The Americas Journal of Plant Science and Biotechnology *©2011 Global Science Books*

Potato Resistance to Insects

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ABSTRACT

Potato, *Solanum tuberosum*, is the fourth major crop and is grown around the world. It is subject to a large number of insect pests, but the Colorado potato beetle, the potato tuber moths and aphids are the most damaging. Crop resistance to these insects can alleviate problems caused by the use of synthetic insecticides. The diversity of wild tuber-bearing *Solanum* species offers a source of resistance to insects and pathogens; however, it has so far been under-utilized. This article reviews progress made in the development of insect resistant potato cultivars, as well as the biological and methodological challenges of developing insect resistant potato varieties. We conclude that the prospects of using wild species in future potato breeding programs are good, but, screening and experimental protocols need to be more holistic given the complexity of insect-potato interactions.

Keywords: aphids, Colorado potato beetle, crop resistance, *Leptinotarsa decemlineata*, *Macrosiphum euphorbiae*, *Myzus persicae*, potato tuber moth, *Phthorimaea operculella*, *Solanum tuberosum*, *Symmetrischema tangolias*, *Tecia solanivora*

Abbreviations: CPB, Colorado potato beetle; **EPG**, electric penetration graph; **QTL**, quantitative trait locus

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INTRODUCTION

The development of agriculture has been based on the development of crop genotypes with good yield that are well adapted to the biotic and abiotic conditions encountered in the regions where they are grown. Producers have been genetically enhancing the ability of crops to resist insects and diseases by keeping the most resistant individuals of production for planting the next season. This process became better understood with the development of modern population and molecular genetics. More recently, approaches to breeding for insect resistance in crops have become more closely matched to underlying genetic models (Painter 1951).

There are numerous examples of the successful use of insect resistant crops in agriculture, such as wheat cultivars with resistance to the Hessian fly or phylloxera resistant grapevines, some of which date back over 200 years (Smith and Quisenberry 1994). These successes demonstrate the potential of crop resistance to reduce the economic impact of insects. However, in an era where chemical insecticides are increasingly effective and accessible, direct insect dam-

Received: 10 March, 2010. Accepted: 10 December, 2010.

Invited Review

age to crops is often perceived to be under total control. However, insecticide control has a range of associated problems including the development of insecticide resistance, increased concerns about the use of petroleum derived products, direct effects on the environment, and possible deleterious effects on the health of users. Crop resistance to insects is seen as an environmentally friendly and sustainable solution to insect pests that could reduce the inputs of chemical insecticides. Recent evidence suggests that growers are increasingly interested in incorporating crop resistance into their integrated pest management strategies (Smith and Quisenberry 1994).

Potato, *Solanum tuberosum*, is the fourth major crop, is grown around the world, and is attacked by a diversity of insect pests. Modern potato varieties have a narrow genetic base and, as a consequence, are usually equally susceptible to most herbivores (Jansky *et al.* 2009). Many insect resistance traits can be imported into cultivated varieties from wild potato relatives. Fortunately, potato breeders have approximately 230 species of wild potato relatives (*Solanaceae*, Section Petota) to choose from when searching for desirable resistance traits (Flanders *et al.* 1999). Wild potatoes are native to the area from the southwestern United States, southward through Mexico and Central America, along the Andes of South America, and into the plains of Argentina, Paraguay, and Uruguay. Most species have a narrow range defined by a specific set of ecogeographic characteristics, but some are more widely distributed. Representative material is available to scientists as continuously maintained accessions in international genebanks. These genebanks also maintain information on different aspects of the accessions including resistance levels to insects (Flanders *et al.* 1999).

The majority of wild *Solanum* species, approximately 64%, are diploid (2x = 24), and most of the remaining species are either tetraploid (4x = 48) or hexaploid (6x = 72) (Jansky *et al.* 2009). Crossability between wild species or with cultivated varieties is mainly determined by having the proper balance of genetic factors contributed by gametes to the endosperm, described by the endosperm balance number. *Solanum* species have consequently been assigned endosperm balance numbers based on their ability to hybridize with each other (Jansky *et al.* 2009). Furthermore, somatic hybridization can be used to overcome the lack of compatibility between wild and cultivated potatoes (Chen *et al.* 2008).

POTATO RESISTANCE TO THE COLORADO POTATO BEETLE

The Colorado potato beetle (CPB) has become a major pest of potato around the world. Originally feeding on a few Solanaceous plant species, it rapidly adapted to potato and spread to many of the regions where the crop is produced. Its biology has been extensively studied (Hare 1990). The fact that both the adult and the larval stages feed on the potato crop is important for the development of insect resistant potatoes. Adults are mobile and have to find a source of food after emerging from hibernation or after moulting in the ground. Oviposition is generally preceded by feeding on a host plant. The first instar larvae are small and tend to remain on the plant material where the eggs were deposited. On a susceptible host plant, adults limit egg numbers according to the capacity of the plant to support feeding by the larvae (Pelletier 1995). Older larvae are more mobile but rarely have to move to another plant to complete their development. Acceptance of the plant as a host is determined by two events: adult choice and establishment by first instar larvae.

Resistant germplasm

1. Sources and variability

Some differences in the biological performance of the CPB have been observed among commercial potato cultivars (Torka 1950; Horton *et al.* 1997; Metspalu *et al.* 2000), but, resistance has not been at a level that eliminates economic impact on the crop. Furthermore, differences in foliar glycoalkaloids are not correlated with negative effects on the biological performance of the CPB (Metspalu *et al.* 2000; Lyytinen *et al.* 2007), suggesting that it is necessary to look for resistance sources outside the cultivated potato germplasm.

Between 1966 and 1986, large-scale screening for resistance to the CPB was conducted in Minnesota providing information on 1686 potato accessions representing 100 species of wild *Solanum* (Flanders *et al.* 1992). Other studies have also assessed resistance levels, but have used substantially fewer species and genotypes (Torka 1950; Carter 1987; Jansky *et al.* 2009). This information has guided the selection of parents for the development of resistant potato cultivars. These studies also demonstrated the variability of resistance within species, and between accessions within the same species (Carter 1987; Jansky *et al.* 2009). Studies conducted at the genotype level (within accessions) provided evidence that resistance varies within accessions, that this variability differs depending on the accession and the species in question, and that it is generally small enough not to greatly influence the development of breeding populations (Bamberg *et al.* 1996; Pelletier and Tai 2001; Pelletier *et al.* 2001). However, fine screening of accessions is recommended if a single genotype is to be used as a parent.

The crossability of wild *Solanum* species with the cultivated potato depends on the difference between the two species for several factors including ploidy and the endosperm balance number, but, interspecific crossing is generally more successful where the wild species is closely related to potato (Jackson and Hanneman 1999). Protoplasm fusion is often the only way to introgress the resistance trait of the wild *Solanum* species into potato germplasm (Xu *et al.* 1991; Chen *et al.* 2004). This method increases the number of candidate species that could be used as resistant parents for breeding CPB resistant cultivars. However, the number of CPB resistant species currently used in breeding programs is limited (see below). These and other species (currently not used in breeding programs) have been used to determine host effects on biological performance of the beetle (**Table 1**).

2. General considerations on the mode of action

Wild and cultivated potatoes contain a variety of glycoalkaloids that are considered protective factors against herbivores. However, total glycoalkaloid levels as well as the concentrations of the most abundant glycoalkaloids are not associated with resistance to the CPB (Flanders *et al.* 1992). Some specific glycoalkaloids like commersonine, dehydrocommersonine, demissine, and leptines, when present in the foliage even in relatively low concentrations, provide better protection than total glycoalkaloid content. Breeding for glycoalkaloid content, as was done for leptines from *S. chacoense*, is relatively difficult since the trait is polygenic, foliage glycoalkaloid content is correlated with tuber content (except for leptines), and glycoalkaloid production is influenced by environmental factors (Tingey 1984).

Wild *Solanum* species also possess trichomes that are generally considered to form a protective barrier against insect herbivory. Species with glandular trichomes were found to be more frequently resistant to the CPB and to some other insects than species without glandular-trichomes (Flanders *et al.* 1992). In potatoes, glandular trichomes are of two types: type-A glandular trichomes are four-lobed, and contain phenolic compounds; type-B are longer trichomes which exude droplets containing sucrose esters of carboxylic acids from their tips (Flanders *et al.* 1992). The presence or density of glandular trichomes does not entirely explain observed differences in resistance levels in potatoes. In some cases it is the nature of the exudates that plays a determining role in providing resistance. The role of glan-

Table 1 List of wild *Solanum* species that were studied for their effects on the biological performance of the CPB.

Species	References
S. acroglossum	Pelletier *et al.* 2007
S. allandiae	Carter 1987
S. berthaultii	Gibson 1979; Casagrande 1982; Mehlenbacher *et al.* 1984; Wright *et al.* 1985; Gregory *et al.* 1986; Groden and Casagrande 1986; Carter 1987; Dimock and Tingey 1987; Castanera *et al.* 1988; Neal *et al.* 1989; Pelletier and Smilowitz 1990; Neal *et al.* 1991; Pelletier and Smilowitz 1991; Steffens and Walters 1991; Flanders *et al.* 1992; Franca and Tingey 1994; Tingey and Yencho 1994; Yencho and Tingey 1994; Yencho *et al.* 1994; Castanera *et al.* 1996; Smilyanets *et al.* 1996; Sikinyi *et al.* 1997; Pelletier *et al.* 1999; Pelletier and Tai 2001; Pelletier and Dutheil 2006; Smilyanets *et al.* 2007
S. brevicaule	Smilyanets *et al.* 2007
S. bukasovii	Carter 1987; Smilyanets *et al.* 2007
S. capsicibaccatum	Sikinyi *et al.* 1997; Pelletier *et al.* 1999; Pelletier and Tai 2001; Pelletier and Clark 2004
S. chacoense	Torka 1950; Hawkes 1958; Sinden *et al.* 1986; Carter 1987; Sagredo *et al.* 1988; Flanders *et al.* 1992; Sikinyi *et al.* 1997; Sanford *et al.* 1998; Yencho *et al.* 2000; Sagredo *et al.* 2006; Smilyanets *et al.* 2007
S. chomatophilum	Pelletier *et al.* 2007
S. comersonii	Hawkes 1958; Flanders *et al.* 1992
S. fendleri	Carter 1987; Lorenzen and Balbyshev 1997
S. jamesii	Hawkes 1958; Carter 1987; Pelletier *et al.* 1999, 2001
S. neocardenasii	Dimock *et al.* 1986; Sinden *et al.* 1991
S. okadae	Pelletier *et al.* 1999; Pelletier *et al.* 2001; Pelletier and Clark 2004
S. oplocense	Pelletier *et al.* 2001; Pelletier and Clark 2004
S. parodie	Smilyanets *et al.* 2007
S. paucissestum	Pelletier *et al.* 2007
S. pinnatisectum	Carter 1987; Sinden *et al.* 1991; Pelletier *et al.* 1999, 2001; Chen *et al.* 2004; Pelletier and Clark 2004
S. piurae	Pelletier *et al.* 2007
S. polyadenium	Gibson 1976b; Carter 1987; Pelletier and Tai 2001; Pelletier and Clark 2004
S. raphanifolium	Sikinyi *et al.* 1997
S. rybinii	Smilyanets *et al.* 2007
S. schiskii	Smilyanets *et al.* 2007
S. stoloniferum	Hawkes 1958; Carter 1987
S. sucrense	Carter 1987
S. tarnii	Pelletier *et al.* 2007; Thieme *et al.* 2008
S. trifidum	Sikinyi *et al.* 1997; Pelletier *et al.* 1999; Pelletier and Tai 2001; Pelletier and Clark 2004

dular trichomes has mainly been studied with *S. berthaultii* (including *S. tarijense*).

3. S. berthaultii (including S. tarijense)

S. tarijense and *S. berthaultii* were initially described by Hawkes as different species, but have since been reclassified as one species, *S. berthaultii* (Spooner *et al.* 2007). The main taxonomic difference between the two former species was the lack of type-B trichomes in *S. tarijense*; however, some accessions labeled as *S. berthaultii* also do not bear type-B trichomes (Pelletier and Smilowitz 1991; Spooner *et al.* 2007). Most of the literature on potato resistance to the CPB is related to those *S. berthaultii* accessions that bear type-B trichomes. Host acceptance and performance of the CPB differ widely even among those accessions that always bear type-B trichomes.

Several authors have demonstrated a reduction in biological performance of the CPB at the larval and the adult stages when confined on *S. berthaultii* (Casagrande 1982; Wright *et al.* 1985; Groden and Casagrande 1986; Neal *et al.* 1991). This reduction in biological performance was associated with the presence of trichomes and their exudates. Exudate from type-A trichomes, containing polyphenol oxidase (Castanera *et al.* 1996), accumulates on the tarsae of small beetle larvae leading to reduced survival (Dimock and Tingey 1987; Neal *et al.* 1991) and reduced leaf consumption (Dimock and Tingey 1988). The ability of *S. berthaultii* to entrap small insects or the appendages of larger ones comes from the reaction of the sticky exudates of type-B trichomes, which contain sesquiterpenoid and sucrose esters (Neal *et al.* 1989), and the polyphenoloxidase contained in type-A trichomes, resulting in quinone formation (Gregory *et al.* 1986; Steffens and Walters 1991). Trichomes also influence beetle preferences among *S. berthaulti* genotypes: Given a feeding choice between *S. tuberosum* and *S. berthaultii*, larvae and adults preferred the foliage of *S. tuberosum*, but adults were more discriminating (Yencho and Tingey 1994). Adult beetles were less attracted to intact leaflets of *S. berthaultii*, or *S. tuberosum* leaflets to which trichome exudates from *S. berthaultii* had been transferred, than to *S. berthaultii* foliage with the trichomes removed (Yencho and Tingey 1994). A leaf extract containing type-B trichome exudates, but not a similar extract from a resistant *S. berthaultii* without type-B trichomes, applied to potato reduced feeding by adult CPB (Pelletier and Smilowitz 1990). Extracts from a *S. berthaultii* clone bearing type-B trichomes when applied to potato foliage did not modify the behavior of adult CPB but reduced consumption while similar extracts from another genotype of *S. berthaultii* without type-B trichomes increased movement of the adults and reduced contact with the plant material (Pelletier and Smilowitz 1991).

However the effects of trichome exudates do not entirely explain the resistance of *S. berthaultii*. The removal of trichome exudates improves feeding by small larvae but does not improve biological performance of the larvae (Dimock and Tingey 1988; Neal *et al.* 1989). *S. berthaultii* foliage, when ingested by the CPB, reduced ovarian development and fecundity. Large amounts of undigested material found in the midgut of the insects suggest that *S. berthaultii* could negatively influence digestion, being a poor nutritional source for the beetle (Franca and Tingey 1994).

Solanum tarijense (mainly *S. berthaultii* accessions without type-B trichomes) has also been identified as resistant (Flanders *et al.* 1992); however only a few studies have ever tried to characterize the factors involved in its observed resistance to the CPB. *S. tarijense* negatively impacts the biological performance of the CPB but has a more pronounced effect on the adults (Pelletier *et al.* 2001; Smilyanets *et al.* 2007). Thanatosis reaction is observed in adults deposited on *S. tarijense* foliage; This reaction is greatly reduced when type-A trichomes are removed, but feeding remains low; The volatile fraction of methylene chloride dip extracts from *S. tarijense* has been shown to act as a feeding deterrent when applied to potato foliage and changes host selection behavior of adult beetles (Pelletier and Dutheil 2006).

Effort has been made to isolate the chemicals responsible for non-trichome based resistance factor(s) in *S. berthaultii*. Bioassay-guided fractionation of methylene chloride leaf rinse extracts lead to the isolation of a polar fraction with low deterrent activity and two nonpolar fractions exhibiting higher specific activity (Yencho *et al*. 1994). The nonvolatile fraction of the extract had more deterrent activity than the volatile fraction.

The variability of resistance levels between *S. berthaultii* accessions, and the prospect of using this plant as a source of resistance has brought questions as to the ability of the CPB to overcome resistance. When confined on *S. berthaultii*, oviposition and larval mortality of the CPB was no longer reduced after two and three generations respectively (Groden and Casagrande 1986). A significant additive genetic component was found when CPB was raised on *S. berthaultii*, indicating the possibility of adaptation of the insect to the wild *Solanum* while maintaining its biological fitness on potato (Pelletier and Smilowitz 1991). An artificial selection study comparing insects grown on potato and on *S. berthaultii* for 10 generations did not produce a significant change in the net replacement rate between the two strains (Franca *et al*. 1994).

Trichome composition varies according to the environment where the accession was originally collected (Gibson 1979). The presence of type-B trichomes is genetically controlled by a single dominant gene (Gibson 1979). The heritability of trichome-related traits measured in a population of *S. berthaultii* × *S. tuberosum* hybrids was variable; Droplet size of type-B trichome exudates was highly heritable (64 ± 8%), the density of type-B trichomes intermediate (22 ± 5%) and the heritability of type-A trichome density was variable (18 to 32%) (Mehlenbacher *et al*. 1984). Genes generally associated with trichomes have been linked to resistance in a hybrid population (Yencho *et al*. 1996). On the other hand, a QTL, not associated with trichomes was also strongly related to resistance against adult CPB (Yencho *et al*. 1996).

Parental lines derived from *S. berthaultii* after six back crosses have been released from Cornell University (NYL 235-4, Q174-2, and NYL 123) (Plaisted *et al*. 1992; De Souza *et al*. 2006; Malakar-Kuenen and Tingey 2006). Furthermore, hybrids derived from *S. tarijense* (PI414150) have been produced and evaluated at the Potato Research Centre, Fredericton, Canada (Pelletier, unpublished data).

4. *S. chacoense*

Solanum chacoense is the wild *Solanum* species that has received most attention for potato resistance to the CPB after *S. berthaultii*. The resistance to the CPB of *S. chacoense* is based on the presence of leptine I and II which are acetylated analogs of chaconine and solanine respectively and are produced only in the foliage (Sinden *et al*. 1991). Field and laboratory comparisons between clones from the same population expressing different level of leptines demonstrated that adult abundance, adult feeding, larval development rate, and larval survival were lower on clones with high levels of leptines (Sinden *et al*. 1986, 1988; Yencho *et al*. 2000) likely because of their strong feeding deterrence.

Somatic fusion is a necessary step for the introgression of *S. chacoense* with crop potato and leads to hybrids that are generally less resistant to adult CPB than the parents, but more resistant to larvae (Jansky *et al*. 1999). Early on, breeders experienced difficulties in maintaining a high level of resistance from *S. chacoense* in populations without sacrificing tuber quality (Torka 1950). The level of leptines remained high when a population of *S. chacoense* × *S. tuberosum* hybrids were backcrossed with *S. chacoense* but decreased when *S. tuberosum* was used (Sanford *et al*. 1998). Two loci, involved in the synthesis of leptines have been identified. These segregate as two complementary epistatic genes, and allow the synthesis of leptinidine and acetyl-leptinidine, respectively (Sagredo *et al*. 2006). Other factors are likely necessary for the production of leptines in quantities sufficient to be an effective defense against the CPB (Sagredo *et al*. 2006).

Parental lines (including ND2858-1 and ND5873-16) issued from *S. chacoense* produced at the North Dakota State University have been used in breeding programs (Lorenzen and Balbyshev 1997; de Souza *et al*. 2006; Thompson *et al*. 2008). The clone, ND2858-1, derived from *S. chacoense* produces leptine I and II but at concentrations that do not explain the high level of resistance observed on this clone (Lorenzen *et al*. 2001). Irradiance and temperature influence the production of glycoalkaloid compounds including leptine I and II and might explain discrepancies with the identification of resistance factors (Lafta and Lorenzen 2000).

5. *S. pinnatisectum*

Very little is known about the mode of resistance to the CPB in *S. pinnatisectum*. The concentration of the glycoalkaloid tomatine might be responsible for part of the resistance of *S. pinnatisectum* (Sinden *et al*. 1991). However, using *S. pinnatisectum* as a scion, but not as rootstock, in a graft with potato foliage increased protection of the potato foliage indicating that the active factor was likely produced and translocated from the foliage (Pelletier and Clark 2004).

The genetics of resistance to the CPB in *S. pinnatisectum* was studied using a resistant 2n hybrid population with *S. cardiophyllum* (Chen *et al*. 2004) and revealed that only two genes are responsible for resistance in *S. pinnatisectum* (Nandy *et al*. 2008). Interspecific somatic hybrids between *S. tuberosum* and *S. pinnatisectum* were regenerated following electrofusion of mesophyll protoplasts (Thieme *et al*. 1997; Chen *et al*. 2008) and some of that material has been developed to the BC_4 stage (R. Thieme, pers. comm.).

6. *S. tarnii*

Foliar consumption and survival of larvae was greatly reduced when beetles were maintained on foliage of *S. tarnii* (Sikinyi *et al*. 1997), but the exact factors involved are not yet known. Somatic fusion was used to produce hybrids between *S. tarnii* and *S. tuberosum*; that material was later back-crossed with *S. tuberosum* (Thieme *et al*. 2008) and is currently at the BC_3 stage (R. Thieme, pers. comm.).

7. *S. polyadenium*

Four-lobed glandular hairs on the leaves and stems of the potato species *S. polyadenium* provide resistance to larvae of the CPB by producing a sticky material that traps larvae or encases their appendages; Larvae with encased feet fall from the plants to die (Gibson 1976b). However, using *S. polyadenium* as a scion, but not as rootstock, in a graft with potato foliage protected the potato foliage indicating that the active factor is also likely produced and translocated from the foliage (Pelletier and Clark 2004). Somatic fusion has been used to produce hybrids between *S. polyadenium* and *S. tuberosum* (Dr. John P. Helgeson, USDA/ARS, Department of Plant Pathology, University of Wisconsin, Madison, WI, pers. comm.); after a few back-crosses with *S. tuberosum*, the fertility of the cross was lost (Dr. H. De Jong, Potato Research Centre, AAFC, Fredericton, Canada, pers. comm.).

8. *S. neocardenasii*

S. neocardenasii foliage is densely covered with sticky trichomes; however, resistance to the CPB found in *S. neocardenasii* has been partly attributed to glycoalkaloids [tomatine and solanocardenine (Sinden *et al*. 1991) and/or solanocardinol (Osman *et al*. 1991)], whereas the removal of the trichomes did not affect the performance of either larvae or adult CPB (Dimock *et al*. 1986).

Table 2 Mean (± SEM) and coefficient of variation (c.v.) of potato, *S. tuberosum*, foliage consumption during a period of 24 h by male or female adult CPB of different ages. The optimal number of samples (N) was calculated based on α=0.05 (Sokal and Rohlf 1995).

Age	Males		Females		Both Sexes		Optimal N		
	Mean ± SEM	c.v.	Mean ± SEM	c.v.	Mean ± SEM	c.v.	♂	♀	Both
3 days	9.35 ± 0.31	0.23	10.61 ± 0.36	0.25	10.05 ± 0.25	0.25	19	27	25
5 days	6.61 ± 0.28	0.28	9.52 ± 0.32	0.25	8.22 ± 0.26	0.32	34	24	33
10 days	6.17 ± 0.25	0.26	10.69 ± 0.50	0.34	8.66 ± 0.37	0.42	17	49	62
17 days	3.97 ± 0.24	0.39	6.83 ± 0.50	0.54	5.59 ± 0.33	0.58	24	78	76

Evaluation (screening) of resistance

Breeding programs aiming to develop potato varieties resistant to insects produce thousands of seedlings for each cross, a result of the complex genetics of resistance traits and of the genetics of potato. All those seedlings have to be evaluated for resistance to the target insect pest in order to select the best parents for the next generation. Similarly, hundreds of accessions of wild *Solanum* species have to be tested in order to find the best sources of resistance. These activities require the use of an efficient and reliable screening method. Early in the breeding process, the amount of plant material available for testing is very limited. The initial evaluation is often performed with one or a few plants from each genotype available. Two approaches have been used, field- and laboratory-based bioassays.

1. Field tests

Planting the potato plant in the field, exposed to natural populations of the CPB is the simplest way of evaluating resistance (Torka 1950). This method is limited by the availability of material from each accession or genotype to be evaluated (Sinden *et al.* 1988). Greenhouse grown tubers are sometimes very small and do not survive well in the field. Plants can be produced from cuttings in the greenhouse but this requires extensive labour to produce and transplant the material in the field. Plants from either production technique are frail, susceptible to lack of water, and susceptible to wind damage for the first few weeks as they establish.

Another disadvantage stems from the biology of the CPB. Because the plant material is usually difficult to produce, there are often few replications. As the CPB tends to aggregate at the border of fields or forests to overwinter, colonization of the test plots is often uneven and leads to variability in defoliation and in the distribution of larvae (Torka 1950; Sinden *et al.* 1988). Plastic lined trenches (Boiteau *et al.* 1994) deployed around the field test prevent colonization by walking resulting in a more even distribution of the adults (Pelletier and Tai 2001; Pelletier *et al.* 2001, 2007). This method will only work if beetles have not overwintered in the field and should be done in a field that was not planted with potato the previous year. Cultivated potato plants, the controls, can be distributed randomly or systematically in the plot to assess the distribution and relative abundances of the beetles.

Field plots are usually replicated and designed as randomized complete blocks (Carter 1987; Bamberg *et al.* 1996; Yencho *et al.* 2000; Pelletier and Tai 2001; Pelletier *et al.* 2001, 2007). Defoliation, expressed as a percentage, or following an index, is usually used as a resistance estimate and evaluated at the end of the larval stage during the first or second generation of the insect. The population of the insect can also be measured throughout the growing season.

2. Data analysis

The analysis of field evaluations of resistance that includes variables related to population development on the plants is difficult because of the relatively large number of variables that must be considered. Some authors have used multivariate analytical approaches, conducting factorial analyses to simplify the data set and make the resulting factors independent (Carter 1987; Pelletier *et al.* 2001, 2007) since population parameters (such as numbers of adults, eggs and larvae) are often correlated (Bamberg *et al.* 1996). This approach results in factors having significant biological meaning that could also be related to antibiotic and antixenotic characteristics of the plant.

3. Lab feeding tests

Laboratory tests can also be used to screen resistant populations. Such an approach allows the use of greenhouse materials, often produced from true seed, when growing that material is not possible in the field. One of the limitations of laboratory tests is the relatively high cost of producing the CPB indoor. Laboratory tests have also been used to test plant materials growing in the field using field caught insects. Both situations require limiting the test to one life stage of the CPB. Since adults and first instars make the decision to accept or reject the plant as a host then these are generally used during tests.

Screening tests with adults are usually limited to the evaluation of the quantity of foliage consumed in a period of time varying from 4 to 24 hours. Foliage consumption will vary with age and sex (Cantelo *et al.* 1987) of adult CPB (**Table 2**) and between overwintered and emerging adults (Pelletier and Smilowitz 1990). If one assumes that an optimal screening test should minimize variability in consumption of potato foliage, then at least 17 young (10-days old) males should be used (**Table 2**). This would require a minimum (likely twice that value) of around 125 cm^2 of foliage, the equivalent of 10 to 15 terminal leaflets from young fully developed leaves, which is a lot to harvest from a single greenhouse grown plant. This amount of foliage could be more easily attained from plants grown from tubers in the field but requires an extra year to produce the tubers. The influence of test duration on results has also been studied (Nandy *et al.* 2008). It was concluded that 8 hours was optimal because it produces a clearer genetic model of the plant resistance traits. However, they also identify the genetic model of the plant resistance trait based on the 8 hours test (other test durations leading to different genetic models) creating a circular argument. The repeatability of adult screening tests (2.5 hour tests) has also been evaluated by running tests twice (the second time after a 24 hour interval) with the same beetles. The relation between consumption of potato and *S. berthaultii* foliage during the two bioassays was poor, with coefficients of determination (r^2) varying from 0.16 to 0.52, and was generally lower with females (Pelletier and Smilowitz 1990).

First instar larvae have been used in screening tests by several teams (Torka 1950; Yencho *et al.* 2000) and are more sensitive than tests using adults or larger larvae (Cantelo *et al.* 1987). First instars are easier to produce in the laboratory in large numbers; however, there are special requirements to insure that all the individuals are synchronized for development. This is especially important for bioassays of short duration where development is measured. Larvae from the same egg clutch emerge over a period of one or two hours. They first need to feed on the chorions of the eggs before they move to the plant foliage. During that time, the head capsule becomes completely schlerotized and goes from yellow through grey to black. At any given time within a few hours from the first larvae emerging, larvae with different head capsule colours can be seen in a single

Table 3 Problematic gelechiids, indicating principal life-history and distribution aspects that determine their interactions with potato crops.

Site of egg laying	Feeding preferences	Main damage
Potato tuber moth [*Phthorimaea operculella* (Zeller)]		
On dead potato leaves and in the soil close to host plant in the field; On tubers in storage (Traynier 1975; Das *et al.* 1993a, 1993b)	Often greater fitness on potato tubers compared to foliage, will also feed on tomato, eggplant and other Solanaceous crops (Traynier 1975; Raman and Palacios 1982)	Damage to shallow and exposed tubers particularly in irrigated fields of warm regions; Severe damage to stored potatoes in cooler Andean regions (Shelton and Wyman 1979; Sileshi and Teriessa 2001; Dangles *et al.* 2009)
Guatemalan tuber moth [*Tecia solanivora* (Povolny)]		
In soil at the base of the stem of flowering potato plants and on exposed tubers (Karlsson *et al.* 2009)	Potato tubers (Dangles *et al.* 2009)	Damage to tubers in fields and stores (Dangles *et al.* 2009)
Andean tuber moth [*Symmetrischema tangolias* (Gyen)]		
On the stem of potatoes (Palacios *et al.* 1999)	Potato stems, leaves, and tubers (Palacios *et al.* 1999; Dangles *et al.* 2009)	Damage to foliage, particularly severe in stems, and damage to tubers in fields and stores (Palacios *et al.* 1999; Dangles *et al.* 2009)
Tomato leaf miner [*Tuta absoluta* (Meyrick)]		
On above-ground foliage (Pereyra and Sanchez 2006)	Tomato preferred over potato, not known to feed on tubers, feeds on a variety of other Solanaceous crops and wild plants (Pereyra and Sanchez 2006)	Mines leaves, fruits, flowers, buds, and stems (Pereyra and Sanchez 2006)

egg clutch. Synchronization of the age of the larvae can be achieved by using "black head" larvae from an egg clutch that has been observed on a regular basis (every 30 minutes). A group of 10 first instar larvae can be used with around 5 cm^2 of foliage for a test of 48 hours and only a few replicates is required (Cantelo *et al.* 1987) making it possible to evaluate resistance from a single plant grown in the greenhouse. First instar larvae can only be used in no-choice type bioassays. They are very reluctant to move from a leaflet or a disk, and if offered the choice of two acceptable leaflets or disks, 75% of the larvae will remain on the first plant material encountered over a period of 4 hours (Pelletier, unpublished data).

Investigating chemical defenses by isolating compounds and testing their effects on pests with *in vitro* bioassays can be inefficient and sometimes ineffective. Assays for chemical composition differences among plants segregating for resistance, an often overlooked alternative, can be more efficient and is sometimes the only effective strategy for identifying defense compounds (Sinden *et al.* 1988).

POTATO RESISTANCE TO GELECHIID MOTHS

Throughout the world, crop potatoes are attacked by the larvae of a diverse assemblage of lepidopteran species. These species occur across a variety of feeding guilds that includes leaf chewers [cutworms, *Peridroma saucia* Hübner, loopers, *Trichoplusia ni* (Hübner) and armyworms *Pseudaletia* spp.], stem-borers [European corn borer, *Ostrinia nubilalis* (Hübner), potato stem borer, *Hydraecia micacea* (Esper)] and leaf miners (tuber moths, see below) (Deedat *et al.* 1983; Kennedy 1983; Landolt 2001; Zeims *et al.* 2008; Dangles *et al.* 2009). Damage by these insects can sometimes increase the incidence of potato pathogens, e.g., corn-borers can increase the incidence of aerial stem rot caused by *Erwinia carotovora* (Jones) (Kennedy 1983) and moth damage to tubers increases fungal-related tuber-rot (Shelton and Wyman 1979; Sileshi and Teriessa 2001). Overall however, above-ground feeding by lepidopteran larvae rarely causes economic losses as many modern varieties of crop potato appear to have generally high tolerance to above-ground damage (Kennedy 1983; Nault *et al.* 2001; Zeims *et al.* 2008).

In contrast to the generally low levels of damage caused by leaf chewers and stem borers, considerable damage can sometimes result from attack by tuber feeding lepidopteran larvae, particularly among stored potatoes in tropical and sub-tropical regions. Among the most damaging tuber feeders are members of the family Gelechiidae, many of which co-occur in Andean potato producing regions (**Table 3**). Among these, *Tecia solanivora* (Povolny) feeds exclusively on potato tubers (Dangles *et al.* 2009), whereas *Symmetrischema tangolias* Gyen and *Phthorimaea operculella* Zeller feed on both the foliage and tubers of potatoes and related plants (Palacios *et al.* 1999; Horgan *et al.* 2007b). A further species, *Tuta absoluta* (Povolny), occasionally feeds on foliage of crop potatoes but not on tubers (Campos 1976), and is primarily a problem in greenhouse tomatoes (Ecole *et al.* 2001; Leite *et al.* 2001; Pereyra and Sanchez 2006). Tuber moths will lay eggs directly on exposed tubers in the field (Sileshi and Teriessa 2001) or in rustic potato stores (Das *et al.* 1993a, 1993b); however, it is not well understood how populations of *S. tangolias* and *P. operculella* on foliage in the field affect subsequent damage to tubers. The occurrence of parasitic *Copidosoma koehleri* Blanchard among tuber moths collected from field infested tubers at Huancayo, Peru, suggest that mining larvae can move directly from foliage to tubers as the potato plants mature and tuberize (F. Horgan, pers. obs.). Moth populations can also build up on foliage, sometimes having developed from infested seed potatoes, and later, at the time of harvest, the newly emerged adults lay eggs on exposed or heaped tubers in the field (Kroschel and Koch 1994).

Recent studies have shown potential partitioning among the tuber moth species complex according to physiological responses to ambient temperatures at different altitudes (Dangles *et al.* 2008). In general, *S. tangolias* occurs at high altitudes (>3000 m a.s.l.), *T. solanivora* occurs at lower altitudes (<2700 m a.s.l.) and all three species can occur at mid-elevations (Dangles *et al.* 2008, 2009). The occurrence of two or more species together can result in greater levels of damage than a single species infestation, presumably because of feeding complementarities among the species (Dangles *et al.* 2009). *Phthorimaea operculella* is common at lower altitudes in regions without *T. solanivora*, and is often highly abundant in coastal regions (i.e., Peru, Campos 1976; Raman 1988). In Peru, it is likely that *P. operculella* infestations of potato stores at altitudes above 3000 m a.s.l. in inter-Andean valleys are due to repeated re-infestations from coastal regions and mid-altitudes during potato transport and by product movement between rustic stores (A.R. Salas and J. Alcazar, Centro Internacional de la Papa, Peru, pers. comm.).

Foliage resistance

Despite gelechiid larvae causing most damage to tubers, and often severe damage in potato storage facilities, the mechanisms of resistance in potato foliage are considerably better understood than resistance mechanisms in tuber (Gurr 1995; Musmeci *et al.* 1997; Malakar and Tingey 1999, 2000). Furthermore, good progress has been made in breeding for resistance to above-ground damage through introgression with trichome-bearing wild potato species (Plais-

Table 4 Foliage resistance sources with associated fitness responses in target insects and proposed mechanisms of resistance.

Insect Responses	Mechanism	Reference
P. operculella		
Nine Australian (Queensland) varieties		
Fewer eggs laid	Chemical (volatile and non-volatile) and mechanical cues determine oviposition on different varieties, trichome densities also affected oviposition, but effects were not consistent.	Valencia 1984
Potato 'tarago', *S. polytrichon*, *S. chacoense*, *S. pinnatisectum*		
Sources affected the numbers of eggs per leaf	Leaf hairs on *S. polytrichon* and potato stimulate oviposition. Reasons for low egg numbers on *S. chacoense* and *S. pinnatisectum* are not known.	Gurr 1995
Many Indian commercial varieties and hybrids (19 varieties)		
Sources affected the numbers of mines per leaf.	Not determined	Parihar and Chandla 1995
***S. berthaultii* (4 accessions), *S. pinnatisectum* (2 accessions), *S. sparsipilum* (3 accessions), *S. tuberosum* × *S. berthaultii* hybrids (4 accessions)**		
Species effects on the numbers (and proportion of total eggs) of eggs on leaves, and on total numbers of eggs laid. Effects on successful establishment of neonates, larval duration, larval survival, pupal weight, and fecundity	High activity of polyphenol oxidase in the exudate *S. tuberosum* × *S. berthaultii* hybrids, and wild species with glandular trichome A reduced larval growth. Type-A trichomes also reduced fecundity. High levels of trichome B repulsed oviposition, but without trichome B, leaf pubescence stimulated oviposition. Significant antixenosis of larvae was related to type A and B-trichomes.	Musmeci *et al.* 1997
***S. berthaultii*, *S. commersonii*, *S. pinnatisectum*, *S. sparsipilum* (3 accessions), *S. spegazzini*, *S. sucrense*, *S. tarijense* (2 accessions), *S. tuberosum* × *S. berthaultii* hybrids (2 accessions)**		
Lower number of mines compared to cultivated potatoes.	Not determined	Arnoné *et al.* 1998
S. berthaultii (2 accessions); Ber331 (trichome A&B), Ber334 (trichome A only)		
Lower proportion of total eggs on leaves and total eggs laid, lower neonate establishment, longer larval duration and lower pupal weight. Overall less damage to leaves	Synergy between type A and type B glandular trichomes proposed as responsible for reducing fitness parameters.	Malakar and Tingey 1999, 2000
***L. hirsutum* Dunal (6 accessions), *L. hirsutum* f. *glabratum* CH Mull. (5 accessions) and cultivated tomato**		
Survival, and number of mines were reduced. Development times increased compared with cultivated tomato. Neonate mortality, pupal mortality and development times were linked to glandular trichome IV and VI densities. Non-glandular trichome V densities were linked to increased larval survival		Gurr and McGrath 2002
***S. tuberosum* × *S. berthaultii* hybrids, Brazilian potato varieties and tomato**		
Lower larval survival, longer larval and pupal development times, lower pupal weights, and higher pupal mortality	Not determined	Rêgo Lopes and Vendramim 2002
Various accessions of *S. berthaultii* (23 accessions)		
Varied effects on numbers and proportion of eggs on leaves, effects on total numbers of eggs laid, and effects on successful establishment of neonates.	Synergy between type A and type B glandular trichomes acting to reduce egg laying. Leaf hairs increased oviposition; Leaf pubescence was positively related to neonate establishment	Horgan *et al.* 2007, 2009a, 2009b
T. absoluta		
***L. hirsutum* f. *typicum* (acc. LA 1777)**		
Less eggs, longer pre-oviposition, and shorter oviposition periods, lower hatchability of eggs, longer larval and pupal development times, lower survival and pupal weight, no effect on sex ratios, and overall fewer mines on the leaves.	Fitness reductions related to hexane leaf extracts.	Ecole *et al.* 2001
***L. hirsutum* f. *glabratum* (acc. PI 134417)**		
Longer larval and pupal development times and lower survival and pupal weights, increased numbers of deformed pupae, no effect on sex ratios, and overall fewer mines on the leaves.	Higher levels of tridecan-2-one and higher densities of glandular trichomes were associated with reduced moth fitness.	Leite *et al.* 2001

ted *et al.* 1992; Malakar and Tingey 1999). However, in spite of the research attention, some simple behavioural and life-history aspects of tuber moths, including aspects of host location and egg-laying by adults, and host finding and penetration by neonate larvae, are still poorly understood; however, these behaviours and the environmental cues through which they are determined, are of key importance to the eventual outcome of moth attack, and to the meaningfulness and interpretation of screening and experimental studies.

Adult female tuber moths are attracted to potato plants largely through chemical stimuli (**Table 4**). Using electroantennogram studies, Das *et al.* (2007) have shown that certain fatty acid derivatives of green leaf volatiles elicit a significantly greater response in female *P. operculella* than in males, suggesting a role for these compounds in host finding for oviposition. Antennae from females further responded to a wide range of compounds that included monoterpenes, sesquiterpenes, and aromatics (Das *et al.* 2007) suggesting that complex blends of chemical compounds in the plant volatiles are responsible for host choice. Similarly, electroantennogram studies on female *T. solanivora* indicate responses to several sesquiterpenes and monoterpenes that are emitted only from foliage (and not from tubers, where the moth larvae feed) and to methyl phenylacetate that is released by flowering potato plants. Methyl phenylacetate is also present in the headspace of potato tubers (Karlsson *et al.* 2009). Which chemical cues determine attraction and oviposition responses have not been separated in these studies; however, choice studies by Valencia (1984) suggest that the egg-laying response is affected by combined chemical and mechanical cues: Discrimination coefficients for different concentrations of Soxhlet leaf extracts indicated repellant effects at high concentrations and attraction at lower concentrations and the non-volatile chemicals α-solanine, zeatin riboside, α-chaconine and chlorogenic acid were oviposition localizers compared to an ethanol (solvent) control; however, overall, more eggs were laid in containers treated with tomatine and glutamic acid; all volatile chemicals (*trans*-2-hexen-1-ol, 1-hexanol, *cis*-3-hexen-1-ol, *trans*-2-hexenal, linalool) tested in the study had repellant effects. It is likely that whichever cues are involved in stimulating oviposition will also indicate the physiological state (herbivore or disease-stressed) and phenological stage of the host plant allowing females to determine the most suitable hosts for developing larvae. However, prior experience with a host plant [i.e., the host plant type (species or variety) on which the adult developed] may also interact with volatile cues to determine ultimate host acceptance and preferences (Landolt 2001).

The site of egg-laying varies between gelechiid species (**Table 3**) and, at least in *P. operculella*, is influenced by the host plant species (Varela and Barneys 1988). Palacios *et al.* (1998) indicate that the eggs of *S. tangolias* are predominately laid directly on the host plant, generally in an axilla in the mid-foliage region of the plant; however, after hatch, the site of larval entry into the stems is affected by plant phenology. *Phthorimaea operculella* appears to alter its site of oviposition according to chemical and mechanical cues from the host plant: In a study by Varela and Bernays (1988), eggs were laid predominantly on the foliage of potato plants but on the soil near datura, tobacco and tomato (all plants were pre-flowering). In contrast, Traynier (1975) found *P. operculella* eggs in the soil near potato and tobacco plants, but not near tomato. Eggs were mainly at the base of the plants, but small numbers occurred up to 2 m from the test plots. Optimum oviposition substrates for *P. operculella* include rough surfaces (with surface depressions large enough to accommodate the eggs), but hairy surfaces also stimulate oviposition (Traynier 1975; Fenemore 1978). In comparative studies with foliage from a range of potential host plants, leaf hairs have been associated with increased egg-laying by *P. operculella* directly on the leaf surface (Gurr 1995; Horgan *et al.* 2007a), whereas glandular trichomes reduced the proportion of eggs laid directly on the plants (Musmeci *et al.* 1997; Malakar and Tingey 1999, 2000; Gurr and McGrath 2002; Horgan *et al.* 2007a). Similarly, unidentified compounds in hexane leaf extracts of *Lycopersicon hirsulutum* f. *typicum* (LA 1777), and associated glandular trichomes, appear to deter egg-laying by *T. absoluta*, a species which does not lay eggs in the soil (Ecole *et al.* 2001). Glandular trichomes are likely to be an effective defense against those gelechiid species that lay their eggs on foliage (i.e., *S. tangolias* and *T. absoluta*) as well as other lepidopteran pests. For example, in field and greenhouse choice experiments, European corn-borer laid fewer eggs and caused less damage on *S. tuberosum* × *S. berthaultii* hybrids NYL 235-4 and K411-2 that were originally bred for resistance to the CPB compared to the popular varieties Atlantic, Superior, Norland and Kennebec (Hanzlik *et al.* 1997), presumably because of glandular trichomes on the hybrids.

Because *P. operculella* (and possibly *S. tangolias* also) varies its site of egg-laying according to host plant identity, then glandular trichomes and other leaf deterrents may serve only to redirect egg-laying rather than reduce it in these species. To our knowledge, no study has adequately addressed this issue; Nevertheless, glandular trichomes derived from *S. berthaultii* bestow resistance against a wide range of herbivores (Neal *et al.* 1990; Hanzlik *et al.* 1997; Malakar and Tingey 1999) and genetic markers associated with trichome defenses are available that will increase the efficiency of potato breeding programs aimed at increasing herbivore resistance (Yencho *et al.* 1996). However, breeding for resistance based on glandular trichomes has associated caveats: There may be possible trade-offs between foliage and tuber resistance, such that breeding for high foliage resistance compromises resistance levels in tubers (Horgan *et al.* 2009b). Furthermore, glandular trichomes can inadvertently increase the susceptibility of potato plants to tuber moths in the field by decreasing the effectiveness of predators and parasitoids (Baggen and Gurr 1995; Gooderham *et al.* 1998; Mulata *et al.* 2004), e.g., *C. koehleri* makes fewer visits and remains for less time on trichome-bearing foliage, resulting in lower levels of parasitism on *P. operculella* eggs; furthermore adult *C. koehleri* can become entrapped in glandular trichomes (Baggen and Gurr 1995). This creates an enemy free space for tuber moths that has been linked to the shift by *P. operculella* in host plant preferences from low-trichome density potatoes to high-trichome density tomatoes in some regions (Mulatu *et al.* 2002).

Leaf trichomes may reduce damage to potatoes even where eggs are laid in the soil, if the trichomes deter dispersing neonates. The distances that neonates can travel to find suitable penetration sites are unknown. Neonates of *P. operculella* undertake exploratory walks following egg hatch that can continue at least up to two hours (F. Horgan, pers. obs.). Furthermore, neonates travel as much as 30cm per minute over non-host plants (Varela and Bernays 1988). Having located a suitable feeding site, the neonates then burrow into the foliage and, depending on the nature of the leaf surface, may construct a protective silk tent (Horgan *et al.* 2007a). Neonates bite and taste the plant surface prior to host-plant penetration. Varela and Barneys (1988) have shown that dichloromethane and methanol extracts of leaf waxes increase the incidence of biting and that dichloromethane reduces the movement of neonate larvae, indicating a role for volatiles and other secondary chemicals in neonate establishment. Leaf pubescence also affects the behaviour of searching neonates (Malakar and Tingey 1999; Horgan *et al.* 2007a). Glandular type-A and type-B trichomes on *Solanum berthaultii* (Hawkes) and on *Solanum tuberosum* × *S. berthaultii* hybrids have been shown to reduce successful neonate establishment (Musmeci *et al.* 1997); However, in a comparative study using a range of *S. berthaultii* accessions, Horgan *et al.* (2007a) found glandular trichomes to generally stimulate neonate establishment. Differences between the results of these studies may be due to the experimental protocols used: Musmeci *et al.* (1997) allowed neonates to colonize cut foliage in a choice experiment, whereas Horgan *et al.* (2007a) assumed that eggs are laid on the host plants, and placed neonates directly onto the leaf surfaces in non-choice tests. Trichomes, restricting larval movement [as in *S. berthaultii* (Malakar and Tingey 2000)] may have stimulated the neonates to penetrate leaf tissues more quickly when applied directly to the leaf surface. Because *P. operculella* lays eggs in both the soil and directly on the host plant, then, where sites of egg-laying are unknown, both protocols should be conducted. Furthermore, to increase the relevance of future such experiments for *P. operculella* and other moth species, the specific sites of egg-laying should be assessed in parallel with neonate establishment experiments.

A number of studies have indicated decreased fitness of *P. operculella* and *T. absoluta* larvae following establishment on the foliage of resistant host plants compared to susceptible or favoured hosts (Musmeci *et al.* 1997; Malakar and Tingey 1999, 2000; Gurr and McGrath 2002): A variety of fitness parameters are detectably altered because of host-plant resistance factors: On resistant plants survival declines, larval development times increase, and larval and pupal weights and sizes decline (**Table 4**). The mechanisms behind these fitness declines are largely unknown and may include the effects of energy losses because of feeding difficulties associated with gumming of legs and mouthparts [Malakar and Tingey 2000; see also Neal *et al.* 1990 for the case of *Myzus persicae* (Sulzer)], the effects of toxic secondary chemicals, and/or the effects of poor nutritive quality of the foliage. Changes in larval survival as plants age give some clues as to the causes of observed fitness declines. For example, older plants of *L. hirsutum* f. *glabratum* (acc. PI 134417) have higher larval mortality, longer larval periods, smaller mines and more females of *T. absoluta* than on susceptible tomatoes. Leite *et al.* (2001) suggest that this is due to increasing levels of tridecan-2-one as leaves age. Evidence for poor nutritive value of resistant foliage is also suggested from observations of longer pupal

Table 5 Tuber resistance sources with associated fitness responses in *P. operculella* and proposed mechanisms of resistance.

Insect response evaluated	Mechanisms	Reference
New Zealand varieties		
Damage to tubers	Not determined	Fenemore 1980
Range of wild species and cultivated landraces (identities not indicated)		
Damage to tubers	Not determined	Raman and Palacios 1982
New Zealand commercial varieties and true potato seed, some wild species (not listed)		
Number of mines, number of tubers damaged	Not determined	Nabi 1984
Four commercial varieties grown in Kenya		
Larval survival, tunnel form, number of tubers damaged	Not determined	Ojero and Mueke 1985
Wild species, hybrids, and traditional varieties over 5 years in Colombia (identities not listed)		
Larval survival, damage	Not determined	Estrada and Valencia 1988
Twenty one commercial varieties		
Number of mines, number of tubers damaged	Eye number related to vulnerability	Das *et al.* 1993a
Twenty three varieties and genotypes		
Larval and pupal development time, larval survival, number of mines, pupal and adult weights, oviposition, population growth rate	No effect of glycoalkaloids, soluble proteins and dietary fiber on moth population growth, but total protein content was positively- and digestible carbohydrates negatively related to moth population growth.	Das *et al.* 1993b
***S. berthaultii*, *S. commersonii*, *S. pinnatisectum*, *S. sparsipilum* (3 accessions), *S. spegazzini*, *S. sucrense*, *S. tarijense* (2 accessions), *S. tuberosum* × *S. berthaultii* hybrids (2 accessions)**		
Larval development time, larval survival, number of mines, pupal weight	Not determined	Arnoné *et al.* 1998
Four Australian commercial varieties		
Neonate establishment, adult emergence, number of mines	Periderm afforded 50% of the protection; most tunnels were made near tuber eyes	Gurr and Symington 1998
Chromosome-doubled regenerates of various hybrid potatoes derived from wild potato relatives		
Damage scores	Not determined	Watanabe *et al.* 1999
***S. tuberosum* × *S. berthaultii* hybrids, Brazilian commercial potato varieties and tomato**		
Larval and pupal survival and development times, pupal weight	Not determined	Rêgo Lopes and Vendramim 2001
Many commercial varieties and true potato seed		
Number of mines, number of tubers damaged	Exposure of tubers (above the soil) was correlated with damage levels.	Sileshi and Teriessa 2001
***S. tuberosum* × *S. berthaultii* hybrids**		
Eggs laid, larval establishment, larval survival, larval size, larval behaviour	Periderm thickness affected neonate penetration of the tuber and oviposition. The periderm is thinner around the eye resulting in increased vulnerability of the eye to larval entry.	Malakar-Kuenen and Tingey 2006
Various accessions of *S. berthaultii* (23 accessions)		
Establishment of neonates, larval and pupal development times, pupal weights	Tuber resistance is determined by i) a periderm barrier to neonate attack and ii) unfavourable nutritional/habitat conditions in the tuber cortex. As the tuber ages both resistance sources break down.	Horgan *et al.* 2007b, 2009b
Various accessions of *S. multiinteruptum* (8 accessions), *S. sparsipilum* (8 accessions) and *S. wittmackii* (9 accessions)		
Establishment of neonates, larval and pupal development times, pupal weights	Resistance in *S. multiinteruptum* is mainly due to periderm protection, whereas resistance in *S. sparsipilum* and *S. wittmackii* is mainly cortex based.	Horgan *et al.* 2010

development times (suggesting carry-over effects of poor nutrition to the non-feeding pupal stage), whereas observations of lower pupal survival and higher proportions of deformed pupae (i.e., Ecole *et al.* 2001; Leite *et al.* 2001) suggest that some resistant foliage may also contain compounds that are toxic to developing larvae. Similarly, adult *P. operculella* reared on its preferred host (potato) had lower female egg loading values and lower lipid content, and had a resulting lower tendency to fly when compared to *P. operculella* reared on a non-preferred host (tomato) (Coll and Yuval 2004), suggesting that adults will more readily disperse away from poor quality hosts.

Tuber resistance

Damage to tubers by gelechiids is considerably more problematic than damage to above-ground foliage. Among poor rural communities in the Andes, where potatoes are stored in rustic storage facilities, losses can be up to 100% (Dangles *et al.* 2009). Under the relatively stable environments of storage facilities *S. tangolias*, *T. solanivora* and *P. operculella* can rapidly build up numbers (Das *et al.* 1993a, 1993b; Dangles *et al.* 2009). To compound the problem, often two or three of the species occur together (Dangles *et al.* 2009). As such, the principal gelechiid tuber moths are as much stored-product pests as they are field crop pests. Infestations of tubers in the field can also be considerable, especially where soil conditions or crop varieties lead to large numbers of exposed tubers (Sileshi and Teriessa 2001). Furthermore, for *S. tangolias* and *P. operculella,* survival and resulting pupal weights are generally higher on tubers than on foliage (F. Horgan pers. obs.); Rêgo Lopes and Vendramim (2001) also found higher survival of *P. operculella* on tubers than on foliage (but surviving larvae had longer development times and lower pupal weights on tubers) except on *S. tuberosum* × *S. berthaultii* hybrids (NYL 235-4 and N 140-201) where larvae did poorly on tubers. Given that tuber moths are better adapted to living on tubers, and given the large number of published tuber screening studies (Fenemore 1980; Raman and Palacios 1982; Nabi 1984; Ojero and Muerke 1985; Estrada and Valencia 1988; Ortíz *et al.* 1990; Das *et al.* 1993b; Chandla 1995; Arnoné *et al.* 1998; Gurr and Symington 1998; Parihar and Watanabe *et al.* 1999; Rêgo Lopes and Vendramim 2001; Sileshi and Teriessa 2001; Horgan *et al.* 2007b, 2010) it is surprising that so little is known about mechanisms of tuber resistance to the moths (**Table 5**). Furthermore, there is little information on which to base hypotheses about tuber resistance, because, other than recording damage levels or herbivore survival, only a few studies have quantified moth fitness responses to resistant tubers (but see Arnoné *et al*. 1998; Malakar-Kuenen and Tingey 2006; Horgan *et al*. 2007b, 2010).

As with foliage, adult moths likely locate tubers based on complex chemical cues emitted from the host plants. These cues will indicate that the plant is at a suitable phenological stage for tuberization. Hence, *T. solanivora* adults are attracted to cues emitted from flowering plants (see above, Karlsson *et al*. 2009) and field observations indicate that *P. operculella* is attracted to flaccid plants and lays its eggs on dead leaves (Traynier 1975; Shelton and Wyman 1979). Karlsson *et al*. (2009) indicate, based on electroantennogram results, that volatile methyl phenylacetate may attract female *T. solanivora* directly to the tubers.

Once eggs hatch, either on foliage or in the soil (see above), the neonates seek out the developing tubers. In the field, the first line of defense against neonate penetration of tubers is tuber apparency: Increasing burial depths reduces damage by both *P. operculella* (Foot 1975) and *S. tangolias* (Palacios *et al*. 1999) because neonates fail to reach deeper tubers. Tuber dept is largely under genetic control (Sileshi and Teriessa 2001), but is seldom regarded in resistance studies. The spatial distribution of tubers in the soil beneath the plant may also influence herbivore attack (Winkler and Fischer 1999), but this has not been studied for potatoes.

On reaching tubers, either in the field or in storage, the next principal barrier to neonate penetration is the tuber periderm. The periderm consists of numerous layers of cork (Cutter 1992). The outer phellem layers contain wax and subarins that form an effective barrier to water. Periderm thickness and chemical composition vary according to potato species, variety, and the environmental conditions during tuber development (Cutter 1992; Tyner *et al*. 1997). The periderm can contribute from 0 to 100% of total resistance in wild potatoes (Horgan *et al*. 2007b, 2010), but, more typically is only a part of the tuber defense with the remainder related to cortex properties (Horgan *et al*. 2007b). Because the periderm is considerably thinner near the tuber eyes, most neonates enter tubers (both commercial varieties and wild potato species) through the eyes (Gurr and Symington 1998; Malakar-Kuenen and Tingey 2006; Horgan *et al*. 2007b). Tunneling through the periderm can reduce larval development times in *P. operculella* by up to one day on some accessions of *Solanum sparsipilum* (Bitter) Juz. et Buk. and *Solanum wittmackii* Bitter, suggesting that even when larvae successfully establish on tubers, penetration of the periderm may have an associated cost (Horgan *et al.* 2010).

Survival, larval and pupal development times, and pupal weights of *P. operculella* reared on tubers of *S. berthaultii* vary between accessions, which indicates that the cortex plays a significant role in tuber resistance based on its nutritive value for developing moths (Horgan *et al*. 2007b); Secondary chemicals, such as glycoalkaloids, appear to play little or no role in the resistance of commercial varieties (Das *et al*. 1993a) and occur at very low levels in *S. berthaultii* (Y Pelletier, unpublished data). However, tubers of *S. wittmackii* have strong antibiotic defenses, such that the establishment of neonates is often lower in tubers with perforated periderms compared to unperforated tubers (suggesting a repellent effect of the cortex and/or induced responses to perforation). Furthermore, larval mortality and tuber abandonment are high and pupal deformities are relatively common when larvae feed on *S. wittmackii* (Horgan et al. 2010). Chemical toxins in the cortex of *S. wittmackii* are therefore largely responsible for tuber resistance in this species (Horgan *et al*. 2010). It is unlikely that such a plant could be used in breeding programs to develop resistant tubers for human consumption.

Das *et al*. (1993a) found the tubers of some commercial varieties to become more susceptible to damage by *P. operculella* as the tubers aged. Similarly, as tubers of *S. berthaultii*, *S. multiinteruptum* and *S. sparsipilum* sprout, their resistance breaks down (Horgan *et al*. 2007b, 2010). This is partly due to a decrease in the protective value of the periderm; however, higher survival rates, shorter development times and heavier pupae suggest that, as the tubers sprout, their nutritional quality for developing larvae often increases (Horgan *et al*. 2007b, 2010). Developing tubers undergo a range of physiological changes, including the disappearance of protein crystals, decreases in saturated and unsaturated fatty acids, hydrolysis of starch, and increases in soluble carbohydrate levels (Cutter 1992; Coleman 2000). In contrast to the studies by Das *et al*. (1993a) and Horgan *et al*. (2007b, 2010), Malakar-Kuenen and Tingey (2006) found increased larval mortality on older tubers of Atlantic and old *S. tuberosum* × *S. berthaultii* hybrid tubers when compared to newly harvested tubers. Difference between these studies may derive from the nature of aging and whether tubers were sprouting and flaccid or dried-out from cold storage. In *S. wittmackii*, older tubers also have lower resistance; however, on this species, other than increased establishment of neonates, *P. operculella* fitness does not increase with sprout development and larval mortality and abandonment of tubers remains high (Horgan *et al*. 2010). Lower resistance against tuber moths on sprouting tubers suggests that resistance is related to tuber dormancy (Horgan *et al*. 2007b, 2010). For example, the highly resistant species *S. multiinteruptum* and *S. wittmackii* occur at high altitudes in the Andes and have notably long dormancies (over seven months in some accessions). In general, wild potato species with relatively longer dormancies tend to be more resistant to tuber moths based on comparative screening of newly harvested tubers (F Horgan, unpublished data).

POTATO RESISTANCE TO APHIDS

Aphids (Hemiptera: Aphididae) are also considered among the most damaging insect pests on cultivated potato (van Emden *et al*. 1969; Radcliffe 1982). They decrease potato yield by consuming phloem sap and by transmitting viruses such as the persistent Potato Leaf Roll Virus and the non-persistent Potato Virus Y (Radcliffe 1982). *Myzus persicae* (Green Peach Aphid) and *Macrosiphum euphorbiae* (Potato Aphid) (Thomas) are the most damaging species, although other species colonize potato crops (Blackman and Eastop 1994) among which *Aphis nasturtii* (Kaltenbach), *Aulacorthum solani* (Kaltenbach) and *Rhopalosiphoninus latysiphon* (Davidson) cause notable damage (Radcliffe 1982). Numerous other aphid species have been collected from potato field traps, but their ability to colonize potato is uncertain (Boiteau 1988; Difonzo *et al*. 1997; Bostan *et al*. 2006). A life-cycle that includes polyphenism (alternate production of alate and apterous morphs by the same genotype, which occurs during summer when aphids feed on potato crops), alternation of sexual and asexual reproduction (Miyasaki 1987; Dixon 1998), a tight relationship with the plant during the host selection process (Powell *et al*. 2006), and endosymbiosis with gut bacteria (Douglas 2003) are key characteristics that contribute to the status of aphids as global agricultural pests.

Sources of resistance

The levels of resistance to aphids have been assessed for a variety of potato cultivars (Adams 1946; Landis *et al*. 1972; Bintcliffe and Wratten 1982; Davis *et al*. 2007). The most recent and most thorough study has not detected any correlation between resistance levels and the abundance of two major aphid species, *M. persicae* and *M. euphorbiae* (Davis *et al*. 2007). The cultivar 'Russet Norkotah' was the most resistant to *M. persicae* and 'Aracy' the most resistant to *M. euphorbiae*. Despite an impact on aphid population growth sufficient to reduce the need for insecticide applications (Davis *et al*. 2007), resistance in cultivated potato depends more on plant physiology and growth habitat than on heritable traits (Radcliffe 1982). Inconsistencies in the results of field assessments between years corroborate this conclusion

(Davis *et al.* 2007).

More than 50 years ago, researchers emphasized the need to improve potato germplasm by introgressing commercial varieties with wild *Solanum* species as sources of novel resistance (Adams 1946; Landis *et al.* 1972). A number of studies have evaluated resistance levels to *M. persicae* and *M. euphorbiae* of *Solanum* species (Radcliffe and Lauer 1968; Quisumbing *et al.* 1970; Radcliffe and Lauer 1970a, 1970b; Gibson 1971b; Radcliffe and Lauer 1971a, 1971b; Sams *et al.* 1976; Radcliffe *et al.* 1981; Flanders *et al.* 1992; Valkonen *et al.* 1992; Flanders *et al.* 1997, 1999). Resistance levels generally differ according to aphid species (Gibson 1971b; Radcliffe *et al.* 1981); However, studies have identified a range of potential sources of aphid resistance for potato including *S. chomatophilum* (Radcliffe and Lauer 1970a; Flanders *et al.* 1992, 1997; Le Roux *et al.* 2007; Pompon et al. 2010b), *S. trifidum* (Radcliffe *et al.* 1981; Flanders *et al.* 1992, 1997; Pelletier *et al.* 2010), *S. stoloniferum* (Radcliffe and Lauer 1970a, 1970b; Gibson 1971b; Radcliffe and Lauer 1971b; Radcliffe *et al.* 1981; Flanders *et al.* 1992; Le Roux *et al.* 2007), and *S. hjertingii* (Radcliffe and Lauer 1970a; Radcliffe *et al.* 1981; Flanders *et al.* 1992). *Solanum etuberosum* was found to be resistant to both aphids and viruses (Valkonen *et al.* 1992; Flanders *et al.* 1997; Novy *et al.* 2002). *Solanum berthaultii*, *S. polyadenium* and *S. neocardenasii* all bear glandular trichomes that have been associated with resistance against other potato herbivores as well (see above; Lapointe and Tingey 1986; Malakar and Tingey 2000; Novy *et al.* 2002; Alvarez *et al.* 2006). To our knowledge, the only commercial variety bred for aphid resistance, ‘King Harry’ (De Jong, W., pers. comm.), has been commercially available since 2004, and has trichome-mediated resistance inherited from *S. berthaultii*.

Mechanisms of resistance

The mechanisms of resistance based on insect responses can be classified as either antixenosis or antibiosis (Panda and Khush 1995). Antixenosis is based on plant factors that interfere with the behaviour of the insects such as the host selection process. Antibiosis mechanisms are caused by plant factors impairing insect physiology. Both types of mechanism are not mutually exclusive and can sometimes be triggered by the same compounds at different concentrations (Niemeyer *et al.* 1993).

Host-plant selection by aphids has been defined as a sequence of six behavioural stages guided by chemical and physical plant characteristics: i) pre-alighting behaviour; ii) initial plant contact and assessment of surface cues before probing; iii) probing the epidermis; iv) stylet pathway activity in the mesophyll; v) salivation; and finally vi) phloem acceptance and sustained ingestion (Powell *et al.* 2006). At each stage, the aphid can reject the plant or resume one of the previous behavioural stages. The pre-alighting stage appears to have little effect on host-plant selection, as aphids have little control over the direction of their flight (Dixon 1998). Before inserting the stylet (probing), aphids evaluate the suitability of the plant surface by antennating while walking on the leaf to detect odour and gustatory cues (Powell *et al.* 1995). Colour also stimulates probing behaviour (Pelletier 1990). Delay in stylet insertion suggests the presence of repellent plant factors in the superficial layers, as for *M. persicae* on *S. polyadenium*, *S. berthaultii*, *S. tarijense*, *S. spegazzinii*, *S. circaeifolium* subsp. *capsicibaccatum*, and *S. stoloniferum* (Alvarez *et al.* 2006; Pompon *et al.* 2010a). Trichomes are responsible for the resistance in *S. polyadenium*, *S. berthaultii*, and *S. tarijense*, whereas stylet derailments are also observed on *S. stoloniferum* and suggest the presence of plant factors impairing stylet penetration. Aphids insert their stylet into intercellular spaces in epidermal and mesophyll tissues, and puncture some cells to gain gustatory information along the pathway towards phloem bundles (Powell *et al.* 2006). Cell puncture frequency can be influenced by symplastic plant characteristics (Chen *et al.* 1997). A longer “pathway phase”, as for *M. persicae* on *S. chomatophilum* (Le Roux *et al.* 2008; Pompon *et al.* 2010a), is thought to be caused by resistance factors detected in the mesophyll. An increase in the number of short probes (< 3 min) is interpreted as unfavourable epidermis tissue because aphids cannot reach deeper tissue during that time (Powell *et al.* 2006). Salivation is the first behaviour performed after reaching phloem bundles and always occurs before phloem ingestion. Ejection of saliva prevents sieve element sealing (Tjallingii 2006), which is part of the plant wound response, by inhibiting the coagulation of bound p-proteins (forisome) (Tjallingii 2006). Although the mechanism is calcium-mediated, the release of saliva is triggered by a drop in phloem sap hydrostatic pressure (Tjallingii 2006). Failure to overcome the plant wound response may result in an extended salivation period and a shorter phloem sap ingestion duration (Tjallingii 2006), as observed for *M. persicae* on *S. stoloniferum* (Le Roux *et al.* 2008), and for *M. euphorbiae* on *S. oplocense*, *S. stoloniferum* (Pompon *et al.* 2010a) and *S. trifidum* (Le Roux *et al.* 2008). Salivation also increases when aphids face nutritionally unbalanced (Ponder *et al.* 2000) or toxic phloem sap (Ramirez and Niemeyer 1999), which is suggested to underlie *S. pinnatisectum* resistance to *M. euphorbiae* (Pompon *et al.* 2010a). Aphids eventually reach phloem sieve elements, where a sustained phloem sap consumption period (> 10 min) can be interpreted as plant acceptance (Tjallingii 1994). Nutritionally unbalanced or toxic phloem sap may also be responsible for difficulties in maintaining phloem sap ingestion, as suggested for *M. persicae* on *S. multiinterruptum* (Alvarez *et al.* 2006), and for *M. euphorbiae* on *S. polyadenium* and *S. tarijense* (Pompon *et al.* 2010a).

Aphids also consume xylem sap in order to regulate the gut content osmotic pressure (Pompon *et al.* 2010c; Pompon 2010). Although xylem sap consumption of *M. euphorbiae* increases on resistant accessions from *S. chomatophilum*, *S. oplocense*, and *S. pinnatisectum* (Le Roux *et al.* 2008; Pompon *et al.* 2010b), its role in host-plant selection is still under investigation.

Electric penetration graphs (EPG) have been used extensively in research on aphid-plant interactions and permit detailed monitoring of aphid host-plant selection behaviour (Tjallingii 1995). However, experimental stresses inherent to EPG manipulation, such as the application of a drop of conductive glue on the dorsum (Pelletier and Giguère 2009), can modify aphid behaviour (Prado and Tjallingii 1999). Ethological observations should complement EPG analyses to prevent misinterpretation of the resistance mechanisms (Prado and Tjallingii 1999; Pelletier and Giguère 2009). Behavioural datasets, such as EPG or ethological observation data, suffers from multicollinearity, which can be handled using multivariate analysis (Quinn and Keough 2002). Multivariate analyses select a subset of relevant variables (Caillaud *et al.* 1995; Sokal and Rohlf 1995), and treats multiple variables simultaneously, both of which reduce type I errors (excessive rejection of the null hypothesis) associated with numerous sequential univariate tests (Quinn and Keough 2002). Multivariate statistics have been successfully used in assessing resistance mechanisms (Caillaud *et al.* 1995; Pompon *et al.* 2010a).

Antibiosis mechanisms are usually indirectly inferred when there is no change in herbivore behaviour between the resistant plant and a susceptible standard (Alvarez *et al.* 2006; Le Roux *et al.* 2008). *Solanum cardiophyllum* and *S. circaeifolium* subsp. *capsicibaccatum* resistance to *M. persicae*, and *S. chomatophilum* resistance to *M. euphorbiae* have been attributed to antibiosis mechanisms (Alvarez *et al.* 2006; Le Roux *et al.* 2008; Pompon *et al.* 2010a). However, these types of indirect observations alone do not provide sufficient evidence for antibiosis since long term behavioural response and induced resistance may be overlooked during the period during which the behaviour is assessed.

Chemical or physical plant characteristics are ultimately responsible for insect resistance (Flanders *et al.* 1992). Glycolalkaloids are known to impact insect performance

(Flanders *et al.* 1992), but total foliar quantity were not correlated with *M. persicae* infestations in potato cultivars, in *S. tuberosum* × wild *Solanum* hybrids, nor in wild *Solanum* species (Mndolwa *et al.* 1984) including *S. berthaultii* (Tingey and Sinden 1982). However, this does not exclude the role of specific alkaloids. No chemical or physical characteristics other that trichomes have been directly attributed to aphid resistance in tuber-bearing *Solanum* species.

Trichome-based resistance occurs in *S. berthaultii* (including *S. tarijense*), *S. polyadenium*, (Gibson 1971a, 1976), *S. neocardenasii* (Lapointe and Tingey 1986), and *S. flavoviridens* (Ochoa 1980). Observed levels of aphid resistance have been positively correlated with trichome densities (Tingey and Laubengayer 1981); however, resistance is significantly improved where two types of glandular trichome, type-A and type-B, are present (Tingey and Sinden 1982) (see above for the description of trichome types). Trichome-mediated resistance to aphids involves several steps (Gregory *et al.* 1986): The insect lands upon the foliage and encounters the type-B trichome exudate, which forms an adhesive coating on the tarsi, and also elicits an antifeedant behaviour through its sesquiterpene content; The insect struggles during attempts to escape and breaks the type-A trichome heads; α- and/or β-polyphenol oxidases are released from the broken head of type-A trichomes and react with a phenolic substrate (chlorogenic acid) to initiate an enzymatic oxidative process leading to the formation of quinones. Eventually, the insect becomes immobilized, ceases feeding, and dies. E-β-farnesene, an aphid alarm pheromone, was proposed to worsen the behaviour disturbance (Gibson and Pickett 1983), but its major effect was later contested since high concentrations of E-β-farnesene were also found in susceptible *S. tuberosum* (Avé *et al.* 1987). However, the concentration and presence of particular compounds vary between species (Avé and Tingey 1986), accessions, and cultural conditions (Avé *et al.* 1987). Despite protecting against aphid damage and virus transmission, due to delayed aphid probing (Lapointe and Tingey 1984), trichome-based resistance has disadvantages. Trichomes are not present on buds and flowers, enabling aphids to colonize these plant parts (Ashouri *et al.* 2001). Under field conditions, depletion of type-A trichomes through ware, especially on the mature leaves that are preferred by *M. persicae* (Tingey *et al.* 1982), and dust on the exudates (Tingey and Sinden 1982) reduce the resistance level. Furthermore, the production of trichome B exudate is strongly associated with unfavorable agronomic traits in *S. berthaultii* × *S. tuberosum* hybrids (Kalazich and Plaisted 1991).

Evaluation of resistance

Understanding the plant factors that influence resistance levels is helpful to guide the selection of resistant parents and develop effective screening protocols. Resistance levels vary among accessions of the same species (Radcliffe *et al.* 1981; Flanders *et al.* 1992). Flanders *et al.* (1997) have related aphid resistance to the geographical origin of wild *Solanum* accessions. High resistance to *M. persicae* was more prevalent than expected in accessions from Mexico-southern United States, Peru, and a region extending from southern Bolivia to northern Argentina. High resistance to *M. euphorbiae* was more prevalent in accessions from Mexico, and west and east-central Peru. Because individuals within accessions are obtained by sexual reproduction then each individual plant is unique, which might explain why resistance levels can vary among plants from the same accession [Sams *et al.* 1976; Pompon *et al.* unpublished data; but see Bamberg *et al.* (2000)]. Resistance levels can also vary between different plant parts (Gibson 1971b; Valkonen *et al.* 1992; Ashouri *et al.* 2001; Le Roux *et al.* 2008; Pompon *et al.* 2010b). However, irrespective of intra-plant variation of resistance levels, *M. persicae* generally prefers senescing leaves (van Emden *et al.* 1969), whereas *M. euphorbiae* prefers flower buds and flowers (Gibson 1971b).

Aspects of aphid biology that promote variation in resistance levels need to be better understood. The occurrence of biotypes is promoted by the long asexual period of the aphid life cycle (van Emden *et al.* 1969; Dixon 1998). Each fundatrix hatching in the spring from the overwintered egg represents a different biotype, potentially having different fitness levels. The resistance levels of a given plant can vary depending on the aphid biotype studied (Gibson and Plumb 1977), e.g. different biotypes of *M. euphorbiae* perform differently on tomato plants carrying the *Mi* gene (Goggin *et al.* 2001). Nevertheless, the resistance of wild *Solanum* species to *M. persicae* was found to be stable in space and time (Radcliffe *et al.* 1974; Radcliffe *et al.* 1988). Endosymbiotic bacteria housed by aphids in specialized cells can influence host-plant range (Douglas 2003; Simon *et al.* 2003) and, as bacteria evolve faster than insects, genetic or epigenetic changes in the endosymbionts might accelerate aphid adaptation to resistant varieties.

CONCLUSIONS AND FUTURE PROSPECTS

The potential of wild potato species as sources of novel resistance to major potato insect pests has been demonstrated through a large number of screening studies conducted over the past 50 years. Furthermore, the successful introgression of wild species with cultivated potato has been achieved and produced some commercially available varieties with improved resistance against the CPB, tuber moths, and aphids. Methods to achieve introgression and secure the transfer of genes and QTLs of interest have improved and will certainly accelerate the pace of cultivar development from wild and cultivated parents. Nevertheless, the availability of introgressed materials is still quite low and very few wild species have been used as resistance sources. Most of the available cultivated hybrids have been developed through introgression with *S. berthaultii* which bears glandular trichomes and for which the mode of action in resistance against the CPB, tuber moths, and aphids is relatively well understood.

Resistance from other wild potato species has been slower in coming. This may partly be due to difficulties in quantifying those elements (either secondary chemicals, volatiles or anatomical barriers to the insects) that determine resistance. Furthermore, direct links between resistance factors and QTLs or major resistance genes have been difficult to establish because of variable responses by target insects to the host materials and variable distributions and levels of the resistance factors in the host plants. Resistance can sometimes change with plant age (as discussed above with trichome defenses to aphids and tuber resistance to moths) and are often heavily influenced by environmental conditions. The identification of the compounds produced by the plant that bestow resistance needs to be improved. The task is likely to become easier with the development of new and advanced metabolomic tools. Along with the development of the genomic tools and the sequencing of the potato genome, breeding for insect resistance is likely to require less time and an increased number of wild parents can be used in breeding programs.

Screening studies have been useful in identifying promising species and accessions for attention in resistance breeding programs. However screening results are seldom published and in some cases, even when published, the identity of the source materials is omitted. Furthermore screening studies are notoriously variable, partly because of the lack of rigour among researchers in standardizing screening methodologies. Tests will often vary screening procedures, plant age, insect age, temperatures and/or the layout of the screening unit. Fine screening with parallel insect-behavioural observations can greatly improve the reliability of results. Although field studies provide real-condition estimation of the resistance level, laboratory assessment of the resistance mechanisms is required to obtain further information on the nature of the resistance. Correlation and associative type experiments can further improve our understanding of resistance mechanisms and improve reliability. Studies that record numerous plant anatomical and chemical parameters and/or insect behavioural and fitness responses end with complex data sets that can be managed and reduced using multivariate statistical techniques. Advances in statistical software and multivariate procedures have therefore become a useful tool in improving knowledge for breeding purposes. Furthermore, multivariate analyses permit researchers to take more holistic views of the interactions between the plants and insects of interest. Most of the studies that have been conducted to date on potato resistance to insects have followed reductionist experimental approaches and few have conducted manipulative experiments. Manipulative experiments, where factors are experimentally manipulated in order to confirm or reject a specific test result (i.e., removal of trichomes, piercing of periderm) are required to determine the processes behind resistance, since correlation and association-type studies will always be subject to the problems of confusing cause and effect, even when multivariate statistics are applied. But, manipulative studies still tend to be reductionist by nature. The popularity of the EPG system has created an abundance of studies on aphid host-plant selection behaviours on resistant plants in many other aphid-plant systems. Since this technique can only address short-term selection behaviour differences between resistant and susceptible plants, it creates a bias towards antixenosis mechanisms. The reduction of research focus on plant-insect interactions to restricted events has been particularly problematic in research on tuber moths: surprisingly, the site of egg laying and the oviposition response of female moths to trichome-bearing plants is still poorly understood. It is unknown whether trichomes deter or simply redirect egg laying (to the soil).

In insects such as tuber moths, that attack both foliage and tubers, the complete life-cycles of the insects and the plants should be considered as trade-off in resistance can occur, or resistance sources can produce unpalatable or poisonous tubers, sometime only under certain environmental conditions. Holistic approaches to the deployment of resistant varieties once these are developed should also be considered. Trichome-bearing potatoes have been associated with increased mortality of natural enemies in the field and can produce preference shifts by pest insects in response to enemy-free space. This could affect the success of resistant varieties as part of integrated pest management strategies. Similar effects on other wild-introgressed potato varieties with distinct resistance mechanisms are perhaps unlikely; nevertheless, potential negative effects should be considered as in the case of all insect management technologies.

The prospects of using wild species in future potato breeding programs are good, especially with the development of new molecular and statistical techniques. We caution that experimental and screening procedures should take more holistic views of the plant-insect system to further improve the success of resistance development and the impact of varietal deployment. The range of wild species and novel resistance mechanisms that is available to breeding programs is large given the improved techniques for attaining introgression. Nevertheless, until now, progress has been limited mainly to introgression of a few trichome-bearing species and particularly *S. berthaultii*. Many other wild potato species hold promise as novel sources of resistance, especially against foliage herbivores.

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