquerrense*			*santolallae* (2x)
Common scab	*commersonii*	*chacoense*				*yungasense* (2x)
Bacterail wilt	*commersonii*	*chacoense* *raphanifolium* *sparsipilum* *phureja* *stenotomum* *microdontum*	*acaule* *polytrichon*		*brachycarpum* *demissum*	
Blakleg and Bacterail soft rot	*brevidens* *brachistotrichum* *bulbocastanum* *commersonii* *hypacrarthrum* *jamesii* *pinnatisectum*	*acroglossum* *berthaultii* *boliviense* *candolleanum* *chacoense* *doddsii* *gourlayi* (2x) *leptophyes* *microdontum* *megistacrolobum* *marinasense* *phureja* *piurae* *sparsipilum* *tarijense* *toralapanum*	*fendleri* *hjertingii* *sucrense*? *stoloniferum*	*gourlayi* (4x) *sucrense*? *andigena* *tuberosum*	*brachycarpum* *demissum* *oplocense* (6x) *schenckii*	
Potato cyst nematodes	*bulbocastanum* *cardiophyllum* *capsicibaccatum*	*boliviense* *gourlayi* (2x) *spegazzinii* *sparsipilum* *vernei*	*acaule* *sucrense*?	*gourlayi* (4x) *sucrense*?	*oplocense* (6x)	*curtilobum* (5x, 4EBN)
Root-knot nematodes		*chacoense* *microdontum* *phureja* *sparsipilum*		*andigena*		
Potato leaf roll virus	*brevidens* *etuberosum* *pinnatisectum*	*candolleanum* *chacoense* *kurtzianum* *marinasense* *phureja* *raphanifolium* *toralapanum*	*acaule* *stoloniferum*		*demissum*	*polyadenium* (2x)
Potato tuber moth	*commersonii*	*sparsipilum* *tarjense*	*sucrense*?	*sucrense*?		
Glandular trichomes	*lignicaule* *wittmackii*	*berthaultii* *tarijense*				x *flavoviridens* (2x) *neocardenasii* (2x) *polyadenium* (2x)

*References: Bamberg *et al.* (1996), Hanneman (1994, presonal communication), Hawkes (1990, 1992, 1994).

spectrum of resistances for the biological constraints (Peloquin *et al.* 1989a, Watanabe 1994). This was demonstrated as ploidy manipulation or analytic breeding scheme (Reviewed in Peloquin *et al.* 1989a, b). However, even with the integration of the knowledge and new concepts, the complicated genetics of potatoes have been made the progress in the potato breeding slowly (Watanbe 1994, 1999a).

In addition to the above difficulties, variable traits may accompany deleterious traits such as highly glycoalkaloid content (Ross 1988). Glycoalkaloids (solanidine in *S. tuberosum* and solasodine in *S. berthaultii*) were quantitatively inherited in potatoes, and presumably the levels of alkaloids were controlled by recessive genes (Yencho *et al.* 1998). Modern tools are now becoming available to alleviate pitfalls in conventional germplasm enhancement in diverse genetic resources (Watanabe *et al.* 1997a).

III-2. Linkage analysis, marker assisted diagnosis and marker assisted selection (MAS)

Selection of target traits by phenotypic evaluation is generally cumbersome with a number of limitations in terms of long time-frame and skills/experience for evaluation, and requires relatively large scale of evaluation and repeated progeny testing. Conventional phenotypic markers such as those used for other crop plants, e. g. rice, wheat, and tomato, are not available for the potatoes (Watanabe 1999a). Recent development of molecular biology provides molecular genetic markers to select genes of interests including quantitative inherited traits as well as single dominant inherited traits.

Molecular markers could also be used for different categories of diagnostics. The specific genetic markers can be employed for analyzing the genetic structure in polyploid for estimating the number of favorable alleles, genotyping, prediction of success in hybridization in terms of involvement of self- or cross-incompatibility (Ehlenfeldt and Hanneman 1988, Fritz and Hanneman 1989), and estimation of the occurrence of the male-sterility in hybridization (Iwanaga *et al.* 1991). Overall utility for these diagnostic purposes shall be referred to Watanabe (1994) and Watanabe *et al.* (1997a).

The present molecular map of the potato has been constructed based on the tomato molecular map using restriction fragment length polymorphism (RFLP) markers (Tanksley *et al.* 1992). Before application of molecular markers, it was impossible to construct a genetic map on potatoes by a classical genetic mean especially due to the heterozygosity and polyploidy of the potato genotypes, however, with the employment of the molecular markers, the first comprehensive linkage map was constructed with a diploid F_1 population using highly heterozygous diploid parental genetics lines (Bonierbale *et al.* 1988). Many RFLP markers as well as other molecular makers are available for the selection of pest resistance related traits on potatoes (**Table 2**): e. g. randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), cleaved amplified polymorphic sequence (CAPS) and sequence characterized amplified region (SCAR) markers. General aspect, advantages and disadvantages of each molecular marker are summarized by Karp and Edwards (1995).

Marker assisted selection is accurate, fast, easy to be manipulated, and effective in cost for use. For this reason, PCR-based markers have been developed after the mapping of target loci using RFLP and/or AFLP markers. PCR-based markers are available for single genes which are related to resistance to PVX, PVY, LB, PCN, and RKN, and for QTL on resistance to LB, PCN and the presence of grandular trichomes (**Table 2**).

Detection of genes for extreme resistance to PVY can be made accurately using CAPS (Sorri *et al.* 1999), SCAR (Kasai *et al.* 1999), and RAPD (Shiranita 1999b); their association with the trait were 100% (77/77 cultivars with diverse genetic background), 100% (103/103), and 97% (31/32), respectively, while an RFLP marker (ADG2) gave 100% (54/54) correspondence (Hamalainen *et al.* 1997).

Recent development of molecular markers have localized resistance genes in potato genome. The followings are examples:

LB

Resistance genes to LB were mapped on potato chromosomes: *R1* on chromosome V (Leonards-Shippers *et al.* 1992) and *R3, R6,* and *R7* on chromosome XI (El-Kharbotly *et al.* 1994, El-Kharbotly *et al.* 1996a, Leister *et al.* 1996). Possible existence of dominant supressors to LB resistance was also proposed using molecular markers (El-Kharbotly *et al.* 1996b). QTL analysis of LB resistance identified multiple chromosome segments on chromosomes II, III, IV, V, VI, VII, VIII, IX, XI and XII (Leonards-Shippers *et al.* 1994, Meyer *et al.* 1998).

PCN

The application of molecular markers mapped *H1* [gene conferring resistance to *G. rostochiensis* pathotypes Ro1 and Ro4 (Kort *et al.* 1977)] on chromosome V (Gebhardt *et al.* 1993, Pineda *et al.*

Table 2. Molecular assisted markers related to pest resistance traits in potato

Pest or related trait	Target gene	Method	Potential markers for MAS	Reference
Potato Virus X	Nx_{phu}	RFLP	*TG424*	Tommiska *et al.* (1998)
	Nb	RFLP	*TG432*	De Jong *et al.* (1997)
	Nb	AFLP	*SPUD237,*	De Jong *et al.* (1997)
	Nb	CAPS	*GP21, SPUD237*	De Jong *et al.* (1997)
	Rx2	RFLP	*TG432*	De Jong *et al.* (1997)
	Rx	RFLP	*GP34, CT100, CT129*	Bendahmane *et al.* (1997)
	Rx	AFLP	*PM4, PM3*	Bendahmane *et al.* (1997)
	Rx	CAPS	*IPM3, IPM4*	Bendahmane *et al.* (1997)
	Rx1, Rx2	RFLP	*CP60, GP21, GP213*	Ritter *et al.* (1991)
	Rx	CAPS	*IPM4-c, 77R*	Kanyuka *et al.* (1999)
Potato Virus Y	Ry_{adg}	RFLP	*TG508*	Hämäläinen *et al.* (1997)
	Ry_{adg}	RFLP	*CP58, CT182, CD17, TG523, ADG1, ADG2*	Hämäläinen *et al.* (1998)
	Ry_{adg}	RFLP	*ADG2*	Shiranita *et al.* (1999a)
	Ry_{adg}	CAPS	*ADG2*	Sorri *et al.* (1999)
	Ry_{adg}	SCAR	*SYRC3*	Kasai *et al.* (1999)
Potato Virus A	Ra_{adg}	RFLP	*GP125, TG508*	Hämäläinen *et al.* (1998)
Phytophthora infestans	*R1*	RFLP	*GP21, GP179*	Leonards-Schippers *et al.* (1992),
	R1	AFLP	*GP21, GP179*	Meksem *et al.* (1995)
	R1	RFLP	*GP21*	El-Kharbotly *et al.* (1996a)
	R1	RFLP	*TG432*	De Jong *et al.* (1997)
	R1	AFLP	*SPUD237*	De Jong *et al.* (1997)
	R3	RFLP	*GP105 (a), TG105 (a), GP185, GP35 (k)*	El-Kharbotly *et al.* (1994)
	R6, R7	RFLP	*GP185 (a), GP250 (a)*	El-Kharbotly *et al.* (1996b)
	Pi (QTL)	RFLP		Leonards-Schippers *et al.* (1994),
	QTL	AFLP		Meyer *et al.* (1998)
Globodera rostochiensis	*H1*	RFLP	*CD78*	Pineda *et al.* (1993)
	H1	RFLP	*CP113*	Gebhardt *et al.* (1993)
	QTL	RFLP		Kreike *et al.* (1993), Kreike *et al.* (1996),
	Gro1	RFLP	*CP51*	Barone *et al.* (1990),
	Gro1	RFLP	*CP56, GP516 (c), CP51 (c)*	Ballvora *et al.* (1995)
	Gro1	RAPD	$OPR10_{700}$	Ballvora *et al.* (1995)
	Gro1	AFLP	*AFLP1, AFLP2*	Ballvora *et al.* (1995)
Globodera pallida	*Gpa* (QTL)	RFLP		Kreike *et al.* (1994)
	Gpa2	RFLP	*GP34, CT100*	Rouppe Van Der Voort *et al.* (1997)
	Gpa2	AFLP	*E+ATG/M+CTA – 148*	Rouppe Van Der Voort *et al.* (1997)
	Gpa2	CAPS	*77L, PM4c, 77R*	Rouppe Van Der Voort *et al.* (1999b)
Globodera spp.	*Grp1*	CAPS	*GP21, GP179*	Rouppe Van Der Voort *et al.* (1998)
Meloidogyne chitwoodi	R_{mc1}	RFLP	*TG523*	Brown *et al.* (1996)
Meloidogyne spp.	R_{mc1}	AFLP	*E+AAC/M+CGA – 170*	Rouppe Van Der Voort *et al.* (1999a)
	R_{mc1}	CAPS	*CT182, M39b*	Rouppe Van Der Voort *et al.* (1999a)
Glandular trichomes	QTL	RFLP		Bonierbale *et al.* (1994)

1993) and *Gro1* (gene conferring resistance to *G. rostochiensis* pathotype Ro1) which is proposed to corresponded to *Fb*, on chromosome VII (Barone *et al.* 1990, Ballvora *et al.* 1995). QTL analysis identified three loci involved in resistance to *G. rostochiensis* pathotype Ro1 on chromosomes III, X and XI (Kreike *et al.* 1993, Kreike *et al.* 1996).

In regard to resistance to *G. pallida*, the nematode resistance locus *Gpa2* (resistance to *G. pallida* pathotype Pa2) was mapped on chromosome XII using information on the genomic positions of known AFLP (Rouppe van der Voort *et al.* 1997) and CAPS markers (Rouppe van der Voort *et al.* 1998). One major locus *Gpa* conferring resistance to

G. pallida pathotypes Pa2 and Pa3, is mapped on chromosome V, and two minor loci on chromosome IV and VII based on the QTL analysis of *S. spegazzinii* were also reported (Kreike *et al.* 1994).

Broad-spectrum resistance both to *G. rostochiensis* and *G. pallida*, regarded as polygenetically inherited, could be ascribed to the action of locus *Grp1* (Rouppe van der Voort *et al.*, 1998). QTL analysis allocated *Grp1* (resistance to *G. rostochiensis* pathotype Po5 and *G. pallida* pathotype Pa2) on chromosome V (Rouppe van der Voort *et al.* 1998). Interestingly, *Grp1* was mapped on a genomic region harboring other resistance factor to viral, fungal and nematodal pathogen (Rouppe van der Voort *et al.* 1998).

RKN

In linkage analysis of RKN resistance, only resistance to *M. chitwoodi* has been mapped on potato genome, while there are many resistances available for various *Meloydogine* species. The *Rmc1* (resistance to *M. chitwoodi*, race 1) locus originates from the wild species *S. bulbocastanum* and localized on chromosome XI (Brown *et al.* 1996). Recently, it has been demonstrated that the resistance *Rmc1* includes not only *M. chitwoodi* and the related species *M. fallax* but also a genetically distinct populations of *M. hapla* (Rooupe van der Voort *et al.* 1999b).

Grandular Trichomes

Based on QTL map constructed by RFLP markers and phenotypic data of grandular trichomes, two quantitative trait loci, one on *chromosome* VI and the other on *chromosome* X were identified to be highly associated with the indication levels of oxidase, phenolic structure and trichome density of type A (Bonierbale *et al.* 1994). For type B trichomes, five QTLs were found for fatty acid sucrose ester levels (Bonierbale *et al.* 1994).

Simple, easy and cost effective markers for MAS are under development. These markers can be the powerful tools for the screening procedures. However, molecular marker closely linked to the target locus sometimes showed a distorted segregation (Ritter *et al.* 1991, Kreike *et al.* 1994).

Testing the applicability of MAS for potato breeding should be made, associated with wider genetic background and variable environmental conditions. The heritabilities (h^2) of the most of the quantitative resistance traits which were mentioned in this review, were low to medium, up to 0.6, so that phenotypic selection of parental lines often resulted in unexpectedly low frequency and low level of resistance progeny (Mendoza 1994). Compared with the conventional phenotypic selection, application of known molecular markers on the QTLs could alleviate such pitfalls, however, an integrated approach for MAS on QTLs should be demonstrated on potatoes; and this is the subject to be provided to materialize the fundamental scientific finding on DNA markers to the real breeding uses. Development of simple selection scheme for a quantitative trait which is controlled by several genes with various gene interactions, could be conducted by integration of the marker technology and a statistical analysis using a multivariate analysis (Tanksley and Nelson 1996, Watanabe *et al.* 1997b). A QTL marker with a highly contributing genomic region could be used for an initial screening for a large population instead of making details analysis by various markers associated with the specific quantitative trait (Alpert and Tanksley 1996, Grandillo and Tanksley 1996). A combination of multivariate statistical package (Nelson 1997), genotype graphics (Watanabe 1994) and QTL map information itself shall enhance the employment of specific molecular markers for quantitative trait selection, and indeed, some experimental result was obtained in simultaneously selecting glandular trichome trait, disease resistances and agronomic traits (Watanabe *et al.* In preparation).

III-3. Recent development in transgenic potatoes

Plant genetic engineering offers opportunities for the creation of pest-resistant potatoes by insertion and expression of foreign genes. Conventional potato breeding has pitfalls described in the previous section. Moreover, controlling and modifying expression of introgressed genes are principally not feasible using conventional technique. Conventional breeding for selection of genotypes with desirable traits without defective effects from introduced genes requires numerous trials. This novel transgenic technique can overcome these pitfalls, and is especially important when desirable genes do not exist in potato genetic resources.

The potato is ranked the fifth among cultivated transgenic crops in 1998 in descending order of area, following soybean, corn/maize, cotton, and canola/rapeseed (James 1999). Some examples in attempting creation of novel transgenic potatoes for pest resistance are summarized in **Table 3** according to types of pests or related traits and inserted genes. Several transgenic cultivars of potatoes have been released as commercial uses since 1995 (USDA 1999).

Future challenges include; 1) new promoters and enhances sequences to drive high levels of expres-

Table 3. Some examples of studies on transgenic potatoes related to pest resistance traits.

	Target pest	Origin of the genes	Main references
Insects	*Phthorimaea operculella* (potato tuber moth)	*Bacillus thuringienses* (CryV-Bt, CryI A (b))	Douches *et al.* (1998). Jansen *et al.* (1995),
	Lacanobia oleracea (tomato moth)	Jackbean lectin	Gatehouse *et al.* (1999)
	Myzus persicae (Sulzer) (aphid)	Bean chitinase	Gatehouse *et al.* (1996)
		Snowdrop lectin	Gatehouse *et al.* (1996)
		Wheat β-amylase	Gatehouse *et al.* (1996)
		Jackbean lectin	Gatehouse *et al.* (1999)
		Proteinase inhibitor	Benchekroun *et al.* (1995)
	Aulacorthum solani (aphid)	Snowdrop lectin	Down *et al.* (1996)
	Leptinotarsa decemlineata (colorado beetle)	*Bacillus thuringiensis* (Cry Ⅲ A, Bt-R)	Perlak *et al.* (1993), Whalon and Wierenga (1994), Wierenga *et al.* (1996)
Virus	Potato leafroll virus	Coat protein	Kawchuk *et al.* (1990), Kawchuk *et al.* (1991), van der Wilk *et al.* (1991), Presting *et al.* (1995), Hoy and Head (1995), Thomas *et al.* (1997), Thomas *et al.* (1999)
		Movement protein	Tacke *et al.* (1996)
		Replicase	Thomas *et al.* (1999)
		Pokeweed antiviral protein	Lodge *et al.* (1993)
	Potato virus X	Coat protein	Hefferon *et al.* (1997), Xu *et al.* (1995), Longedijk *et al.* (1992), Lawson *et al.* (1990), Hoekema *et al.* (1989), Hemenway *et al.* (1988)
		Mammalian oligoadenylate synthetase	Truve *et al.* (1993)
		Movement protein	Tacke *et al.* (1996)
		Pokeweed antiviral protein	Lodge *et al.* (1993)
	Potato virus Y	Coat protein	Hassairi *et al.* (1998) Hefferon *et al.* (1997), Wefels *et al.* (1993), Lawson *et al.* (1990)
		Movement protein	Tacke *et al.* (1996)
		Pokeweed antiviral protein	Lodge *et al.* (1993)
		Replicase	Pehu *et al.* (1995)
	Potato virus S	Coat protain	Mackenzie *et al.* (1991)
	Cucumber mosaic virus	Pokeweed antiviral protein	Lodge *et al.* (1993)
Viroid	Potato spindle tuber viroid	Double-stranded RNA-specific ribonuclease	Sano *et al.* (1997)
		Ribozyme	Yang *et al.* (1997)
Fungi	*Fusarium sambucinum* (Fusaruim dry rot)	Cucumber anionic peroxidase	Ray *et al.* (1998)
	Phytophthora infestans (Late blight)	Cucumber anionic peroxidase	Ray *et al.* (1998)
		H_2O_2-generating glucose oxidase	Wu *et al.* (1995)
		Chimeric gene (Barnase and barstar)	Strittmatter *et al.* (1995)
		Osmotin	Liu *et al.* (1994)
Bacteria	*Erwinia cartovora* (Erwinia soft rot)	Pectase lyase	Wegener *et al.* (1996)
		Cucumber anionic peroxidase	Ray *et al.* (1998)
		H_2O_2-generating glucose oxidase	Wu *et al.* (1995)
		Cecropin B	Allefs *et al.* (1995)
		Antimicrobical peptide	Allefs *et al.* (1996)
		T4 phage lysozyme	Düring *et al.* (1993)
	Pseudomonas solanacearum (bacterial wilt)	Cecropin lytic peptide analogue	Montanelli *et al.* (1995)

sion in the correct tissues at the relevant stages, 2) a wider range of more acceptable selectable markers, 3) new vectors, 4) routine protocols if traits are to be modified by over-expressing or antisensing several genes sequentially or simultaneously, 5), reliable selection methods under field conditions for commercially available transgenics under greenhouse condition, and 6), evaluation of the effects of environment on transgene expression and trait development and stability (Davis 1996).

Recently, concern about genetically modified (GM) food has been intensified, especially in Europe and Japan. Social-scientific aspects are important for further development and utilization of transgenic plants; 1) intellectual property right, 2) public concern, and 3) regulation (Watanabe 1999b, 1999c, Watanabe and Sonoda 1999, Watanabe and Iwanaga 1999). These components are not only negligible but also important issues which shall be discussed in separate review papers in terms of cultivar adoption, access and benefit sharing of germplasm and fundamental consideration of employment of the genetic engineering.

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