

Insect Pests of Potato

Global Perspectives on
Biology and Management

Edited by

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Biological Control of Potato Insect Pests

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INTRODUCTION

Predators and parasitoids which actively seek out the pest have an enormous potential to suppress potato insect pests in the context of a truly integrated pest management approach, locally adapted to include essential cultural controls, pest thresholds, and a variety of compatible intervention tactics such as biopesticides, pheromone-based technologies, trap cropping, and selective insecticides. Here we discuss arthropod predators and parasitoids of major potato pests, with an emphasis on those pests more or less specific to the potato crop. This excludes specific discussion of such important groups as leafhoppers, scarab grubs, and wireworms, which are, nevertheless, the key pests in many potato fields. Microbial control agents, including viruses, bacteria, fungi, and entomopathogenic nematodes, are described in Chapter 16, as are natural products such as botanical and semiochemical preparations.

NATURAL ENEMIES OF MAJOR POTATO PESTS

Colorado Potato Beetle (Coleoptera: Chrysomelidae)

The Colorado potato beetle (CPB; *Leptinotarsa decemlineata* (Say)) now ranges throughout most of the North Temperate Zone, with the exception of the British Isles, most of China, and South and Southeast Asia. Since it is native to northern Mexico and the southwestern USA, almost all of its current range represents an expansion, and all of its cultivated hosts – principally potato, eggplant, and tomato – are also novel (Weber 2003). In addition to studies of natural enemies in North America and Eurasia, a number of classical and one neoclassical biological control introductions have been attempted against CPB.

Since the first review of natural enemies of Colorado potato beetle by Walsh and Riley (1868), only one major species of native predator in North America

has been added to that early list. This section reviews primarily the research published since Ferro's (1994) review of the arthropod and microbial natural enemies. Soon after that date, the introduction of imidacloprid, which is a highly effective systemic neonicotinoid for control of CPB, decreased interest in its biological control in North America and elsewhere. This occurred despite pesticide resistance remaining an ever-present risk with this insect (see Chapter 2), and the repeated lesson that resistance risk is mitigated by a suite of alternative tactics such as crop rotation and other cultural practices, as well as microbial and biological controls (Alyokhin 2009). CPB resistance to neonicotinoids has since appeared in several growing areas; however, growers now have a number of other novel insecticide classes with which to suppress CPB (see Chapter 13).

The recent growth of organic potato culture has increased interest in non-chemical controls as part of sustainable CPB management. For instance, in the USA, certified organic potato plantings almost tripled to just over 1% of total potato acreage between 1997 and 2007, while the overall acreage decreased by 13% (ERS 2012). Furthermore, only a portion of those acres grown using organic techniques are certified organic. This trend, as well as the expansion of CPB to the east in Asia, where it is threatening to impact the crops of the two leading potato-growing nations, China and India, has also heightened interest in possibilities for classical biological control with the three species of CPB parasitoids commonly attacking the pest in North America.

CPB populations in North America are commonly preyed upon by several species of native and exotic lady beetles, a specialized carabid which is also a pupal parasitoid, a few species of asopine stink bugs, two species of tachinid parasitoids, and a variety of generalist arthropod predators, including predatory bugs of the genera *Orius*, *Geocoris*, and *Nabis*, Carabidae, Cantharidae, and Opiliones (Heimpel and Hough-Goldstein 1992, Ferro 1994, Hilbeck and Kennedy 1996).

Egg Parasitoids

Egg parasitoids are rare in North America. However, the eulophid *Edovum puttleri* Grissell (1981) was introduced each growing season to eggplant and also potato, from New Jersey Department of Agriculture insectary rearings, during the period 1981 to 1997 (Schroder and Athanas 1989, Tipping 1999). The population, derived from field collections in Colombia (Medellin and Palmira [Valle], between 1000 and 1500m elevation), where it parasitizes a related species *L. undecimlineata* (Stål) (Grissell 1981), is not winter-hardy in North America (Schroder and Athanas 1989) or in Europe (Pucci and Dominici 1988). It is also ineffective in cooler weather in which potatoes are grown (Cloutier *et al.* 2002).

Van Driesche and Ferro (letter to B. Puttler, 1987), Acosta and O'Neil (1999), and O'Neil *et al.* (2005) made several explorations for CPB natural enemies, including cold-hardy *E. puttleri* in cooler habitats in Central America and Colombia. Also, Cappaert *et al.* (1991) reported *E. puttleri* on native CPB

populations in the Mexican state of Morelos. These efforts did not discover strains better adapted to North American conditions. However, the higher elevations of Colombia are still not thoroughly explored.

E. puttleri is no longer available from any source in North America or Europe. Hamilton and Lashomb (1996) demonstrated that a program of biointensive pest management for New Jersey eggplant was economically viable, as it was apparently for the crop in Italy (Colazza and Bin 1992). Unfortunately, the lower value per acre of potato, as well as the parasitoid's poorer performance on this crop (Colazza and Bin 1992), led to its abandonment for commercial potatoes well before its demise in eggplant. In the warmer latitudes where it might better prosper in the potato crop, CPB is not much of a pest and/or potato is grown in the cooler portion of the year. For *E. puttleri* (at least the Colombian strain) there is a crop-parasitoid mismatch: the potato crop is grown under cooler conditions compared to eggplant, and the parasitoid may also, for other reasons, prefer eggplant to potato (Vasquez *et al.* 1997). The wild host from which it was collected, *Solanum torvum* Swartz, is very closely related to eggplant, as reflected in their interfertility, architecture, and foliar texture (Daunay 2008).

Parasitoids: Myiopharus spp.

Myiopharus aberrans and *M. doryphorae* are common tachinid parasitoids of CPB in North America. They both appear to be specialists on CPB. *M. doryphorae* was also recorded from sunflower leaf beetle, *Zygogramma exclamationis* (Fitch), in Canada, even though *M. macellus* (Reinhard) is much more common on this host beetle (Charlet 2003). López and Ferro (1990) and López *et al.* (1992) discovered that both of these species overwinter within the adult host, and emerge the subsequent spring. Both species larviposit into the CPB larvae, and many of the larvae laid by *M. doryphorae* from the second week of August onwards remain within the host, probably as a first instar. They develop within the overwintering adult and emerge in the spring (López *et al.* 1997a). Second and third CPB instars are the preferred hosts.

CPB larvae have a broad repertoire of defensive behaviors against the two tachinids (López *et al.* 1997b), suggesting co-evolution of CPB with this natural enemy. Ramirez *et al.* (2010) also found some similar, and some different, defensive responses to generalist predators in Washington state larval populations. Both tachinid species guard the parasitized host following successful larviposition during certain times, usually in late summer, when the preferred hosts are in short supply. This is the same period during which superparasitism may occur, even though, for most of the year, larvipositing flies do not parasitize previously parasitized hosts (López *et al.* 1995).

Unlike *M. doryphorae*, *M. aberrans* females shift in late season to larvipositing directly into adult CPB by rapidly gaining access to their vulnerable abdominal dorsum when the host raises its wings to fly. This larviposition behavior appears again in *M. aberrans* on early-season post-diapause CPB (López *et al.*

1997b). With this early- and late-season parasitization of adult CPB, the two *Myiopharus* apparently have a significant differentiation of niche relative to the common beetle host. The late emergence of *M. doryphorae* does not allow a build-up of its numbers early in the season to suppress CPB numbers enough to prevent crop damage even though, later on, parasitism may reach 50–80% (e.g., Tamaki *et al.* 1983). Horton and Capinera (1987) found high rates of parasitism by *M. doryphorae* in Colorado in early season both on potato and on the weed *Solanum sarrachoides* Sendtner. Interestingly, this was an area in which CPB, though present on potato, was not an economic pest (Horton and Capinera 1987).

Carabid Predator–Parasitoid, Lebia grandis Hentz

CPB was not the original host of *Lebia grandis*; instead, it was the so-called false potato beetle, *L. juncta* Germar. This *Leptinotarsa* species is native to the southeastern USA. Only after the CPB invaded its range was *L. grandis* discovered as a predator on the CPB (Weber *et al.* 2006). The carabid's larval life cycle was not known until a classical biological control program exported the carabid to France, by boat, in the 1930s. Chaboussou (1939) discovered that first-instar *L. grandis* larvae sought out CPB prepupae or pupae soon after they dug into the soil, and he reared them successfully for introduction into France. This effort ultimately failed, probably due to climatic mismatch, with the target area having too dry summers. *L. grandis* is not present north of southern Maine in eastern USA (Alyokhin, pers. comm.), and is less able to complete larval development at low temperatures (<20°C) than is its host (Weber, unpubl. data). Groden (1989) and Weber *et al.* (2006) considered this species to be the most promising CPB natural enemy, because of its faithfulness to the host and voracity of feeding. In cage studies, Szendrei and Weber (2009) showed the per capita suppression by *L. grandis* to be far superior to that of *C. maculata*. Field studies using molecular gut analysis to assess predation also showed that *Lebia* had the highest predation rate, along with the pentatomid *P. maculiventris* (Szendrei *et al.* 2010). Although *L. grandis* is difficult to rear in the lab, it is worthy of conservation biocontrol in the field, especially by use of selective insecticides, and of further study to determine its limiting factors and possibilities for in-field augmentation.

Candidates for Classical Biological Control

Because of their host specificity and the lack of native *Leptinotarsa* and related genera in Eurasia, *Lebia grandis* and *Myiopharus* spp. are candidates for classical biocontrol in warm humid areas of the Palearctic. Introduction of *Myiopharus* (apparently *M. doryphorae*) was attempted but failed in France, along with shipments of *Lebia grandis* (Trouvelot 1931). Another attempt with 11 shipments from Canada in 1958–1963 to the far-western USSR (Zakarpatsia region of Ukraine) also failed, probably due to lack of knowledge of overwintering habits

(Sikura and Smetnik 1967). Current improved knowledge of all three species bodes well for future introductions. However, classical weed biocontrol programs in Eurasia may possibly give rise to non-target concerns. *Leptinotarsa* species are being considered to target exotic weedy *Solanum eleagnifolium* Cavanilles in the Mediterranean (Hoffmann *et al.* 1998, Sforza and Jones 2007). Furthermore, *Zygogramma suturalis* (F.) is already established to suppress exotic ragweed *Ambrosia* (Reznik 1991), with other *Zygogramma* under discussion (Gerber *et al.* 2011). Given that all species involved (weeds, their introduced herbivores, CPB, and its natural enemies) are exotic to Eurasia, potential conflicts require a balancing of the various pest and damage concerns amongst the exotic species.

Predatory Stink Bugs: *Perillus* and *Podisus*

Many studies have tested augmentation of the North American native asopine pentatomids *Perillus bioculatus* and/or *Podisus maculiventris* in the USA, Canada, and southern Europe (reviewed in Hough-Goldstein 1998). Both species have been introduced to Europe (Jermy 1980, Stamopoulos and Chloridis 1994, Manole *et al.* 2002). Colazza *et al.* (1996) found *P. maculiventris* was superior to the South American *Perillus connexivus* Bergroth in field tests with potato in central Italy. *P. maculiventris* is a generalist predator, whereas *P. bioculatus* is thought to be more of a specialist on CPB, although it is capable of attacking a wider prey range (Saint-Cyr and Cloutier 1996). Nymphs of *P. bioculatus* benefit from group feeding, and a number of factors influence the success of nymphs and their dispersal in the field (Hough-Goldstein *et al.* 1996, LaChance and Cloutier 1997). Adults and nymphs of both species are attracted to their respective aggregation pheromones (Aldrich 1999), and are also sensitive to plant volatiles (Sant'ana and Dickens 1998, Weissbecker *et al.* 1999).

P. bioculatus releases are clearly capable of drastically reducing CPB egg numbers in the field (Cloutier and Baudin 1995, Hough-Goldstein 1998). However, mass-rearing them for augmentative release in potatoes is difficult to justify economically (Tipping *et al.* 1999), even with refinements in diet for rearing (Rojas *et al.* 2000). An alternative source for *Podisus* is early-season field-trapped insects. For small plantings, they can be attracted with pheromone and set up in a “field nursery”, probably situated in an early-planted trap crop. This allows reproduction of the enclosed adults and subsequent dispersal of nymphs out of the coarse-screened field enclosures and into the surrounding crop (Aldrich and Cantelo 1999). Such an approach relies on a background of conservation biocontrol to support the endemic predatory bug population (Perdikis *et al.* 2011); namely, having a diversified ecosystem with alternate prey for this generalist predator to thrive in the rest of the season, and to generate sufficient numbers for capture and emplacement in the potatoes in the early spring. A commercial system to attract *P. maculiventris* (Predator Rescue) was marketed by the Sterling Company in Spokane, Washington, USA, but is now not marketed for retail.

Coleomegilla maculata (DeGeer) and other Coccinellidae

Throughout its range, the CPB is preyed upon by a variety of coccinellid species (see, for example, Snyder and Clevenger 2004, Szendrei *et al.* 2010). Of those, the most studied is *Coleomegilla maculata*, a North American omnivorous species capable of developing on a variety of pure and mixed diets (Weber and Lundgren 2009). In North America it is most abundant in late summer in corn (maize) fields, feeding on corn pollen, Lepidoptera larvae, and aphids (Nault and Kennedy 2000, Lundgren *et al.* 2004). Adults overwinter adjacent to cornfields and other late-season habitats. Both larvae and adults consume CPB eggs and early-instar larvae, and their phenology may be well-synchronized with reproduction of overwintered CPB populations colonizing potato crops. During this period, their predation was found to be an important source of mortality for CPB eggs in North Carolina (Hilbeck *et al.* 1997) and in Massachusetts (Hazzard *et al.* 1991). Potato fields following corn in crop rotation were heavily colonized in Massachusetts (Hazzard *et al.* 1991). However, in North Carolina overwintered coccinellids dispersing in spring often moved to small grain fields before potatoes had emerged, and thus were less abundant in potatoes (Nault and Kennedy 2000).

In mulched and tilled potato field plots in Maryland, Szendrei and Weber (2009) found that *C. maculata* preferred rye-straw mulched plots in spite of the higher density of CPB in the tilled plots, and that in field cages *Lebia grandis* adults were far more effective per capita than *C. maculata* adults at reducing CPB numbers *ab ovo*. PCR-based gut content analysis showed that, in the field, of the four major predators, *C. maculata* adults were least likely to consume CPB, even when adjustments were made for its more rapid digestion of CPB marker DNA (Szendrei *et al.* 2010). However, *C. maculata* may in many situations be several times more abundant than either *L. grandis* or pentatomid predators (e.g., Hilbeck and Kennedy 1996, Szendrei and Weber 2009). Depending on their numbers, as well as on prevalence of eggs and small instar CPBs, and alternate prey, *C. maculata* may or may not be an important predator for pest suppression. This is consistent with Ferro's (1994) mixed conclusion regarding the importance of this species for CPB biological control.

Because of their abundance, fecundity, and ease of rearing, several authors have considered augmentative or inundative releases of *C. maculata*. Giroux *et al.* (1995) concluded that third-instar larvae would be the optimal stage for inundative releases because of their ability to prey on CPB eggs and early-stage larvae, and their inability to disperse from target fields by flight.

Cultural Effects: Mulching and Native Vegetation

Mulching with grain straw suppresses Colorado potato beetle populations; however, it is unclear whether this is due to a positive benefit for natural enemies (as Brust 1994 concluded), a behavioral effect on the pest insect, and/or other factors (see Chapter 10 and references therein).

Interaction of CPB Natural Enemies

Interaction of CPB natural enemies has been investigated both for practical and for theoretical reasons (Moldenke and Berry 1999). Lynch and colleagues (see Chapter 9) discuss the interactions of these and other potato pests and natural enemies. In potatoes, using green peach aphid and CPB respectively as focal pests, Straub and Snyder (2006) and Szendrei and Weber (2009) both emphasized that the identity of the natural enemies is more important than simply their diversity or evenness. Identifying key predators requires an objective assessment not just of their presence but also of their predation (both day and night) on the focal pest (Weber *et al.* 2008). Molecular-based assessment of predation of CPB in Maryland potatoes (Greenstone *et al.* 2007, 2010, Szendrei *et al.* 2010) has indicated that, among the four most abundant predators sampled, *P. maculiventris* adults and *L. grandis* were highest ranked in terms of per capita predation, and that *C. maculata* larvae and adults, and other stinkbug lifestages, including *P. bioculatus* nymphs and adults, were less effective predators of CPB. This information can guide future choices about what species should be targeted for conservation or augmentation in the potato system.

Potato Tuberworms (Lepidoptera: Gelechiidae)

Three species of Lepidoptera (Gelechiidae) are known as potato tuberworms because the larvae bore into potato tubers in the field and in potato stores. The potato tuberworm (PTW, *Phthorimaea operculella* (Zeller)) is by far the most widespread. The PTW originated in the Andes, but is now present in all potato-growing regions with the exception of colder north temperate areas; in many regions this is the insect responsible for the largest potato losses (Rondon 2010). *Tecnia solanivora* (Povolný) (Guatemalan potato tuberworm, GPTW) has in the past 20 years spread from central America into Venezuela, Colombia, and Ecuador, and more recently to southern Mexico (Cruz Roblero *et al.* 2011) and the Canary Islands, thus threatening invasion of Africa and Eurasia (Povolný and Hula 2004). The Andean potato tuberworm (*Symmetrischema tangolias* (Gyen)) originated in Peru and Bolivia, but is now also found in Ecuador and Colombia, typically at above 2800–3000m elevation (Palacios *et al.* 1999, Dangles *et al.* 2008). This species has also spread to Australia including Tasmania, New Zealand, and reportedly Indonesia (see Fig. 6.1). It is important to realize that while some authors lump these species together as “potato tuberworm complex”, they differ in many aspects of biology and damage (Dangles *et al.* 2008). Thus, appropriate pest management approaches, including specialist natural enemies, may be species-specific. The vast majority of ecological and management experience has been with *P. operculella*, including that with native and introduced biological controls.

Potato Tuberworm, Phthorimaea operculella

The PTW is by preference a leafminer; the ovipositing female prefers foliage over tubers, attacking eggplant (aubergine, brinjal), tomato, tobacco, and a

number of other non-tuberous solanaceous crops, weeds, and wild plants (Rondon 2010). It may also bore in above-ground stems. Foliar damage to potatoes is usually not economically important (Rondon 2010). However, as foliar quality declines due to natural or chemically-induced senescence near the end of the potato-growing cycle, tubers come under attack by larvae moving down from the canopy, and by females ovipositing directly on exposed tubers or through cracks in the soil (Kroschel 2006). During the pre-harvest period, when tubers are still in the ground, degree and duration of tuber exposure is a critical factor in PTW infestation of the harvested crop (Alvarez *et al.* 2005). This in turn depends on soil type, moisture, tillage (particularly hilling), cultivar-dependent tuber depth, and, of course, population of PTW. If tubers are left above ground in the process of harvest, additional infestation is invited (Von Arx *et al.* 1990, and other studies).

Growers with access to controlled temperature storage typically arrest any PTW infestation there. However, many regions, especially in developing countries where potatoes are a staple, have few such storage facilities, and store the harvest in rustic conditions – under trees, in sheds, or simply in piles – where their exposure to further PTW development and reproduction can result in huge losses, often up to 100%. In rustic storage, farmers often cover the tuber stores with plant remains, including potato haulms from the harvested crop. Use of PTW-infested halms is particularly detrimental to stores because the remaining larvae have direct access to the tubers (Kroschel 2006).

Native Natural Enemies

A variety of natural enemies attack PTW in all growing regions where it occurs. Particularly prevalent are larval and egg-larval parasitoids in the hymenopteran families Braconidae and Ichneumonidae. A well-studied example is the situation in South Africa (reviewed by Kfir [2003]), in which five species of native parasitoid wasps were found to attack PTW, in each case allowing larvae to develop to just before pupation before killing the host. Rates of parasitism often ranged around 70%, but unacceptable tuber infestation still often resulted. These native species have a variety of other hosts, since the crop is native to South America. Also, a variety of coccinellids, chrysopid larvae, predatory Heteroptera, carabid and staphylinid beetles, and earwigs prey on PTW eggs and larvae (Kfir 2003).

The range of native parasitoids and predators present in South Africa is typical of that in other regions; however, parasitism rates may vary. For example, in Israel, Coll *et al.* (2000) found that five indigenous braconids and ichneumonids attacked PTW larvae. However, their overall level of parasitism was below 10% in commercial fields, with the exception of up to 40% larvae parasitized on volunteer plants that harbored high densities of PTW. That study was particularly notable for its examination of the predator complex and evaluation of its suppressive effects on PTW using emplaced eggs with and without fine-mesh exclosures. The most important predators in that system were *Coccinella septempunctata*,

Chrysoperla carnea, *Orius* spp., and four identified ant species, causing about 80% mortality in the field. To the best of our knowledge, that has been the only quantitative assessment of predation in the field for PTW, although many other studies have noted species of parasitoids and predators, and nominal rates of parasitism. Kroschel and Koch (1994) found in Yemen that the native larval parasitoid ichneumonid *Diadegma mollipla* Holmgren and the egg parasitoid *Chelonus phthorimaeae* Gahan (Braconidae), along with native predators, helped suppress potato tuberworm. Unfortunately, poor cultural practices (particularly the planting of infested tubers) frequently resulted in high levels of damage.

Classical Biological Control of Potato Tuberworm

Beginning in the mid-20th century, the Commonwealth Institute of Biological Control (CIBC) undertook a classical biological control effort against PTW. That resulted in the introduction of several hymenopterous parasitoids, native to South America, into South Africa and many other potato-growing areas. *Copidosoma koehleri* Blanchard (Encyrtidae), an egg-larval polyembryonic parasitoid, and the larval solitary koinobiont *Apanteles subandinus* Blanchard (Braconidae), established in South Africa and greatly increased the levels of parasitism in larvae of PTW in the field (Kfir 2003). Subsequently, PTW damage was significantly and permanently reduced in South Africa, Zimbabwe, Zambia, and other countries of southern Africa (Kfir 2003). In Zimbabwe, PTW was eliminated as a pest (Mitchell 1978). In Australia, introductions of the braconids *Orgilus lepidus* Muesbeck and *A. subandinus*, and the egg parasitoid *C. koehleri*, remain a major factor controlling PTW in potato fields without insecticides (Horne 1990). *O. lepidus*, which was introduced but did not establish in South Africa, is the most important parasitoid, and effectively seeks out the host using volatiles produced by PTW damage to foliage (Keller and Horne 1993). Natural enemies form the basis in Australia for a biointensive IPM program including all potato pests such as PTW, aphids, and noctuid and geometrid larvae (Horne 1990, Horne and Page 2008). In New Zealand, *A. subandinus* is the most important parasitoid, reaching high levels of PTW parasitism especially on foliar populations (Herman 2008) where insecticide treatments were reduced or absent. Another braconid, *Diadegma semiclausum* (Hellén), which was introduced to New Zealand to suppress diamondback moth, reached up to 24% parasitism. All three species of parasitoids have been established in India as well (Kroschel 2006), increasing modest parasitism by native species (Chandla and Verma 2000). The International Potato Center has rearings of these species available for future classical biological control introductions against PTW (CIP 2012), and is assessing target areas worldwide for suitability of introductions (Sporleder et al. 2011).

Guatemalan Potato Tuberworm

The GPTW (*T. solanivora*) differs from PTW in its apparent preference for tubers over the above-ground plant parts (Torres et al. 1997), and also in its

thermal response (Dangles *et al.* 2008). Similarly, study of the natural enemies in the field, mainly since its invasion of northwestern South America, has revealed that the natural enemy complex also differs (Osorio *et al.* 2001). In Colombia, two anthocorid bugs are important predators, along with lycosid and salticid spiders, Carabidae, Coccinellidae, Staphylinidae, and Tenebrionidae (Osorio *et al.* 2001). Two unidentified parasitoid wasps, *Apanteles* sp. (Braconidae) and *Trichogramma* sp. (Trichogrammatidae), were commonly associated with GPTW. Intriguingly, an unidentified tachinid fly was associated with GPTW as well (Osorio *et al.* 2001). *C. koehleri*, native to the Andes, seems to be specialized on PTW and not GPTW. Báez and Gallegos (2011) showed that 36% and 25% of eggs of PTW were parasitized when offered separately and in a mixture with the other two tuberworm species, respectively. In a similar setting, the parasitism of GPTW was only 1% and 2%, respectively. This suggests that one of the principal natural enemies of PTW is not effective on GPTW eggs.

Andean Potato Tuberworm

APTW (*S. tangolias*) is even less-known than GPTW, and less widespread, being cited as a pest in Peru and Bolivia (Palacios *et al.* 1998) although the three tuberworm species are now sympatric in parts of Colombia and Ecuador, where they have been observed to increase crop damage when two or three species occur together (Dangles *et al.* 2009). Infestation is primarily in stems in the field, but tubers are infested both in the field and in storage (Palacios *et al.* 1998). In Australia and New Zealand, it is known as tomato stem borer, and also attacks other fruiting *Solanum* crops. Little information specific to APTW parasitoids and predators is yet available (see Chapter 6). However, Sánchez-Aguirre and Palacios (1996) and Báez and Gallegos (2011) showed that APTW was not a preferred host of *C. koehleri*.

Inundative Biological Control

Several efforts at inundative parasitoid releases have resulted in variable, often unsatisfactory, suppression of PTW in the field and in storage. Inundative releases of exotic parasitoids, particularly *C. koehleri*, have been employed against PTW in the field (e.g., Pokharkar *et al.* 2002, in India; Pucci *et al.* 2003, in Italy) with mixed results, probably due to the sensitivity of the species to desiccation and hot temperatures (Kfir 2003). Inundative approaches with *C. koehleri* and *Trichogramma* species have also been tried against PTW in rustic storage (Keasar and Sadeh 2007, Mandour *et al.* 2012). Rubio *et al.* (2004) evaluated *Trichogramma lopezandinensis* for control of *T. solanivora* (GPTW) in Colombian potato stores and determined that young female parasites, released at 3-day intervals, were necessary for best results. For stored potatoes, a combination of microbial controls (PTW granulosis virus and/or *Bt*), proper sanitation, and storage, as well as use of repellent botanicals, has proven more reliable than parasitoids (Kroschel and Koch 1996, Chandla and Verma 2000, Hanafi 2005, Mandour *et al.* 2012; see also Chapter 16, this volume).

Summary of Biological Control of Tuberworm Species

Additional research is critical for biological control; in many regions PTW biocontrol is poorly understood, as are the biocontrol possibilities for GTPW and ATPW. In the field, predators are consistently present, and at least sometimes are a major source of mortality (Coll *et al.* 2000); these must be researched, recognized, and promoted wherever possible. In the field, native parasitoids play a variable role, often not sufficient to adequately suppress PTW (e.g., Kfir 2003). However, introduced parasitoids from the presumed native range of PTW, and also possibly from outside the native range, have the potential to play a major role in suppression of PTW in the crop, depending on climate and potato culture (Kroschel 2006). Classical biological control may also play a role in the future of GPTW and APTW. Introduced and native parasitoids, as well as predators, are expected to be more successful when supported by practices of pesticide reduction and selection, along with conservation biocontrol (Baggen *et al.* 1999, Horne and Page 2008), which provide resources such as nectar in such a way as to selectively favor natural enemies over the pest, as well as protection from desiccation and from temperature extremes.

Pheromones are known for all three species of potato tuberworms; pheromone-based technologies such as attract-and-kill schemes (Kroschel and Zegarra 2010) are powerful and promising tools which should be selective and compatible with natural enemies. Cultural controls must provide the foundation for protection of tubers from exposure to tuberworm infestation, and continued protection of the tubers during and after harvest. Otherwise, the benefits of biocontrol during the growing season are lost (Kroschel 2006). Simple techniques such as solarization (Gallegos *et al.* 2005) should also be pursued as appropriate. Storage practices can easily be the downfall of potatoes by PTW infestation. A combination of temperature control, sanitation, and exclusion at the outset of storage and over time, and safe biopesticides such as PoGV and/or *Bt*, are most promising where secure refrigeration is not available. Inundative biocontrol with parasitoids is not the most efficient means of control of PTW in potato stores; biopesticides are more reliable and economical in this environment (see Chapter 16).

Hadda Beetle and Potato Lady Beetle: *Epilachna* spp. (Coleoptera: Coccinellidae)

Epilachna species form a large genus of phytophagous coccinellids which feed chiefly on foliage of the Solanaceae, Cucurbitaceae, Fabaceae, and Asteraceae. The systematics of this group is confused; as a result, many specific names in the literature are not correct (Richards and Filewood 1990, CABI 2010). The most important species attacking potato and other solanaceous plants is the hadda beetle, or 28-spotted lady beetle, *Epilachna vigintioctopunctatum* (F.) (also placed in the genus *Henosepilachna*, and taken here to include *E. sparsa* (Herbst); nomenclature follows CABI (2010)). The geographic range of this species includes South, Southeast, and East Asia, Oceania including Australia

(CABI 2010), and, recently, New Zealand (MAFBNZ 2010, David Yard (MAFBNZ), pers. comm. 2012). This species was also detected in Brazil by Schrodner *et al.* (1993), has spread to Argentina (Folcia *et al.* 1996), and persists on wild nightshades in Brazil (Araujo-Siqueira and Massutti 2004). The other important solanaceous feeder is the potato lady beetle (also known as the large 28-spotted lady beetle), *Epilachna vigintioctomaculatum* Motschulsky. It is the most damaging potato pest in China (most notably in northern China; see Chapter 7), and a pest of potatoes in eastern Russia (Ivanova 1962; AgroAtlas 2012), Korea (Lee *et al.* 1988), and Japan (Nakamura 1987).

Hadda Beetle, Epilachna vigintioctopunctatum

Throughout much of its range, hadda beetle is the principal foliar feeder on potatoes and eggplant, and second only to potato tuberworm among potato pests. Schaefer (1983) reported at least 15 species of parasitoids and 4 predator species. Cannibalism is also significant (Patalappa and ChannaBasavanna 1979; Nakamura *et al.* 2004). In India and Pakistan, hadda beetle is attacked by three predatory bugs: *Rhynocoris fuscipes* (F.) (Reduviidae), *Cantheconidea furcellata* (Wolff) (Pentatomidae), and *Geocoris tricolor* F. (Lygaeidae) (Patalappa and ChannaBasavanna 1979, Schaefer 1983, CABI 2010). In southeastern China, Tu and Wang (2010) reported that *Campylomma chinensis* Schuh (Hemiptera: Miridae) was an important predator. Published observations of generalist predators, such as other coccinellids, have not been detailed, but unattributed egg and larval mortality of hadda beetle suggests that predators, many of them nocturnal, can be major mortality factors (e.g., Nakamura 1976, Nakamura *et al.* 1988). Where predator observations have been made on *Epilachna*, as with *E. varivestis* in USA and Mexico, a large number of species of coccinellids, carabids, reduviids, pentatomids, and chrysopids have been found as predators (Schaefer 1983).

For hadda beetle, the most important of the parasitoids are the gregarious larval-pupal eulophids *Pediobius foveolatus* (Crawford) and *P. epilachnae* (Rohwer), the eulophid egg parasitoid *Oomyzus ovulorum* (Ferriere) (formerly *Tetrastichus*), and chalcidids *Uga* spp. These three genera are also recorded from *Epilachna ocellata* Redtenbacher, a closely-related potato pest of northern India (Chandel *et al.* 2007, CABI 2010). Parasitism, particularly by *Pediobius*, frequently reaches 75% on wild nightshades, as well as on potato and eggplant (Patalappa and ChannaBasavanna 1979, Rajagopal and Trivedi 1989; Nakamura *et al.* 2004). Sheng and Wang (1992) found a peak of 28.5% parasitism on potato, and later a peak of 64.5% on *Solanum nigrum*, followed by a precipitous decline of both host and parasitoid due to high temperatures in mid-July. Other studies in India (see Rajagopal and Trivedi 1989), Bangladesh (FAO 2003), and Thailand (Kernasa *et al.* 2002) confirm the importance of *P. foveolatus* as a natural enemy of hadda beetle. There are at least 11 generations per year reported in China (Sheng and Wang 1992), and as many as 18 generations in

India (Rajagopal and Trivedi 1989). Females oviposit into larvae, mainly of the third and fourth instars, and between 10 and 30 adults usually emerge from the resulting larval “mummies” (Lall 1961). Adult longevity is greatly increased by feeding on dilute honey in the laboratory (Sheng and Wang 1992). As early as 1954 Puttarudriah and Krishnamurti observed the seasonally high parasitism on both potato and eggplant, and tested the effects of early chlorinated hydrocarbon and calcium arsenate insecticides on *P. foveolatus*. They urged growers to withhold sprays against hadda beetle when parasitism reached about 70%, and demonstrated the negative effects of the DDT, BHC, and toxaphene, but not the arsenical, on the parasitoid. Fenvalerate, abamectin, and particularly dichlorvos severely affected larval survival inside the host in lab tests, especially within 7 days of oviposition by *P. foveolatus* (Wang et al. 1998). Schaefer et al. (1986) reported *Tetrastichus* sp. to be hyperparasitic on *Pediobius* at several locations in China.

Potato Lady Beetle, *Epilachna vigintioctomaculatum*

For the potato lady beetle, *P. foveolatus* is not as important a parasitoid as for the hadda beetle, but appears to be the same wide-ranging species (Peng and Bao 1988). Lee et al. (1988) studied potato lady beetle on potato and eggplant crops, and reported that, in South Korea, *Nothoserphus affissae* (Watanabe) (Proctotrupidae) was the dominant parasitoid. *Uga menoni* (Kerrich) and *P. foveolatus* were also present, the latter only near the end of the season, except in southern Korea, indicating lack of winter hardiness. The authors advocated leaving the late-season wild plant host *Solanum nigrum* intact as a refuge for *E. vigintioctomaculatum* and its parasitoids. Zhuang and Sun (2009) constructed life tables for this pest, and considered predation and rainfall to be the most important mortality factors in Daqing, in far northeastern China. They mentioned spiders and lady beetles (not identified) as predators, and an average of 22% of pupae as being parasitized (parasitoids not specified). Three species of Tachinidae, *Medina collaris* Fallen, *M. separata* (Meigen), and *Bessa parallela* (Meigen), have also been reported from Japan (Schaefer 1983), but their impact on the target species was not quantified.

Annual Inoculation of *Pediobius* against *Epilachna* in USA

P. foveolatus was exported from India (original host, hadda beetle) and is the basis for a 40-year history of annual inoculative releases against *Epilachna varivestis* Mulsant (Mexican bean beetle) in eastern North America (Kogan 1999, Robbins et al. 2010). The parasitoid is also available through four commercial vendors in the USA (White and Johnson 2010). Releases are made each year because it does not overwinter. In New Jersey, where the state Department of Agriculture rears and releases *P. foveolatus*, area-wide control has now suppressed *E. varivestis* numbers on bean and soybean crops by ~95% compared to densities in the 1980s (Robbins et al. 2010). A trap crop is typically employed

to attract the overwintering hosts, which functions as an in-field nursery for the lab-reared parasitoids (Robbins *et al.* 2010). This strategy could also be employed with Asian *Epilachna* species.

Summary of Role of Biological Control for Epilachna Potato Pests

To make optimal use of natural enemies in suppressing *Epilachna* pests of potatoes, overwintering adult aggregations (see Chapter 7) should be targeted in temperate regions for destruction to reduce immigrating pest numbers, which otherwise commonly outstrip predator and parasitoid suppression. Staging and managing trap crops as in-field nurseries for *Pediobius* parasitoids, using the model of the New Jersey scheme for Mexican bean beetle, would likely result in early-season biological control establishment and effectiveness against Asian *Epilachna* spp. There is a need for more selective insecticides for *Epilachna* control which would conserve the oft-abundant natural enemies. Although *Bacillus thuringiensis tenebrionis* (Btt) is not toxic to *Epilachna* (specifically, *E. varivestis*; Krieg *et al.* 1987), there have been reports of strains toxic to coccinellids (e.g., Peña *et al.* 2006), and these, if selected and deployed carefully to avoid harming predatory coccinellids, could function in concert, rather than against, the beneficial insect guild.

Andean Potato Weevil (Coleoptera: Curculionidae)

There are at least 14 species which make up the Andean potato weevil species complex: *Premnotrypes latithorax* (Pierce), *P. suturicallus* Kuschel, *P. vorax* (Hustache), and 9 other *Premnotrypes* spp., as well as *Rhigopsidius piercei* Heller and one other species in this genus. The four named species are the most important, according to Kühne *et al.* (2007). They are distributed from Andean Venezuela south to northern Chile and Argentina, mostly at between 2800 and 4500 m in altitude; they are often the only important pest above 3800 m (Kühne *et al.* 2007, Kroschel *et al.* 2009).

All Andean potato weevils are specialists on tuberous *Solanum* spp. including all potato species. They are univoltine in Peru and Bolivia, corresponding to a single potato season, but two to three generations occur to the north, where rainfall allows longer or even continuous potato crops. Adults of all species are flightless, and colonize new hosts by walking. Emergence from dormancy is variable by species and growing region, and *P. suturicallus* and *P. vorax* are reported to survive a few months if starved. On potatoes, they feed modestly during the first half of the night, copulating and ovipositing numerous eggs at the base of the plant. Larvae seek out the tuber and enter it to complete their development in four instars. In the soil, almost all larvae of *Premnotrypes* spp. typically emerge from the tuber to pupate, but *Rhigopsidius* spp., in contrast, pupate within the tuber (Kühne *et al.* 2007).

In traditional communal potato culture, a system of “sectoral fallow”, still practiced in parts of Peru and Bolivia, limited potato plantings to blocks of

~100ha, which were rotated each year amongst 7–10 similar blocks. Long fallow periods of several years were designated for grazing rather than crops. Under such a system, the Andean potato weevil typically damaged less than 10% of tubers, and these would typically be fed to animals or made into *chuños* (traditional freeze-dried potato meal). Within the past several decades, the communal land tenure, and along with it the rotational system of sectoral fallow, has been dismantled. Small plots of potatoes and other crops raised on private plots in uncoordinated individual rotations accompanied the ascendancy of Andean potato weevil to key pest status throughout most of the upper-elevation growing areas of South America (Parsa 2010, Parsa *et al.* 2011, Rios and Kroschel 2011).

Natural Enemies

The natural enemy complex appears to be lacking in specific natural enemies. No parasitoids have been discovered despite prolonged and intensive efforts (Parsa 2010). Known predators are six genera of carabids: *Harpalus turmalinus* Erichson, *Hylitus*, *Meotachys*, *Metius*, *Notiobia* including *N. schnusei* Van Emden, and *Blennidus*, a predatory tenebrionid (*Metius* sp.) (Alcalá and Alcázar 1976, Alcázar and Cisneros 1999, Kaya *et al.* 1999), and a predatory ant found in potato storage (Garmendia 1961). Kroschel *et al.* (2009) caught carabids in abundance along with weevil adults when plastic barriers were combined with pitfall traps. The authors stated that high carabid numbers, and their association with lower weevil populations, indicated an “important role in improved natural control of Andean potato weevils”. They also suggested two methods of favoring carabids over weevils: removal of barriers after ~95% of weevil captures, to allow the later-colonizing carabids to move into new potato plantings, and selective release by growers of carabids captured in traps along with the weevils. The carabids identified are thought to be generalists (Parsa 2010), although there is no quantitative data on their diets; they readily accept weevil eggs as food, and some prefer early-instar larvae (Alcázar and Cisneros 1999, Loza and Apaza 2001, Yábar *et al.* 2006). Wild birds and toads also prey on weevil adults, likely with minimal impact, but chickens at harvest time may be useful (Alcázar and Cisneros 1999). Predators may have been negatively impacted across the region with adoption of broad-spectrum synthetic pesticides (Parsa 2010), of which the most commonly used are carbofuran and methamidophos (Kühne *et al.* 2007). Both these chemicals are extremely toxic to most invertebrates and vertebrates, including humans (Orozco *et al.* 2009, Pradel *et al.* 2009).

Biological Control in Context of IPM for Andean Potato Weevil

Within this changing spatiotemporal context, the IPM strategies that are considered most promising are crop rotation away from sources of emerging weevils (Rios and Kroschel 2011), development of practical barriers to weevil movement (Kroschel *et al.* 2009), use of natural barriers such as streams as well as ditches (Parsa *et al.* 2011), trap crops and baits prior to planting (Gallegos

and Castillo 2011), border treatments of newly immigrated weevil concentrations, manipulation of harvest timing and storage (Kühne *et al.* 2007), and use of entomopathogens, including *Beauveria*, and particularly cold-adapted and virulent *Heterorhabditis* sp. nematodes (Kaya *et al.* 2009; see also Chapter 16, this volume). It is likely that predation on Andean potato weevils has a useful supporting role in the field when cultural controls are in place, and chemical control is judicious and selective in nature. Molecular approaches to identifying and quantifying subterranean predation, as used by Juen and Traugott (2007) for wireworms and Lundgren *et al.* (2009) for western corn rootworm larvae, could yield surprising information regarding unseen trophic relationships. Given the dearth of knowledge on the predator fauna, more research on carabids and possible other arthropods as natural enemies of Andean potato weevil complex is much needed.

Potato Psyllid (Hemiptera: Triozidae)

The potato psyllid (*Bactericera cockerelli* Sulc) (Hemiptera: Triozidae), native to the Rocky Mountain region of the USA and northern Mexico, has recently expanded its range to the entire western USA, including California, Oregon, and Washington, southern Canada, including Ontario, as well as Mexico and Central America, and New Zealand, with major impacts on potatoes, tomatoes, peppers, and other solanaceous crops (Crosslin *et al.* 2010, Munyaneza 2010, Rehman *et al.* 2010). The damage, including zebra chip disease of potatoes, is now unequivocally associated with the transmission by potato psyllid of the recently-discovered *Candidatus* Liberibacter psyllaurosus/solanacearum (see Chapter 4). In response to increasing potato damage, “At present, application of insecticide targeted against the potato psyllid [is] the only way to effectively manage zebra chip” (Munyaneza 2010). In California, recommendations call for monitoring by yellow sticky cards and plant sampling, coupled with insecticide applications (UC IPM Online 2009).

Predators in Rocky Mountain States

Natural enemies identified as preying on the potato psyllid include predatory bugs in the genera *Nabis*, *Geocoris*, *Orius*, *Anthocoris*, and *Deraeocoris*, and also adult and larval *Hippodamia* (Coccinellidae), larval Chrysopidae, and Syrphidae (Knowlton 1933a, 1933b, 1934a, 1934b, Knowlton and Allen 1936). Romney (1939) noted that “numerous predators (coccinellids and chrysopids) reduce the numbers of eggs and nymphs to a varying degree from year to year,” but it is not clear whether this was on wild hosts in Arizona or on crops in Colorado. Among those early works, field observations on predation were generally not detailed. However, Pletsch (1947) noted “an exceedingly heavy and aggressive population of [coccinellid] adults and larvae feeding on psyllids” on tomato in Bozeman, Montana, especially *Hippodamia parenthesis* (Say), *H. convergens* Guerin, *H. quinquesignata* Kirby, *Coccinella novemnotata* Herbst, and *C. transversoguttata*

Faldermann. He also considered lacewings (Chrysopidae) among the most important predators, and ascertained that newly eclosed lacewings as well as later instars fed readily on potato psyllid eggs.

Al-Jabr (1999) found that two species of Chrysopidae (*Chrysoperla carnea* and *C. rufilabris*) had promise for potato psyllid suppression on greenhouse tomatoes, consuming (under laboratory conditions) a mean of 24.4 and 17.5 nymphs per day during a larval development period of 12 and 8 days, respectively. Development and survival was comparatively worse on green peach aphid prey, with *C. rufilabris* not completing larval development. In laboratory choice trials, both species consumed both prey species without preference. A field trial of augmentation of *C. carnea* eggs in Colorado potatoes failed to show suppression of either potato psyllid or green peach aphid populations at 7 and 14 days post-release (Al-Jabr 1999).

Early Work with Parasitoids, and Changing Context

A parasitoid “*Tetrastichus* sp.” was mentioned by Romney (1939), and described later by Burks (1943) as *Tetrastichus triozae*. Pletsch (1947) in Montana and Johnson (1971) in Colorado concluded that *Tetrastichus* (now *Tamarixia*) *triozae* was not a promising biocontrol agent for potato psyllid. However, that assessment was based largely on the parasitoid’s localized occurrence and late phenology, which does not pertain in mild climate areas where infestations are worst now (California, Texas, Mexico, Central America and New Zealand). Johnson (1971) also noted high pupal mortality in the field. Lab studies by Pletsch (1947) showed that oviposition was only in fourth- and fifth-instar nymphs.

Natural Enemies of Invasive Psyllid Populations in California

Butler *et al.* (2010) examined endemic biological controls on potatoes grown in southern California, and on a common weed in the crop environment, *Solanum americanum* P. Miller, which also supported the psyllid. Over 90% of natural enemies were in the following groups: hymenopterous parasitoids *Tamarixia triozae* (Eulophidae) and *Metaphycus psyllidis* Compere (Encyrtidae), *Chrysopa* (Chrysopidae), spiders (Araneae), predaceous bugs *Orius tristicolor* (White) (Anthocoridae), *Geocoris*, *Nabis*, and various Miridae, the coccinellids *Hippodamia convergens*, *Coccinella septempunctata*, and *Harmonia axyridis*. Cage exclusion studies with potato and *S. americanum* showed similar and significant suppression of nymphal populations (Butler *et al.* 2010). The recorded parasitism rates by *T. triozae* were less than 20% (Butler and Trumble, 2012).

Introduction to New Zealand, and Natural Enemies There

Following the discovery of potato psyllid on the North Island of New Zealand in 2006, and its rapid spread to most areas of both principal islands (Teulon *et al.* 2009), chemical control was the main response for severely affected greenhouse

crops, including tomato and peppers, and for field-grown potatoes (Walker *et al.* 2011). The natural enemy complex in unsprayed psyllid-infested potatoes on North Island includes many of the same higher taxa found to be important in California, with the widespread Australian native lacewing *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae) and the endemic *Melanostoma fasciatum* (Macquart) (Diptera: Syrphidae) judged in preliminary studies to be most important (Walker *et al.* 2011). These two species, as well as *Coccinella undecimpunctata* L., *Harmonia conformis* (Boisduval), *Nabis kingergii* Reuter (Hemiptera: Nabidae), and Linyphiidae (Araneae), were common in unsprayed potato fields, and all consumed potato psyllid nymphs and adults in laboratory assays (MacDonald *et al.* 2010, Larsen *et al.* 2011, Walker *et al.* 2011). The native psyllid *Trioza vitreoradiata* (Maskell), which feeds on native woody plants, has a predator community including *M. tasmaniae* and *Drepanacra binocula* (Newman) (Hemerobiidae); coccinellids *Harmonia conformis*, *Adalia bipunctata* (L.), and *Halmus chalybeus* (Boisduval); and the predatory mirid *Sejanus albisignata* (Knight). All six of these species preyed on potato psyllid in lab no-choice tests, with *D. binocula* and the first two coccinellids considered the most promising predators of potato psyllid except in tomato crops, where the coccinellids avoided the crop (Gardner-Gee 2011). No parasitoids or entomopathogens were found in the field study by Walker *et al.* (2011), but an undescribed *Tamarixia* was discovered in 1997 in New Zealand (Workman and Whiteman 2009, Workman 2009) and is now in culture (Gardner-Gee 2011).

Candidates for Classical Biological Control

The North American native eulophid *Tamarixia triozae* has been studied in Mexico (Luna Cruz 2010, Rojas Rojas 2010) and then exported from Koppert Mexico to quarantine in New Zealand (Workman and Whiteman 2009, Workman 2009). *T. triozae* prefers fourth- and fifth-instar nymphs for oviposition, but undertakes host-feeding particularly on younger nymphs (this feeding was not quantified) (Rojas Rojas 2010). Both females and males benefit enormously from non-prey food. In the laboratory, honey increased the lifespan of females from a mean of less than 2 days with water only, to more than 46 days. Females in the lab averaged 143 parasitized hosts in their lifetime; the population doubling time appears to be significantly less than that of potato psyllid (Rojas Rojas 2010). Its reported host range is restricted to the psyllid families Calophyllidae, Psyllidae, and Triozidae, for a total of 7 genera in 13 species, including the potato psyllid (Jensen 1957, Zuparko *et al.* 2011). It is quite sensitive to commonly used insecticides (Luna Cruz 2010). A single unidentified sphegigastrine pteromalid was reared from *T. triozae* by Pletsch (1947), and two hyperparasitoid *Encarsia* species have been documented in California on tomato and pepper crops at totals between 5.3% and 6.9% (Butler and Trumble 2011).

Greenhouse infestations of potato psyllid in Ontario on tomatoes and peppers have been suppressed with releases of *T. triozae* (OMAFRA 2012, Workman and

Whiteman 2009), and this application may become more widespread (including in New Zealand, if the parasitoid is released from quarantine). Koppert Mexico (2012) sells the species commercially, and permission to import to Canada has been issued by the Canadian Food Inspection Agency (2011).

New Zealand researchers have begun screening of *T. triozae* against the diverse native psyllid fauna (83 described species), as well as to compare its performance against potato psyllid with the newly-discovered New Zealand *Tamarixia* sp. No-choice tests against four native psyllid species showed only one species partially accepted, without adult emergence (Gardner-Gee 2011).

Compere (1943) described the encyrtid *Metaphycus psyllidis* from *B. cockerelli* on peppers in Southern California. Until the report of Butler *et al.* (2010), there were no subsequent published observations. It is one of only three species of *Metaphycus*, all in the New World, which parasitize psyllids (Guerrieri and Noyes 2000).

Spread of Liberibacter and the Context for Psyllid Microflora

As molecular tools are used to discover more information about the occurrence and transmission of the pathogenic bacterium *Ca. L. psyllauros/solanacearum*, there are major implications for the management both of the potato psyllid and the pathogen. Studies of potato psyllids in New Zealand (Berry *et al.* 2010) have shown a large proportion of insects carry the *Liberibacter*; furthermore, in New Zealand field studies, PCR shows putative presence in plants of four plant families other than Solanaceae. This in turn raises the possibility that additional reservoirs and pathogen-vector relationships may develop. Molecular confirmation of a distinct haplotype of *Ca. L. psyllauros/solanacearum* in carrot psyllid and symptomatic carrots in Finland (Munyanze *et al.* 2010, Nelson *et al.* 2011), and the report of zebra chip symptomatic potatoes infested with *Bactericera nigricornis* (Forster) in northern Iran (Fathi 2011), suggest wider occurrence of *Ca. L. psyllauros/solanacearum*. Molecular studies also reveal that the pathogen is universally present in first-instar nymphs through adults on potato (Hansen *et al.* 2008), and that pathogen transmission by potato psyllid is very rapid, putting a premium on management tools providing rapid death and/or cessation of feeding and/or repellency (Buchman *et al.* 2010, Yang *et al.* 2010, Peng *et al.* 2011).

The symbiotic flora of potato psyllid may also yield possibilities for management of the pathogen, including biological control within the symbiont community. Psyllid bacteriocytes harbor the obligate symbiont *Candidatus Carsonella ruddii* which is maternally transmitted (reviewed in Baumann 2005), and may also contain secondary symbionts. All potato psyllids studied contained *Carsonella*; many contained *Liberibacter*; some also contained *Wollbachia*, *Acinetobacter*, and/or *Methylibium* (Alvarado *et al.* 2010, Nachappa *et al.* 2011). Furthermore, there are indications that parasitoids can promote secondary symbiont transmission in psyllids (Hansen *et al.* 2007). Together with the potential for oral ingestion of RNAi constructs for potato psyllid control (Wuriyanghan

et al. 2011), one can imagine using the same technology to achieve elimination of *Ca. L. psyllauros/solanacearum* from its psyllid host, or transgenerational passage of a secondary symbiont which is antagonistic to the *Liberibacter*, or even transmission of *Liberobacter*-antagonistic symbionts into potato psyllid by its parasitoid.

Overall Context for Sustainable Potato Psyllid Management Including Biocontrol

Returning to the agroecological level, it is essential to recognize the importance and potential value of population suppression of potato psyllid by native and introduced natural enemies, in, near, and distant from agroecosystems. This population suppression works to reduce many losses and risks: crop quantity and quality loss, spread of *Liberibacter*, spread of potato psyllid on local to global scales, insecticide resistance, provocation of secondary pest outbreaks, and other deleterious effects of pesticides to non-target organisms including humans. In combination with more selective chemical controls, semiochemical tactics (see Guédot *et al.* 2010), cultural manipulations, and crop resistance, biological control must play an important role in sustainable management of potato psyllid.

Aphids (Hemiptera: Aphididae)

Several species of aphids feed on potatoes throughout the world; the most important are green peach aphid (*Myzus persicae* Sulzer), potato aphid (*Macrosiphum euphorbiae* (Thomas)), buckthorn aphid (*Aphis nasturtii* Kaltentbach), and foxglove aphid (*Aulacorthum solani* (Kaltentbach)); they may vector several damaging viruses in a persistent or non-persistent manner (Ragsdale *et al.* 1994; Flint 2006). Virus transmission is of highest concern for growing seed potatoes, which are used to plant subsequent crops (Nakata 1995, Flint 2006). In potatoes, aphids rarely reach populations which lower potato yields by their feeding alone, due to natural enemy complexes typically including Coccinellidae, predatory bugs in genera *Orius*, *Nabis*, and *Geocoris*, lacewings, spiders, syrphid fly larvae, and/or predatory gall midge larvae (Cecidomyiidae), as well as aphid-specific parasitoids, typically solitary koinobionts in family Aphididae (Hautier *et al.* 2006, Straub and Snyder 2006). Alyokhin *et al.* (2005, 2011), using a 34-year record of aphid and natural enemy populations on potatoes in northern Maine, concluded that pest populations were regulated in a density-dependent manner. Predators suppressed buckthorn and potato aphids, potato aphids were also suppressed by entomopathogenic fungi, green peach aphids were negatively affected by interactions with the former two species, and parasitoids did not significantly affect any of the three aphid populations. Management implications of this study were that chemical controls should minimize impacts on predators and entomopathogenic fungi, and that non-damaging populations of

buckthorn and potato aphids should be allowed to develop, because these might help prevent population increase in green peach aphid, which is recognized as a more effective virus vector in potatoes (Alyokhin *et al.* 2011). Insecticide applications often only temporarily suppress aphid populations, resulting in decimation of natural enemies and subsequent resurgence of aphids within a few weeks (Ito *et al.* 2005, Horne and Page 2008). Evolution of insecticide resistance in aphids aggravates this phenomenon (Hardin *et al.* 1995). Even insecticides applied specifically against aphids (e.g., pirimicarb, Jansen *et al.* 2011) and those allowed in organic farming (Jansen *et al.* 2010) are often damaging to aphid antagonists. However, there are several more-or-less specific aphidicides which minimally impact aphid predators and parasitoids, avoiding pest resurgence (Hautier *et al.* 2006). Border treatments may reduce chemical quantities by over 90% while achieving similar aphid population suppression, due to concentration of colonizing alates in field edges (Carroll *et al.* 2009). Sampling of alate aphids has recently shown that they carry a wide variety of entomopathogens and also larval parasitoids, which inoculate colonizing populations with these natural enemies (Feng *et al.* 2007, Huang *et al.* 2008). In some areas, if potatoes are grown using certified seed (reducing concerns of virus transmission), avoidance of all insecticide applications may be practical (e.g., Ito *et al.* 2005, Ito and Furukawa 2009). Lack of knowledge of widely varying aphid and virus levels has encouraged prophylactic treatment with systemic insecticides and/or calendar foliar treatments which are often not needed (Ragsdale *et al.* 1994).

BIOLOGICAL CONTROL INTERACTION WITH OTHER MANAGEMENT METHODS

Interaction with Chemical Control

There are countless instances of non-selective insecticides impairing natural enemy function, up to and including decimating their numbers and causing resurgence both of the target pests, and of other herbivores in the absence of their respective natural enemies. In potato systems, there is no shortage of examples. Horne and Page (2008) show resurgence of potato aphid (*M. euphorbiae*) populations approximately 1 month after pyrethroid application against lepidoptera larvae. The pyrethroid esfenvalerate was highly toxic to *C. maculata* and *Chrysoperla carnea* (Stephens), natural enemies of CPB (Hamilton and Lashomb 1997), as was fenvalerate and methamidophos to *E. puttleri* (Obrycki *et al.* 1986), endosulfan, methamidophos, and permethrin to PTW parasitoid *Orgilus lepidus* (Symington 2003), and imidacloprid to *C. maculata* (Lucas *et al.* 2004). All of these insecticides are commonly used in potato applications. Insecticides specific to targeted key pests, such as *Bt* strains for lepidoptera or CPB, and the aphidicides pymetrozine and flonicamide, are highly compatible with arthropod natural enemies (Ferro 1994, Jansen *et al.* 2011). Deployment of border treatments, even with relatively non-selective materials, also has the

potential for large cost savings (Carroll *et al.* 2009); additional delayed benefits also accrue, by conservation of predators and parasitoids. Conversely, effectiveness of natural enemies serves to avoid pesticide applications, thereby mitigating or delaying insecticide resistance on the part of target pests (Alyokhin *et al.* 2008). Interactions of predators with multiple prey may heighten this effect (Mallampalli *et al.* 2005).

Interaction with Biopesticides and Nematodes

Microbial biopesticides can be extremely selective in favor of natural enemies; for instance, *Bacillus thuringiensis tenebrionis* (Btt) does no harm to coccinellids regardless of application method (Lucas *et al.* 2004, Kühne 2010). Ramirez and Snyder (2009) found a fascinating synergistic effect on Colorado potato beetle between above-ground generalist predators and below-ground pathogens (*Beauveria* and the nematodes *Heterorhabditis marelatus* and *Steinernema carpocapsae*). Negative interaction between arthropod natural enemies and entomopathogens is of concern. For example, *Beauveria* strains varied from harmless to quite pathogenic against *C. maculata*, making at least 6 of 10 strains tested unacceptable for these non-target effects (Todorova *et al.* 2000).

Interaction with Cultural Controls

If adequate cultural controls are not in place, biological control will often not succeed either through excessive pest populations or through frequent insecticide applications, or through both. For instance, for potato tuber moth, covering tubers with intact (not cracked) soil during the growing season restricts their infestation of the potato plant to the canopy, both avoiding tuber damage and providing access to hosts for a suite of parasitoids and predators which can attack them there (Von Arx *et al.* 1990, Kroschel 2006). Crop rotation is necessary to provide a foundation for biological control as part of an integrated, sustainable approach to Colorado potato beetle management (Alyokhin *et al.* 2008); it is also essential for Andean potato weevil management, and possibly beneficial to hadda beetle and potato lady beetle management (see above).

Interaction with Crop Resistance

Plant cultivar affects the success of natural enemies through a variety of mechanisms, including access to the host over time (e.g., positive effect on *C. maculata* predation on CPB feeding on tomatoes, Lu *et al.* 1996). Studying potato and tomato host plants, Baggen and Gurr (1995) found a negative lethal effect of glandular trichomes of tomato, and Gooderham *et al.* (1998) found a negative non-lethal effect of non-glandular foliar pubescence on the potato tuber-worm parasitoid *Copidosoma koehleri*. Therefore, plant resistance to pests can be favorable or detrimental to natural enemies, depending on the mechanism

involved and the pest and the beneficial species. [Arpaia et al. \(1997\)](#) proposed that predation could in theory slow or accelerate evolution of CPB resistance to *Bt*-transgenic potatoes, and showed that *C. maculata* could decrease this undesirable selection – a process which could also work to slow pest resistance to non-transgenic crop resistance.

CURRENT AND FUTURE RESEARCH NEEDS

The potato crop is surprisingly tolerant of foliar damage that is inflicted by many of the important potato pests ([Alyokhin 2009](#)). Pest damage at certain growth stages can even result in overcompensation, as demonstrated for Guatemalan potato tuberworm by [Poveda et al. \(2010\)](#). Yet pest management practices rarely take this compensatory capacity, or any scientifically established pest thresholds, into account ([Alyokhin 2009](#)). Chemical control is the dominant pest management tactic for potato pests (see Chapter 13), often applied too frequently and/or in excess. This has negative consequences for pest management. In the short run, target pests and other species resurge because their natural enemies are no longer present. Also, especially in developing countries, pesticide exposure reaches dangerous levels ([Giri et al. 2009](#), [Orozco et al. 2009](#)). In the long term, pesticide resistance causes more pest damage, and increased expense in attempting to control it. In order for biological controls to contribute to management of potato insect pests, pesticide applications must be based on rational decision-making, be more selective for the target pest(s), and take account of these short- and long-term risks. For this to happen, potato growers must be more knowledgeable regarding both the risks and the benefits of more sustainable strategies ([Kroschel et al. 2012](#)).

Conservation Biocontrol

There are ample opportunities for enhancing the performance of both native and introduced natural enemies using reduced applications of selective insecticides or bioinsecticides only when necessary (e.g., [Horne and Page 2008](#)). Moreover, provision of food resources for parasitoids and predators based on scientific knowledge of their requirements, which is quite poor at the present moment, would further benefit natural enemies. Companion plantings may provide some biocontrol benefits (e.g., [Patt et al. 1997](#)) or fail altogether ([Moreau et al. 2006](#)) if their multiple benefits and risks are not known. The example of parasitoid-selective flowering plants offered by [Baggen and Gurr \(1998\)](#) and [Baggen et al. \(1999\)](#) is both directly relevant to potato pest biocontrol, and a powerful paradigm for sorely-needed practical research to develop conservation biocontrol tools. Some very easy steps to provide in-field resources for natural enemies could, a number of studies suggest, increase the longevity and fecundity of parasitoid adults from 2-fold to 20-fold.

Predation impact on pest populations is poorly known, and is often more effective than we realize. Furthermore, it is probably easy to increase, once we

have a better understanding of predator biology and ecology. The few studies where exclusion cages have tested the magnitude of suppression by predators (e.g., Coll *et al.* 2000, Butler and Trumble 2012) show that surprises are in store both for the existing power of insect predation, and for the increased potential of predation through conservation.

Augmentative and Inundative Biocontrol

Potato value as a crop makes inundative biocontrol using parasitoids or predators an economically dubious proposition. Inundative control using egg parasitoids to protect potatoes from potato tuberworm has only been attempted on a research basis, and even then has not been promising (Horne and Page 2008). Inundative control of Colorado potato beetle with the exotic egg parasitoid *Edovum puttleri* has only been economically viable in eggplant, a much more valuable crop, when registered pesticides were not effective on CPB (Ferro 1994, Hamilton and Lashomb 1996). Similar practical considerations pertain to possible inundative control with predatory stink bugs in the potato crop.

Augmentative control, on the other hand, has a place where the crop environment is supportive of natural enemies but they are not present early enough in the crop cycle, or in high enough numbers, to provide adequate control. Rearing costs may still discourage large releases, but these are not always necessary if in-field conditions (including in-field nurseries) can be established which allow natural enemies optimal conditions to reproduce, as with wild-caught *Podisus maculiventris* against CPB (Aldrich and Cantelo 1999) and lab-reared *Pedobius foveolatus* against *Epilachna varivestis* in beans (Robbins *et al.* 2010). Candidates for augmentation include *P. foveolatus* against *Epilachna* beetles, especially in temperate Asia where it overwinters poorly or not at all (as in Korea, where it only became a mortality factor late in the growing season (Lee *et al.* 1988)); *Copidosoma koehleri* where there are low populations at some times of the season but climatic conditions allow successful survival in the field; and possibly the potato psyllid parasitoid *Tamarixia triozae*.

Classical and Neoclassical Biocontrol

A number of the major potato pests, including Colorado potato beetle, potato tuberworm, Guatemalan potato tuberworm, and potato psyllid, have invaded large new areas of potatoes and related crops. Because of non-target risks, classical biological control programs consider only specialized natural enemies, and they must continue to take this approach. However, there are still many opportunities, within this framework, to export natural enemies from areas of pest origin, or from areas of origin of closely related species (a so-called neoclassical approach), creating associations of target pests and novel natural enemies. Colorado potato beetle parasitoids, the carabid beetle *Lebia grandis*, and two species of specialist tachinid parasitoids in the genus *Myiopharus*, could

benefit potato, eggplant, and tomato agroecosystems in the Old World. The last time such an introduction was attempted was almost 50 years ago, in the USSR (Sikura and Smetnik 1967), before much of the biology, including the overwintering habit of the tachinids, was known. Climatic matching today would yield a broader range of opportunities than for early efforts, when the beetle was restricted to France and adjacent western Europe. For CPB, there is also still the possibility that an egg parasitoid or other effective natural enemy may be found on other *Leptinotarsa* species. Unfortunately, this seems unlikely given the fruitless effort already expended.

Classical biocontrol programs for potato tuberworm have yielded immense returns in crop yield and pest control savings, particularly in southern Africa and Australia. For the three parasitoids most commonly introduced, each region has had a unique combination of relative successes and failures. The failure of some species to establish or to play a significant role in pest suppression may in the future yield to an understanding of biotypes along with more sophisticated climatic models and matching. With the expansion of the Guatemalan potato tuberworm may come opportunities to suppress invasive populations in South America, or in potentially invaded areas such as Africa, with natural enemies yet to be determined.

A potato psyllid classical biological control program for New Zealand is already underway. However, it is not clear that candidate species will ultimately be introduced in this newly invaded territory, both because of non-target concerns, and because native psyllid predators that are already present may be capable, with management, of adequately suppressing the invasive pest.

The Epilachninae are an extremely diverse group offering many possibilities for natural enemy matching. The importation of *Pediobius foveolatus* from India to combat a Mexican pest, *Epilachna varivestis*, in temperate USA, is an example of successful biocontrol in this group of pests. In contrast, for Asian *Epilachna* pests of potatoes and related crops, because potentially powerful endemic natural enemy complexes including parasitoids are already present, the best approach is to research and implement suppression of these pests through conservation and augmentation, combined with appropriate cultural controls and application of monitoring and thresholds with selective chemical or microbial treatments if needed.

Interaction with Future Technologies, Practices, and Growing Regions

Potatoes are grown under an increasingly extreme diverse range of locations, conditions, and pest pressures (see Chapter 1). If our expectation is for this ancient crop to provide even as large a proportion of our food needs tomorrow as it does today, we will have to employ a much more diverse set of tactics, and to combine them in a much more sophisticated manner. These tactics will not employ themselves; they must be brought to and made accessible

to the potato grower – who lives and farms under a vast range of economic and environmental conditions. This will require a practical and knowledge-intensive participatory approach (e.g., FAO 2003, Ortiz *et al.* 2004, Dangles *et al.* 2010), which researchers have, to date, rarely taken. Furthermore, IPM must be locally adapted and take into account all pests impinging on the crop, otherwise inappropriate management practices for novel pests – even minor pests or non-pests – may disrupt the entire crop system (Horne and Page 2008, 2009; Kroschel *et al.* 2012). Researchers and growers will have to answer a myriad of questions and will need to apply the answers in a judicious manner, or suffer the consequences of poor pest management and wasted resources. Successful tactics of the future may range from apparently simple ones like intercropping potatoes with onions, which is reported to greatly reduce hadda beetle (Potts 1990), or nursery crops for parasitoids of pest *Epilachna* beetles, to the high technology of detecting insect predation using quantitative PCR, or applying RNA interference to cure insect vectors of their potato huanglongbing. Only if these tactics respect the beneficial organisms in and surrounding potato agroecosystems around the globe are they likely to succeed in providing the opportunity for sustainable management of potato insect pests.

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