

# Colorado Potato Beetle Management on Potatoes: Current Challenges and Future Prospects

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## ABSTRACT

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) is the most important insect defoliator of potatoes that can completely destroy potato crops. Its current range covers about 16 million km<sup>2</sup> in North America, Europe, and Asia and continues to expand. A complex and diverse life history, combined with an impressive ability to develop insecticide resistance, make the Colorado potato beetle a challenging pest to manage. Beetle populations on commercial farms are usually suppressed by insecticides, which are likely to remain the predominant approach for the foreseeable future. In addition, the beetles can be controlled through the use of relatively common cultural practices, with crop rotation being the most effective and easily implemented approach. In spite of a long history of breeding efforts, no commercial cultivars resistant to the Colorado potato beetles are currently available on the market. Natural enemies are usually incapable of reducing beetle densities below the economically damaging levels and have to be used in combination with other control techniques. Unfortunately, there will never be a “silver bullet” solution to preventing the damage caused by this insect. The only sustainable way to protect potato crops is to integrate multiple control techniques into a scientifically sound management approach. This is not an easy task, but the only alternatives are recurrent crop losses in combination with environmental degradation.

**Keywords:** biological control, crop protection, cultural control, insecticides, integrated pest management, *Leptinotarsa decemlineata*, life history, potato

## CONTENTS

PEST STATUS .....	10
LIFE HISTORY .....	11
CHEMICAL CONTROL .....	12
CULTURAL CONTROL .....	13
PLANT RESISTANCE .....	13
BIOLOGICAL CONTROL .....	13
OTHER CONTROL METHODS .....	14
IMPORTANCE OF AN INTEGRATED APPROACH .....	14
FUTURE DIRECTIONS .....	15
EPILOGUE .....	15
ACKNOWLEDGEMENTS .....	15
REFERENCES .....	15

## PEST STATUS

The Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) is native to Mexico. Wild populations feed mostly on buffalobur, *Solanum rostratum*, *Solanum angustifolium*, and several related species in the family Solanaceae (Casagrande 1987). It was first collected in the U.S. in 1811 by Thomas Nuttall. Additional collections were subsequently made in 1819-1820 near the Iowa-Nebraska border by Thomas Say, who later described the species as *Doryphora decemlineata* (Casagrande 1985; Jacques 1988).

Although the Colorado potato beetle was initially exposed to potatoes, *Solanum tuberosum*, before 1820 (Casagrande 1985), the first major outbreak did not occur until 1859. Severe damage was observed on potato fields about 100 miles west of Omaha, Nebraska (Jacques 1988). Following the outbreak, eastward expansion of the beetles' geographic range was very rapid, with beetles reaching the Atlantic coast of the U.S. and Canada in 15 years (Casa-

grande 1987). Westward expansion was somewhat slower, limited in part by scarcity of potatoes (Riley 1877). The first serious damage to potatoes in Colorado was reported in 1874 (Riley 1875). However, ten years earlier Walsh (1865) observed a considerable beetle population feeding on *S. rostratum* in Colorado, eventually resulting in Colorado being incorporated into the generally accepted common name; Colorado potato beetle (Jacques 1988).

The first European population of Colorado potato beetles was discovered in Germany and subsequently eradicated in 1877. Quarantine measures and eradication campaigns were largely successful in keeping the pest out of Europe for the next 45 years until 1922, when self-propagating populations were finally established in France (Feytaud 1950). By the end of the 20<sup>th</sup> century, the pest had become a problem all over Europe, Asia Minor, Iran, Central Asia, and western China (Jolivet 1991; Weber 2003). Its current range covers about 16 million km<sup>2</sup> in North America, Europe, and Asia and continues to expand (Weber 2003). Potentially, the beetle could spread to temperate areas of

East Asia, Indian subcontinent, South America, Africa, New Zealand, and Australia (Vlasova 1978; Worner 1988; Jolivet 1991; Weber 2003).

Currently, the Colorado potato beetle is considered to be the most important insect defoliator of potatoes. Both adults and larvae devour entire leaves without discriminating among leaf tissues. Approximately 40 cm<sup>2</sup> of potato leaves are consumed by a single beetle during the larval stage (Ferro *et al.* 1985; Logan *et al.* 1985), and close to 10 cm<sup>2</sup> of foliage per day are consumed during the adult stage (Ferro *et al.* 1985). Once the foliage is gone, beetles can feed on stems and exposed tubers, though the latter two constitute a suboptimal diet. Colorado potato beetle is very prolific, with one female laying 300-800 eggs (Harcourt 1971). If left uncontrolled, the beetles can completely destroy potato crops.

## LIFE HISTORY

Colorado potato beetles are a multivoltine species with a facultative overwintering diapause that takes place at the adult stage and is induced by a short-day photoperiod (de Kort 1990). After diapause initiation, the beetles either burrow into the soil in the field, or move towards field edges by flight and walking, presumably orienting themselves towards tall vegetation common in hedgerows (Voss and Ferro 1990a; Weber and Ferro 1993; French *et al.* 1993). Upon arrival to overwintering sites, pre-diapause migrants immediately burrow into the soil to diapause (Voss and Ferro 1990b). Flight muscles of the diapausing beetles undergo significant degeneration (Stegwee *et al.* 1963).

Refractory phase of the diapause, during which the beetles do not react to changes in environmental conditions, lasts for approximately 3 months. Diapause is then terminated by temperatures above +10°C (de Kort 1990). The beetles usually accumulate 50-250 degree-days (DD, 10°C base temperature) before they appear on the soil surface (Ferro *et al.* 1999). Males and females exit their diapause simultaneously (Ferro *et al.* 1999). Based on the results of mostly laboratory research, the beetles appear to use both visual (de Wilde *et al.* 1976; Zehnder and Speese 1987) and olfactory (Visser and Nielsen 1977; Visser and Ave 1978; Thierry and Visser 1986; Landolt *et al.* 1999; Dickens 2000) cues to orient towards host vegetation. However, their ability to actively search and find hosts over long distances in the field is somewhat uncertain (Boiteau *et al.* 2003).

In some beetles, diapause may last for two or more years (Isely 1935; Trouvelot 1936; Wegorek 1957a, 1957b; Ushatinskaya 1962, 1966). The incidence of an extended diapause varies among beetle populations and may depend in part on environmental conditions. In Washington State, 16-21% of overwintering adults emerged after two winters, and up to 2% emerged after three winters (Biever and Chauvin 1990). In upstate New York, 0-7.2% of the beetles spent more than one winter in dormancy (Tauber and Tauber 2002). In western Ukraine, 0.4-6.5% of beetles overwintering in sandy soils remained dormant for two years, but all beetles overwintering in clay soils emerged after the first winter (Ushatinskaya 1962, 1966).

Although overwintered adults usually die during the second summer of their lives, up to 25% of the overwintered population may enter the second diapause (Isely 1935; de Wilde 1962; Jermy and Saringer 1955; Minder and Petrova 1966). However, overwintering and spring mortality among such beetles is very high (Isely 1935; Minder and Petrova 1966), and their contribution to population maintenance and growth is likely to be generally insignificant.

Dispersal and migration are tightly incorporated in the life cycle of the Colorado potato beetle. Colorado potato beetles are capable of moving both by flight and by walking, and can easily fly several kilometers (Weber and Ferro 1994a). Incursions across the Baltic Sea to Scandinavia imply that given favorable wind speed and direction, Colorado potato beetles can fly more than 100 km (Wiktelius 1981). Thus, flight is very important for the Colorado

potato beetle to be able to colonize new habitats and escape from hostile environments, as well as for gene flow between isolated populations. Walking is relatively less important, because beetles are able to walk only several hundred meters at a maximum speed of about 1 cm/s (Ng and Lashomb 1983).

Beetle flight initiation is strongly related to air temperature, starting at 15°C and reaching 100% for unfed overwintered adults at 20°C (Caprio and Grafius 1990). The Colorado potato beetle has three distinct types of flight (Voss and Ferro 1990a). The first is short-range, local, or trivial flight. This is a low-altitude flight with frequent turning which occurs strictly within the host habitat. It may serve to distribute eggs within a field, or for mate-finding. For both sexes, this flight serves a short-range "bet-hedging" function, and allows the beetle to distribute its offspring in both space and time (Solbreck 1978). The second type of flight is long-range or migratory flight. This is a straight-line, often downwind flight over the distances of several hundred meters or more, used for colonization of new areas. It is not necessarily connected with the immediate search for a new host habitat as shown by Caprio and Grafius (1990), who observed beetles flying over potato fields obviously suitable for colonization. The third type of flight that can be distinguished is diapause flight. It is a low altitude, directed flight, which often starts with a spiraling ascent from the crop to an approximate 5 m altitude, and a subsequent orientation towards tall vegetation. The beetles fly to wooded sites or uncultivated field areas where they immediately burrow into the soil to diapause (Voss and Ferro 1990a).

Both sexes perform all three types of flight patterns (Weber and Ferro 1994a). Zehnder and Speese (1987) reported a 50:50 sex ratio of beetles caught in windowpane traps throughout the growing season. However, Voss and Ferro (1990b) showed that significantly more males than females engaged in local flight activity, possibly in search of mates. Hough-Goldstein and Whalen (1996) reported that almost twice as many overwintered males immigrated into fields by flight compared to overwintered females, though a portion of their data probably reflected local flight activity, especially later in the season (Voss and Ferro 1990a; Hough-Goldstein and Whalen 1996). Additionally, Weber and Ferro (1994b) found that overwintered males departed from a non-host habitat more readily than females, but were more likely than females to remain in a potato field.

Colorado potato beetle is a polygamous species, with both males and females performing multiple copulations with different partners (Szentesi 1985). Behavioral activities during courtship form a loose pattern with limited sequential order. Males guard females following the copulation, and display aggressive behavior towards other males (Szentesi 1985). However, duration of such guarding is usually rather short (personal observations). Between 5 and 20% of all copulations do not result in sperm transfer (Thibout 1982). Sexually mature females produce an airborne sex pheromone, which acts as a long-range attractant for males (Edwards and Seabrook 1997). In addition, there is a difference between the sexes in the composition of cuticular hydrocarbons (Dubis *et al.* 1987), which might be perceived by contact chemoreception and play an important role in sex recognition (Jermy and Butt 1991). Male beetles also produce an airborne pheromone, but it is attractive to both sexes and should be classified as an aggregation pheromone (Dickens *et al.* 2002).

Boiteau (1988a) determined that at least three matings are required to completely fill the female's spermatheca and argued that multiple matings are necessary for the females to realize their full reproductive potential. Conversely, neither sperm number nor fecundity was positively correlated with number of matings in the study by Orsetti and Rutowski (2003). Furthermore, there was a significant decrease in hatch rate with an increase in matings, demonstrating a cost of polyandry (Orsetti and Rutowski 2003). Further investigations are needed to address this apparent contradiction.

When a summer generation female mates with two different males, the first male fertilizes 28-48% of the eggs, indicating incomplete sperm precedence (Boiteau 1988a; Alyokhin and Ferro 1999a; Roderick *et al.* 2003). Post-diapause females can lay eggs utilizing sperm from the pre-diapause mating from the previous fall; however, the number of offspring produced by such females is lower compared to spring-mated females (Ferro *et al.* 1991; Baker *et al.* 2005). Therefore, beetles usually mate again after diapause termination in the spring. Mating starts before beetles leave for the host habitat, with at least half of the population mating within the overwintering sites (Ferro *et al.* 1999). Sperm from spring mating takes complete precedence over overwintered sperm from the previous year's mating (Baker *et al.* 2005).

Mating status affects beetle flight. Gravid Colorado potato beetle females engage in a considerable amount of flight activity (Ferro *et al.* 1999; Alyokhin and Ferro 1999b), allowing them to distribute eggs within and between host habitats. However, they fly significantly less than unmated females (Alyokhin and Ferro 1999b), probably because both migration and reproduction are physiologically demanding for females, and these two processes are known to interfere with each other (Rankin *et al.* 1986), or because increased mobility improves their chances to find a mate. In contrast, mated males increase their flight activity, probably to maximize the number of copulations with different mates (Alyokhin and Ferro 1999b) and to increase genetic diversity of their offspring (McCauley and Reilly 1984). Unlike flight of the summer-generation beetles, flight of the post-diapause beetles is not affected by their mating status (Ferro *et al.* 1999).

Females do not usually start ovipositing until they accumulate at least 51 DD since emergence from pupae (Alyokhin and Ferro 1999b). Depending on temperature, development from egg to adult takes between 14-56 days (de Wilde 1948; Ferro *et al.* 1985; Logan *et al.* 1985). The fastest development occurs between 25-32°C and appears to differ among populations of different geographic origins. The larvae have a tendency to rest and feed on the upper surface of leaves at low ambient temperatures, probably increasing their exposure to solar radiation (May 1981). As ambient temperatures increase, they tend to move under leaves (Lactin and Holliday 1994) or to the inner part of the potato canopy (May 1981). Because of this behavioral thermoregulation, their temperatures are more optimal for physiological development than air temperatures to which they are immediately exposed to (May 1981). Pupation takes place in soil near plants where the larvae have completed their development at an average depth between 5-12 cm (Feytaud 1938).

Overall, a complex and diverse life history makes the Colorado potato beetle a challenging pest to control. This insect employs "bet-hedging" reproductive strategies, distributing its offspring in both space (within and between fields) and time (within and between years) (Solbreck 1978; Voss and Ferro 1990a). As a result, targeting its populations with insecticide applications and other control methods is a rather difficult task.

## CHEMICAL CONTROL

Search for chemicals capable of controlling the Colorado potato beetle started in 1864 (Gauthier *et al.* 1981) and continues until the present day. The first major breakthrough came in 1871, when Riley (1871) determined that recently discovered insecticide Paris green (copper[II]-acetoarsenite) was highly efficient against the Colorado potato beetle. This chemical was quickly adopted by commercial growers, and was later supplemented by other arsenicals, mostly lead arsenate and calcium arsenate (Brown 1951; Gauthier *et al.* 1981; Casagrande 1987). DDT was first tested against the Colorado potato beetle in 1939, and became the chemical of choice for most potato farmers in mid-1940s (Hitchner 1952; Gauthier *et al.* 1981). This was quickly followed by

cyclodiene organochlorines, organophosphates, carbamates, and other organic insecticides (Casagrande 1987). Currently, chemical control still remains the foundation of the Colorado potato beetle management on commercial potato farms.

A wide variety of secondary plant compounds deter feeding by Colorado potato beetle adults and larvae in laboratory tests (e.g., Hsiao and Fraenkel 1968; Drummond and Casagrande 1985; Alford *et al.* 1987; Hough-Goldstein 1990; Szczepanik *et al.* 2005). In field tests, neem seed extract containing azadiractin suppressed populations of Colorado potato beetle larvae and adults, resulting in a decrease of defoliation on test plots (Zehnder and Warthen 1988). Similarly, application of a crude limonoid extract containing 78% limonin and 18% nomilin resulted in as much as a 75% reduction in seasonal egg density and as much as 41% reduction in seasonal adult incidence (Murray *et al.* 1995). Since secondary compounds may both deter feeding and act as insecticides (Zehnder and Warthen 1988; Murray *et al.* 1995), it was not clear which of those two effects was responsible for decreasing beetle populations. None of these plant-derived chemicals are as lethal to the Colorado potato beetles as synthetic insecticides, and their use in commercial production is very limited.

Unfortunately, Colorado potato beetles proved to have remarkable adaptability to a wide variety of poisons. DDT failure in 1952 (Quinton 1955) was the first reported case of this pest's resistance to synthetic organic insecticide. Resistance to dieldrin was observed in 1958, quickly followed by resistance to other chlorinated hydrocarbons (Hofmaster *et al.* 1967). Since then, failures have been reported for most major classes of insecticides. Not every beetle population is resistant to all compounds that have been observed to fail against this pest. However, both cross-resistance and multiple resistance are common within the tested populations (Harris and Svec 1981; Ioannidis *et al.* 1991; Heim *et al.* 1992; Stewart *et al.* 1997; Alyokhin *et al.* 2006; Mota-Sanchez *et al.* 2006; Alyokhin *et al.* 2007).

Resistance mechanisms may be highly diverse even within a relatively narrow geographical area (Ioannidis *et al.* 1991) and include enhanced metabolism involving esterase, carboxylesterases and monooxygenases, target site insensitivity, as well as reduced insecticide penetration and increased excretion (Rose and Brindley 1985; Argentine *et al.* 1989; Ioannidis *et al.* 1991; Ioannidis *et al.* 1992; Wierenga and Hollingworth 1994; Anspaugh *et al.* 1995; Zhu *et al.* 1996; Lee and Clark 1998; Clark *et al.* 2001). There is also some evidence of behavioral resistance by avoidance of treated foliage (Hoy and Head 1995; Alyokhin and Ferro 1999c).

Insecticide resistance is most prevalent in the Northeastern United States (Forgash 1985; Whalon and Ferro 1998). This could be at least partially explained by intensive chemical use in this area, insufficient crop rotation, favorable climate (Casagrande 1987) and possibly hybridization between two genetically distinct beetle races (Hsiao 1985). However, resistant populations are found across the entire distribution range (Hofmaster *et al.* 1967; Forgash 1985; Boiteau 1988b; Ioannidis *et al.* 1991; Heim *et al.* 1992; Stewart *et al.* 1997; Noronha *et al.* 2001; Stankovic *et al.* 2004; Pourmirza 2005; Benkovskaya *et al.* 2006; Mota-Sanchez *et al.* 2006; Mohammadi Sharif *et al.* 2007; Sukhoruchenko and Dolzhenko 2008).

Beetle propensity to develop insecticide resistance may be caused by an unfortunate confluence of several factors. First, to be able to feed on plants in the family Solanaceae, which have high concentrations of toxic glycoalkaloids in their foliage, this species had to evolve physiological capabilities to detoxify or tolerate poison (Ferro 1993; Bishop and Grafius 1996). This created pre-adaptations to being exposed to man-made toxins. Secondly, high beetle fecundity increases the probability of random mutations. It also guarantees the rapid increase in numbers of resistant mutants once such mutation has occurred (Bishop and Grafius 1996). Thirdly, narrow host range further increases selection pressure by reducing the size of an unstructured refuge where

susceptible genotypes may escape exposure to chemicals (Bishop and Grafius 1996; Whalon and Ferro 1998).

## CULTURAL CONTROL

Colorado potato beetle populations can be reduced through the use of relatively common cultural practices, with crop rotation being the most effective and easily implemented approach. It had been first recommended for managing this pest as early as 1872 (Bethune 1872). In the rotated field, peak density of the beetle egg masses could be less than 10% of that of the non-rotated field (Lashomb and Ng 1984). Wright (1984) reported that when potatoes were planted following a non-host grain crop (rye or wheat), early season adult densities were reduced by 95.8%. Unfortunately, high beetle mobility necessitates a separation of 0.3-0.9 km between the rotated fields to maximize efficiency of this technique (Weisz *et al.* 1994; Hough-Goldstein and Whalen 1996; Weisz *et al.* 1996; Sexson and Wyman 2005). Still, crop rotation remains the single most important cultural control against the Colorado potato beetle.

Manipulating planting time may help to suppress the second-generation larval populations. Because summer-generation adults emerge later in the season on the late-planted crop, the short-day photoperiod stimulates reproductive diapause, largely eliminating the second-generation larval impact on the crop. Early planting also eliminates the second generation larvae, in this case because the crop is already being removed at the time of their emergence (Weber and Ferro 1994a). However, agronomic and economic considerations often constrain the window of time when planting is possible, reducing the feasibility of these techniques.

Planting trap crops that attract beetles away from the main crop may be effective in intercepting overwintered beetles colonizing a field in the spring (Weber and Ferro 1994a), as well as the beetles moving away from senescing potatoes late in the season (Hoy *et al.* 1996). Chausov (1976) reported that the number of insecticide applications necessary to protect 200-500 ha potato fields was reduced by half after planting 2-5 ha of a trap crop. Hunt and Whitfield (1996) used perimeter potato trap rows to protect plots planted to tomatoes, which is a less preferred beetle host. Tomato yield in trap-cropped plots was 61-87% higher than in control plots. Martel *et al.* (2005) used synthetic kairomone previously shown to be attractive to the Colorado potato beetles (Dickens 2000) to further enhance effectiveness of potato trap crop. Male-produced aggregation pheromone (Dickens *et al.* 2002) may also be potentially used for a similar behavioral manipulation, but its field testing (Kuhar *et al.* 2006) has been somewhat inconclusive. Unfortunately, design and implementation of trap crops requires a substantial commitment of grower time. Therefore, it is rarely used on commercial farms.

Mulching may increase the time required by the beetles to find potatoes (Ng and Lashomb 1983), increase the proportion of beetles leaving the area by flight (Weber *et al.* 1994), and increase predation on eggs and larvae (Brust 1994). Larval populations of the beetle were significantly reduced in straw-mulched plots of potato (Stoner 1993) and eggplant (Stoner 1997). A peak of the small (1<sup>st</sup>-2<sup>nd</sup> instar) larval populations was observed 1-2 weeks later on the mulched potato fields than on the unmulched ones (Stoner 1993). A 6-10 cm layer of wheat straw produced 2.5-5 fold decrease in potato defoliation (Zehnder and Hough-Goldstein 1990; Brust 1994). Although not feasible in large-scale production, mulching can be very useful on small fields and garden plots.

## PLANT RESISTANCE

Potatoes can tolerate 30-40% defoliation during early growth stages, 10-60% defoliation during middle growth stages, and up to 100% defoliation late in the season without noticeable yield reduction (Hare 1980; Cranshaw and Rad-

cliffe 1980; Ferro *et al.* 1983; Shields and Wyman 1984; Zehnder and Evanylo 1988). However, voracious beetle appetite combined with high rates of population growth often result in defoliation exceeding tolerable levels. Furthermore, most commercial growers consider defoliation unacceptable even when presented with scientific evidence of the contrary. Therefore, development of resistant varieties remains to be an important task.

Host plant resistance has been considered an option for the Colorado potato beetle control since the 19th century (Saunders and Reed 1871). Breeding attempts focused mostly on developing cultivars with high levels of resistance to beetle feeding (Fisher *et al.* 2002). Approaches included incorporation of germplasm from other species of *Solanum* through cross-pollination (Plaisted *et al.* 1992; Lorenzen and Balbyshev 1997) or electrofusion of protoplasts (Cheng *et al.* 1995), transgenic insertion of *Bacillus thuringiensis* genes (Ebora and Sticklen 1997), and a combination of several of these methods (Coombs *et al.* 2002, 2003; Cooper *et al.* 2004). Unfortunately, potato breeding is complicated by tetraploidy in *S. tuberosum* (Grafius and Douches 2008). Despite all efforts, no commercial cultivars resistant to the Colorado potato beetles are currently available on the market (Flanders *et al.* 1992; Fisher *et al.* 2002; Grafius and Douches 2008).

Potatoes were among the first successful transgenic crop plants (An *et al.* 1986). Genetically modified potatoes expressing *Bacillus thuringiensis* delta-endotoxin that is toxic to the Colorado potato beetle were registered and sold in the U.S. from 1995-2000. Although well-received at first, they were discontinued after only five years of use because of consumer concerns about genetically modified crops, grower concerns of their agronomic performance compared to non-transformed varieties, and competition with a new and highly efficient insecticide imidacloprid (Grafius and Douches 2008).

Certain soil amendment practices may make potato plants partially resistant to the Colorado potato beetle. In the study by Alyokhin *et al.* (2005), beetle densities were lower in plots receiving manure soil amendments in combination with reduced amounts of synthetic fertilizers compared to plots receiving full rates of synthetic fertilizers, but no manure. Unlike beetle abundance, plant height and canopy cover were comparable between plots receiving manure and synthetic fertilizer. Furthermore, tuber yields were higher in manure-amended plots. Thus, the difference in beetle density was unlikely to be explained simply by poor plant vigor in the absence of synthetic fertilizers. Subsequent field-cage and laboratory experiments (Alyokhin and Atlihan 2005) confirmed that potato plants grown in manure-amended soil were indeed inferior Colorado potato beetle hosts compared to plants grown in synthetically fertilized soil. The observed negative effects were broad in scope. Female fecundity was lower in field cages set up on manure-amended plots early in the season, although it later became comparable between the treatments. Fewer larvae survived past the first instar, and development of immature stages was slowed down on manure-amended plots. In the laboratory, first instars also consumed less foliage from plants grown in manure-amended soils (Alyokhin and Atlihan 2005).

## BIOLOGICAL CONTROL

A number of arthropod species attack the Colorado potato beetle, and some of them show potential as biological control agents (Hough-Goldstein *et al.* 1993). Predaceous stink bugs *Perillus bioculatus* and *Podisus maculiventris* (Hemiptera: Pentatomidae) have been shown to have a significant impact on the Colorado potato beetle by feeding on its larvae. Inundative releases of these predators suppressed beetle density by 62% (Biever and Chauvin 1992), reduced defoliation by 86% (Hough-Goldstein and McPherson 1996), and increased potato yields by 65% (Biever and Chauvin 1992) over the untreated control. The lady beetle

*Coleomegilla maculata* (Coleoptera: Coccinellidae) preys on eggs and small larvae (Grodén *et al.* 1990; Hazzard *et al.* 1991). Total mortality of eggs from the *C. maculata* predation can reach 37.8% for the first generation and 58.1% for the second generation (Hazzard *et al.* 1991). Ground beetle *Lebia grandis* (Coleoptera: Carabidae) feeds on the Colorado potato beetle eggs and larvae as an adult, and develops ectoparasitically on the Colorado potato beetle pupae and prepupae at its larval stage (Chaboussou 1939; Weber *et al.* 2006). The parasitic wasp *Edovum puttleri* (Hemiptera: Eulophidae) that is native to South America and Mexico was found to parasitise 71-91% of Colorado potato beetle egg masses on eggplant, killing 67-79% of the eggs per mass (Lashomb *et al.* 1987). As a result, it was very effective for control of Colorado beetle in eggplant crops in New Jersey for several years. The level of parasitism is somewhat lower in potatoes, rarely exceeding 50% (Ruberson *et al.* 1991; van Driesche *et al.* 1991). Performance of *E. puttleri* in the field can be further improved by the supplementary use of an artificial carbohydrate source (Idoine and Ferro 1990). The parasitic fly *Myopharus doryphorae* (Diptera: Tachnidae) has been reported to cause 30-70% parasitism of the second beetle generation in the field (Tamaki *et al.* 1983; Horton and Capinera 1987; Lopez *et al.* 1993).

In addition to the discussed natural enemies, there is a number of other species, mainly generalist predators, which occasionally feed on the Colorado potato beetle. Fourteen species of ground beetles, three species of lady beetles, and a spider, *Xysticus kochi*, are known to feed on the Colorado potato beetle in the former Soviet Union (Sorokin 1976). Eight species of *Lebia* and five other ground beetle species attack this pest in Mexico (Logan 1990). The ground beetle *Pterostichus chalcites* has been observed feeding on the Colorado potato beetles in Delaware (Heimpel and Hough-Goldstein 1992), and the phalangid *Phalangium opilio* preys on the beetle's eggs and small larvae (Drummond *et al.* 1990).

Entomopathogenic nematodes (Rhabditidae: Steinernematidae and Heterorhabditidae) are obligatory generalist insect parasites with a free-living stage, known as the infective juvenile, that seeks a suitable insect host in the soil. Augmentative releases of nematodes may cause up to 100% mortality of Colorado potato beetle late instars and pupae in laboratory and small-scale field experiments (Toba *et al.* 1983; Berry *et al.* 1997). However, control efficacy is highly variable among the studies, and depends on nematode species and strains, environmental conditions, and release rates (MacVean *et al.* 1982; Toba *et al.* 1983; Wright *et al.* 1987; Cantelo and Nickle 1992; Berry *et al.* 1997). Overall, Colorado potato beetle appears to have lower susceptibility to nematode infection compared to many other insect species due, in part, to its effective immune response through hemocytic encapsulation of penetrating infective juveniles (Thurston *et al.* 1994).

*Beauveria bassiana* (Hyphomycetes) is a generalist entomopathogenic fungus that is known to reduce Colorado potato beetle densities in potato fields. Commercial formulations of this fungus can be applied using a regular pesticide sprayer and have some use in organic agriculture. They have been shown to reduce beetle populations by up to 75% (Cantwell *et al.* 1986), although control is usually less efficient compared to conventional insecticides (Campbell *et al.* 1985; Hajek *et al.* 1987). Most mortality is the result of foliar sprays, but the horizontal infection from sporulating cadavers to healthy fourth instars going to the soil for pupation may further diminish beetle populations (Long *et al.* 2000).

Although use of natural enemies is a valuable option for Colorado potato beetle control, usually they are not able to reduce beetle densities below the economically damaging levels and have to be used in combination with other control techniques (Ferro 1994). Unfortunately, none of the known biological control agents are capable of removing enough beetles to compensate for their high reproductive output. Augmenting natural enemy populations to match

that of the Colorado potato beetle is usually not practical because of the high rearing and handling costs (Ferro 1994).

## OTHER CONTROL METHODS

Digging plastic-lined trenches along a field border will intercept migrating Colorado potato beetles. Compared to control fields without trenches, surrounding fields with such a barrier reduced the population of immigrating overwintered adults by 47-49%, and the population of summer-generation adults by 40-90% (Boiteau *et al.* 1994). Up to 95% of captured beetles are retained in the ditch (Misener *et al.* 1993).

Beetle diapause habitat can be manipulated to enhance its overwintering mortality. In the experiment of Milner *et al.* (1992), wheat straw mulch was applied to the overwintering sites in the fall, and then removed together with the layer of snow covering it in January. This procedure rapidly depressed soil temperatures, and led to a significantly lower beetle survival rate (approximately 7% at disturbed habitats vs. approximately 26% at the undisturbed habitats).

Heat treatment, usually employing propane flammers, can be used to control Colorado potato beetles, particularly adults colonizing potato crops early in the season. Beetle mortality following exposure to high temperatures ranges between 30-100% (Khelifi *et al.* 2007). Surviving beetles often suffer from the degeneration of leg muscles and antennae muscles, which impairs their movement and ability to feed (Pelletier *et al.* 1995). However, the window of opportunity for using this approach is fairly narrow because potato plants above 10 cm in height also sustain serious damage (Khelifi *et al.* 2007).

The pneumatic control technique consists of using an artificially created air current to dislodge the beetles from potato plants. Dislodged Colorado potato beetles are then sucked inside the tractor-mounted machine, which essentially function as a giant vacuum cleaner. In the study by Boiteau *et al.* (1992), the vacuum collector removed 40% of small larvae, 27% of large larvae, and 48% of adults from the foliage. Similarly, Lacasse *et al.* (1998) reported on a 24% capture of the first and second instars, 58% of the third instars, and 61% of the fourth instars. Alternatively, the dislodged beetles could be allowed to fall on the ground between rows of potato plants and immediately burned by a propane burner. Burning dislodged beetles results in more efficient control compared to using the vacuum cleaner approach because the beetles could no longer survive by falling on the ground and waiting until the vacuum collector passed by (Khelifi *et al.* 2007). Using this combined technique, Laguë *et al.* (1999) achieved a better control efficiency compared to insecticide-treated plots.

## IMPORTANCE OF AN INTEGRATED APPROACH

Casagrande (1987) described the long history of the Colorado potato beetle control as "135 years of mismanagement." Unfortunately, 20 years later the situation is no different. Growers are still relying almost exclusively on insecticides for controlling this pest. Despite much talk about its benefits, integrated pest management (IPM) is still far from being universally adopted by commercial potato growers. Currently, insect pest control on potatoes, particularly in North America, is largely based on using the chloronicotinyl insecticide imidacloprid. Most potato growers apply imidacloprid in furrow at planting or directly to seed tubers. Relatively few farmers practice even first level chemically based IPM by scouting their fields and applying foliar formulation of imidacloprid when insect populations exceed economic threshold levels. Virtually no one practices more advanced forms of IPM on a large commercial scale.

Reliance on a single control technique is a dangerous case of "putting all eggs into one basket," with the fallacy of such an approach being repeatedly and expensively demonstrated throughout the history of pest control. Therefore,

diversification of a pest management “portfolio” is an important task facing commercial potato growers. However, simple replacement of imidacloprid by some other chemical (or even a non-chemical control method) will never provide a lasting solution to pest control in potato fields. Development of a “silver-bullet” non-chemical control method is no more likely than the development of a “silver-bullet” insecticide. For example, in the study by Groden and Casagrande (1986) oviposition and survival rates on resistant wild potato species *S. berthaultii* became comparable to those on susceptible *S. tuberosum* after only two generations of selection. Pelletier and Smilowitz (1991) and França *et al.* (1994) confirmed existence of genetic variability in several performance attributes for adaptation to *S. berthaultii*, although França *et al.* (1994) argued that adaptation is not always going to be as rapid as reported by Groden and Casagrande (1986). Similarly, Cantelo *et al.* (1987) observed gradual adaptation to feeding on another resistant wild potato, *Solanum chacoense*, after 12 months of selection. In another example, efficiency of annual crop rotation for reducing field colonization by overwintering adults is diminished when a portion of the population remains in extended diapause for two or more years (Whalon and Ferro 1998). Selection towards a higher proportion of populations entering multiyear diapause in rotated fields has been reported for another leaf beetle, the northern corn rootworm (*Diabrotica barberi*) (Levine *et al.* 1992). Clearly, it is essential that not only do we have a variety of techniques available for suppressing pest populations, but also that these techniques are actually integrated together into a unified multiple attack strategy.

## FUTURE DIRECTIONS

Chemical control is likely to remain the foundation of the Colorado potato beetle management for the foreseeable future. However, the general trend in production agriculture is towards gradual decrease in indiscriminate use of insecticides. Development and registration of new insecticides is an increasingly complicated and costly process. At the same time, older chemistries are being lost to resistance or removed from the market because of environmental concerns. Insecticide purchases are becoming increasingly costly, and frequent applications create bad publicity. As a result, there is an increasing tendency towards adopting more sustainable approaches that are based on understanding pest biology and combining chemical and non-chemical control techniques.

Integrated pest management is particularly important in dealing with the Colorado potato beetle because of its impressive ability to develop insecticide resistance. At the end of the era of abundant and cheap insecticides, insecticide susceptibility in pest populations should be treated as a valuable genetic resource (Hueth and Regev 1974; Bourguet *et al.* 2005). Reducing insecticidal pressure on pest populations is the most commonly proposed strategy to its preservation (McGaughey and Whalon 1992; Tabashnik 1994; Caprio 1998, Carrière and Tabashnik 2001). Replacing some of the sprays with non-chemical control techniques is the easiest way to implement this strategy. Therefore, the use of cultural control, particularly crop rotation specifically targeting the Colorado potato beetle, is likely to become more wide-spread in the near future.

Availability of resistant cultivars will greatly facilitate beetle management in commercial potato production. Unfortunately, after more than a century worth of breeding efforts, no resistant variety has been discovered. Although a number of resistance factors have been identified in wild potato species, their introgression into *S. tuberosum* has resulted in the transfer of undesirable growth and tuber traits typical of the wild species (Tingey and Yencho 1994; Grafius and Douches 2008). Commercial acceptability of a new variety is determined by numerous characteristics, including maturity, disease resistance, dormancy, storage quality, appearance, and cooking quality. Maintaining the above

characteristics while incorporating a new insect resistance trait is a difficult task, although certain progress has been made (Tingey and Yencho 1994). It is not likely that a beetle-resistant variety will appear on the market any time soon.

Using genetic engineering provides a shortcut towards developing a commercially viable potato variety. However, current unwillingness of Japanese and European markets to accept them because of perceived threats to human health and the environment provides a major obstacle to the development of this technology. As a result, it is not a significant part of most potato breeding programs (Grafius and Douches 2008). If genetically modified food crops become more acceptable to a general consumer, insect-protected potatoes are likely to make a comeback. Their reappearance is likely to happen first in Asia (perhaps excluding Japan), Eastern Europe, Africa, and then in North America because public mistrust of transgenic crops is generally smaller in these areas.

Biological control of the Colorado potato beetle is likely to remain a major challenge. Up-to-date, foreign exploration has failed to produce an effective biological control agent that would become established in major potato-growing areas and bring Colorado potato beetle populations under control. The latest South American expedition exploring for new arthropod natural enemies also returned pretty much empty-handed (O’Neil *et al.* 2005). A new bacterium species, *Chromobacterium subtsugae*, has been found to be toxic to the Colorado potato beetle (Martin *et al.* 2004). However, its field efficiency as a biological control agent still remains to be determined. All in all, chances of finding a new natural enemy capable of beetle control look increasingly dim. Augmentation of the known agents can sometimes suppress beetle populations below economically damaging levels. However, it is expensive and is not usually feasible in a low-value crop like potatoes (Ferro 1994). On the bright side, gradual replacement of broad-spectrum insecticides by more selective compounds is currently underway on commercial farms, allowing conservation of existing natural enemies (mostly generalist predators). Although usually incapable of completely preventing beetle damage, these natural enemies nevertheless contribute to reducing beetle numbers. A more judicious use of pesticides is likely to increase their role in controlling the Colorado potato beetles.

## EPILOGUE

Over the years, the Colorado potato beetle has proven to be an extremely difficult pest to manage. A life history that is well-suited to agricultural habitats, together with a remarkable adaptability, challenges many generations of potato growers. Despite all scientific and technological advances, the beetle remains a major threat to potato production. Unfortunately, there will most likely be no “silver bullet” solution to the problem created by this insect. The only sustainable way to protect potato crops is to integrate multiple control techniques into a scientifically sound management approach. This is not an easy task, but the only alternatives are recurrent crop losses in combination with environmental degradation.

## ACKNOWLEDGEMENTS

Ryan Guillemette helped with editing and proofreading this manuscript.

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