Population Dynamics of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae): Measuring the Effects of Methyl Salicylate and Predator Recruitment in Potato[1]

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Abstract Methyl salicylate is an organic compound produced by potato and other plants in response to insect herbivory. In other studies the compound has been shown to be attractive to numerous predatory arthropods. Experiments were conducted in Virginia to evaluate methyl salicylate lures for attracting natural enemies in potato plots to manage populations of *Leptinotarsa decemlineata* (Say). Abundance of predatory arthropods and *L. decemlineata* life stages were measured in plots treated with and without 90 day, 5 g slow-release packets of methyl salicylate (95% methyl salicylate [Predalure™]). Mortality of *L. decemlineata* eggs and small larvae was estimated by calculating the difference in numbers of individuals recruited to subsequent stages using a stage-specific life table approach. Methyl salicylate treatment had no impact on predator recruitment or mortality of *L. decemlineata* eggs and small larvae, compared with nontreated plots. Cumulative mortality of *L. decemlineata* ranged from 87.9 - 89.2% in 2010 and from 81.9 - 94.8% in 2011. The dominant arthropod predators observed on potatoes included *Hippodamia convergens* Guerin-Meneville, *Coccinella septempunctata* L., and *Perillus bioculatus* (F.).

Key Words *Leptinotarsa decemlineata*, potato, population dynamics, methyl salicylate, natural enemies

Methyl salicylate, also referred to as oil of wintergreen, is an herbivore-induced plant volatile compound. Several studies have shown that methyl salicylate has the potential to attract beneficial insects such as anthocorids (Drukker et al. 2000), geocorids, syrphids, chrysopids, and coccinellids (James 2003, James and Price 2004), as well as predatory mites (Dicke et al. 1990). This has led to the development of a commercially-available synthetic methyl salicylate lure, Predalure™ (AgBio Inc., Westminster, CO), to enhance biological control in gardens and crops by aiding in the recruitment of natural enemies. Methyl salicylate also has been shown to have a repellent effect on pest insects such as aphids (Glinwood and Pettersson 2000, Mallinger et al. 2011). Dickens (2000, 2006) found that methyl salicylate is one compound of a blend of potato plant volatiles that is attractive to Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). Thus, it is not known what effect Predalure could have in potato IPM systems.

Leptinotarsa decemlineata is one of the most important insect pests of potato (*Solanum tuberosum* L.) in North America and Europe (Hare 1990, Alyokhin 2009).

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Uncontrolled populations can completely defoliate potato potentially leading to a total loss of tuber production (Hare 1980). Widespread insecticide resistance problems over the past 50 years have created a strong interest in the development of integrated pest management approaches for this insect (Cassagrande 1987, Alyokhin et al. 2008, Alyokhin 2009).

Leptinotarsa decemlineata has many important natural enemies that can reduce population levels (Weber 2013). These include the predaceous ground beetle *Lebia grandis* Henz (Coleoptera: Carabidae) and several species of Coccinellidae as well as a few parasitoids including *Edovum puttleri* Grissell. Research has shown that mortality of *L. decemlineata* from natural enemies can be quite high. For example, the predacious lady beetle *Coleomegilla maculata* De Geer can cause up to 37.8% mortality in the first generation of *L. decemlineata* eggs and an additional 58.1% mortality of eggs in the second generation (Hazzard et al. 1991, Alyokhin 2008). In addition, inundated releases of the predatory stink bugs, *Perillus bioculatus* (F.) (Hemiptera: Pentatomidae) and *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), reduced beetle densities by 62% and decreased defoliation of potato by 86% (Biever and Chauvin 1992, Hough-Goldstein and McPherson 1996, Alyokhin 2008). Moreover, the parasitic wasp *E. puttleri* can parasitize up to 91% of *L. decemlineata* egg masses on eggplant and up to 50% of egg masses on potato (Lashomb et al. 1987, Ruberson et al. 1991, Van Driesche et al. 1991, Alyokhin 2008). However, most natural enemies of *L. decemlineata* typically do not sufficiently reduce densities to an acceptable level of control (Hare 1990), forcing growers to rely on insecticides or other means of control.

Using a chemical such as methyl salicylate to attract natural enemies into areas where the *L. decemlineata* is present could contribute to control of the pest by adopting an IPM approach. Methyl salicylate has the potential to protect and enhance natural enemies whereas at the same time reducing the number of insecticide applications needed within a field. Thus, potato plots inundated with methyl salicylate (via Predalure™ (=95% methyl salicylate)) could influence *L. decemlineata* population dynamics by attracting or repelling adults, and by attracting natural arthropod predators that may consume *L. decemlineata* eggs and larvae. Because research has shown methyl salicylate to be attractive to natural enemies, but also has a component of volatiles attractive to *L. decemlineata*, the impact of using this lure is unknown. The purpose of this study, therefore, was to determine the effect of methyl salicylate (Predalure) on *L. decemlineata* population dynamics.

Materials and Methods

Field plots. The experiment was arranged in a randomized complete block design in 2 fields at the Virginia Tech Eastern Shore Agricultural Research and Extension Center (ESAREC) located in Painter, VA, during the 2010 and 2011 growing seasons. Experimental plots of 'Superior' potatoes were planted on 25 March 2010 and 13 April 2011 in rows spaced 0.9 m apart with plants seeded ≈0.28 m within rows. Potatoes were established and maintained using standard agricultural procedures including fertilizer, herbicide, and fungicide applications according to the commercial vegetable guidelines for Virginia (Wilson et al. 2012); no insecticides were applied to experimental plots. Four replicate blocks were used in each experiment with each block assigned a treated plot containing methyl salicylate release packets and an untreated plot without methyl salicylate release packets. Plots were established as 4 planted rows of potato ≈3.7 m wide and 7.6 m long and separated by a minimum of 10 m of bare ground. Mean weekly temperatures were calculated from weather data collected during each test (Table 1).

Methyl salicylate application. The experiments were setup on 23 April and 10 May 2010 and on 3 May 2011 when the potato plants were <0.5 m and had not yet bloomed and *L. decemlineata* adults had just begun to colonize the field. In each of the experiments, treated plots of potato received two 90 d, 5 g slow-release packets of Predalure (95% methyl salicylate). For the treated plots, methyl salicylate release packets were fastened with binder clips to wooden stakes 25 cm above the ground and were placed every 2 m in the middle of the plot.

Sampling *L. decemlineata* and arthropod predators. Plots were sampled every 2 - 5 d after the experiment began. All *L. decemlineata* egg masses, small larvae (instars 1 and 2), large larvae (instars 3 and 4), and adults were counted from 10 randomly-selected plants in each plot. The average number of eggs per egg mass was determined by counting the number of eggs in 10 randomly-selected egg masses. The average number of eggs per egg mass multiplied by the number of egg masses was used to calculate the total number of eggs in each of the treated and untreated plots at each sampling.

Visual counts of all predatory arthropods were recorded every 3 - 7 d from 10 randomly selected plants in each plot. In 2010, predators were collected and returned to the laboratory for identification. In 2011, predators were identified during sampling based on experience from the previous year, but were not removed from plots. Parasitoids were not detected through visual counts and, because *L. decemlineata* egg masses were not collected, the impact of parasitoids on *L. decemlineata* mortality was not assessed.

Data analysis. The seasonal dynamics of *L. decemlineata* populations in the 2 treatments was assessed visually by plotting the numbers in each life stage against accumulated degree-day (DD). Degree days were calculated using the Wisconsin model developed by Delahaut (1997), which assumes a minimum developmental temperature threshold of 11°C for *L. decemlineatea*. We then analyzed the data on the numbers of eggs, small larvae, large larvae, and adults collected in each treatment in each year using the Kiritani-Nakasyji-Manly (KNM) method for multicohort data (Kiritani and Naksuji 1967, Manly 1976, Young and Young 1998). The KNM method provided estimates of the area under the population curve (AUC) for each life stage, which

Table 1. Mean weekly temperatures (°C) recorded in Painter VA, 2010 and 2011.

Week	2010*	2011**
1	16.1	16.6
2	23.9	17.8
3	17.8	20.9
4	18.1	26.2
5	22.2	23.9
6	25.3	26.7

* Trial set up on 23-Apr., weekly temperature recordings start the day after trial set-up.

** Trial set up on 3-May, weekly temperature recordings start the day after trial set-up.

represents the cumulative sum of individuals collected for each stage; the analysis also provided estimates of the numbers entering and dying in each stage.

The data on the mean number of individuals entering and mean number dying in each life stage under each treatment in each year were examined using a chi-square test of homogeneity of distributions (Ott and Longnecker 2001) with the effect of year as a blocking factor tested using the Cochran-Mantel-Haenszel test. The null hypothesis for the homogeneity test is that of no difference in the distributions with respect to the proportion of individuals in each life stage between treatments (Ott and Longnecker 2001). When the test indicated that the null hypothesis was rejected ($P < 0.05$), we conducted individual tests of the proportions of individuals in each life stage to determine which stage or stages were responsible for the observed difference in the population distributions between the treatments. All statistical analyses were conducted using JMP 10 (SAS 2013).

The data on predators collected within the treatment plots were pooled across block and year for each treatment. From these data, we calculated the relative abundances of each taxa and the Shannon-Weiner index of diversity as a measure of community structure in each treatment (Krebs 1998, Dively 2005). A significant difference in the estimated Shannon-Weiner indices for the 2 treatments was determined using a permutation/randomization approach as described in Manly (1997).

Results

***Leptinotarsa decemlineata* populations.** The seasonal dynamics of *L. decemlineata* life stages with respect to DD are shown in Fig. 1. Stage-specific population levels were higher in 2011 compared with 2010 (Fig. 1; Table 2). In 2010, peak oviposition of *L. decemlineata* occurred between 10 and 19 May and the peak number of small larvae occurred between 14 May and 7 June (Fig. 1a, b). In 2011, peak oviposition occurred between 10 and 23 May and peak small larvae populations were observed between 21 May and 1 June (Fig. 1c, d).

The results of the multicohort analysis of the data with the KNM method are presented in Table 2. The homogeneity analysis showed that there was a significant difference in the distribution of the proportions of individuals entering each life stage (χ^2 = 746.58, df = 3, $P < .0001$; Table 2; Fig. 2A). There was also a significant difference between the distributions after blocking for year (χ^2 = 724.65, df = 1, $P < .0001$). Individual analysis of each of the life stages showed that overall the proportion of individuals entering the egg stage was significantly higher in untreated plots compared with the methyl salicylate -treated plots (χ^2 =262.47, df = 1, $P < 0.0001$). However, a significantly greater proportion of small larvae (χ^2 =4.559, df = 1, $P = 0.0327$), large larvae (χ^2 = 162.87, df = 1, $P < 0.0001$), and adults (χ^2 = 15.25, df = 1, $P < 0.0001$) entered the respective stages in the methyl salicylate -treated plots.

The analysis also showed that there was a significant difference between the treatments in the distribution of the proportions of individuals dying within the immature stages (χ^2 = 731.18, df = 2, $P < 0.0001$; Fig. 2B). A significantly greater proportion of individuals died within the egg (χ^2 = 918.11, df = 1, $P < 0.0001$) and small larval (χ^2 = 73.49, df = 1, $P < 0.0001$) stages in untreated plots compared with methyl salicylate -treated plots.

Natural enemy abundance. In both years, the 3 most abundant predatory insects found in potato plots were the convergent lady beetle, *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae), seven-spotted lady beetle, *Coccinella*

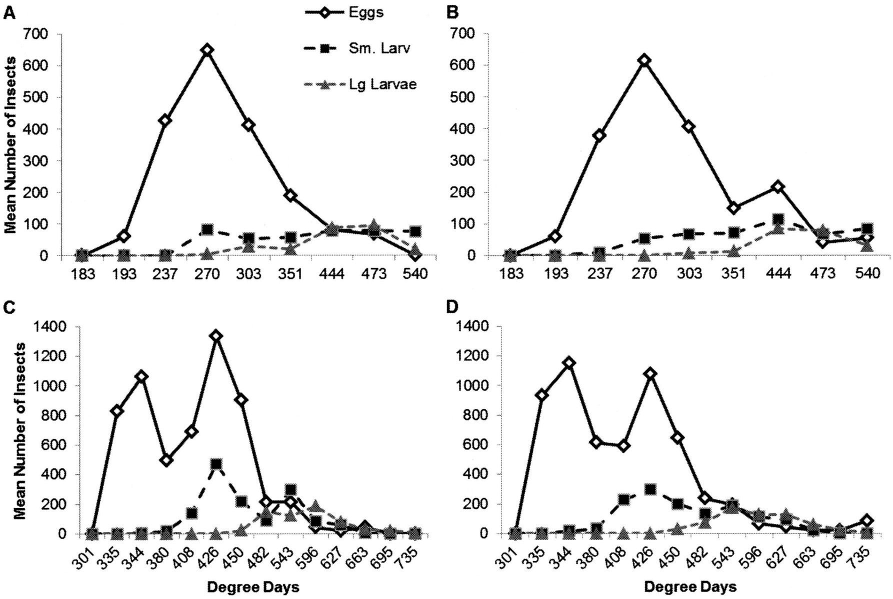

Fig. 1. Mean number of *Leptinotarsa decemlineata* eggs, small larvae, and large larvae per ten plants per plot (n = 8) in A) untreated potatoes in 2010, B) potatoes treated with methyl salicylate in 2010, C) untreated potatoes in 2011, and D) potatoes treated with methyl salicylate in 2011 in Painter, VA.

septempunctata L. (Coleoptera: Coccinellidae), and the two-spotted stink bug, *P. bioculatus* (Fig. 3). Other arthropod predators observed in low numbers included *P. maculiventris, L. grandis, C. maculata, Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), chrysopid eggs, various spiders, and predatory mites. The latter 3 groups were not identified to species. The permutation/randomization analysis showed that there was no significant difference (P = 0.331) in the Shannon-Weiner index for the predatory species collected in untreated (1.567) and methyl salicylate -treated (1.598) potato plots.

Discussion

Our experiments showed the cumulative mortality for *L. decemlineata* based on the egg and small larvae mortalities ranged from 81.9 - 94.8%, which is similar to the cumulative mortality of 91.2% reported by Cappaert et al. (1991b), who observed *L. decemlineata* populations on a native host plant in Mexico. Mena-Covarrubias et al. (1996) also reported a cumulative mortality of *L. decemlineata* eggs and small larvae ranging from 82 - 99% on horse nettle in Michigan.

Arthropod predators likely play a significant role in early-stage mortality of *L. decemlineata* (Weber 2013). In a study evaluating natural enemies of *L. decemlineata* in Mexico, Cappaert et al. (1991a) observed that over half of the insect natural enemies within their field site consisted of Pentatomidae, Carabidae, and Coccinellidae. We

Table 2. Results of the multicohort analysis with the Kiritani-Nakasuji-Manly method for data on *Leptinotarsa decemlineata* collected in potato plots at Painter, VA.

Year	Treatment*	Stage	AUC**	Mean Number Entering Stage	Mean Number Dying in Stage
2010	Untreated	Egg	40702.8	7638.2	5580.9
		Small Larva	10887.1	2057.3	1131.4
		Large Larva	6789.6	925.9	
		Adult	1428.6	172.6	
2010	Treated	Egg	42501.6	9627.2	7003.5
		Small Larva	11836.2	2623.8	1582.0
		Large Larva	5536.9	1041.8	
		Adult	2022.1	234.8	
2011	Untreated	Egg	76453.9	18837.5	13000.7
		Small Larva	23457.8	5836.8	4864.9
		Large Larva	13437.1	971.9	
		Adult	2313.6	150.0	
2011	Treated	Egg	74615.5	11832.3	6177.9
		Small Larva	21965.5	5654.4	3511.6
		Large Larva	13329.3	2142.8	
		Adult	2983.0	244.1	

* Treated plots received two 90 d, 5 g slow-release packets of Predalure (95% methyl salicylate).
** AUC is the mean area under the stage frequency curves for 4 replicates (blocks).

also primarily observed those same 3 families and some of the same species in Virginia. Heimpel and Hough-Goldstein (1992) observed a similar composition of predators in Delaware potato fields, compared with the predators we observed in VA. Researchers found *C. maculata*, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), *L. grandis*, *P. maculiventris*, and *P. bioculatus* associated with *L. decemlineata*. In our study, the 3 most abundant natural enemies observed were *H. convergens*, *C. septempunctata* and *P. bioculatus*. As previously mentioned, *P. bioculatus* can reduce *L. decemlineata* populations in potato, specifically when *L. decemlineata* populations are low (Tamaki and Butt 1978). Research has shown that *H. convergens* is associated with *L. decemlineata* populations in Mexico (Cappaert et al. 1991b) and feeds on *L. decemlineata* eggs (Cappaert et al. 1991a, Hough-Goldstein et al. 1993).

Although *C. septempunctata* was one of the most abundant predators detected in this trial, findings from other researchers indicate that this predator may not particularly feed on *L. decemlineata*. Snyder and Clevenger (2004) examined the survivorship of 4 Coccinellidae, 2 native species *H. convergens* and *Coccinella transversoguttata*

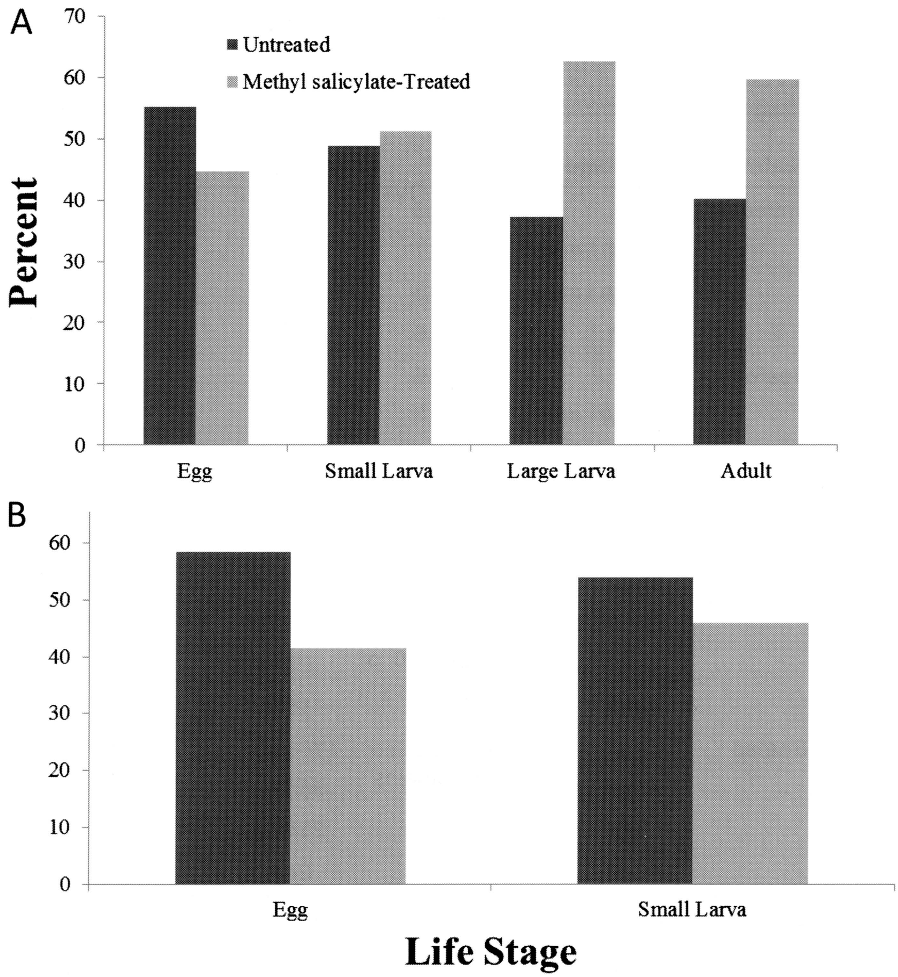

Fig. 2. Percentage of eggs, small larvae, large larvae, and adults in untreated and methyl salicylate-treated plots of potato at Painter, VA; (A) Percentage of total number entering each life stage (B) Percentage of total number dying within each life stage.

Brown (Coleoptera: Coccinellidae), and 2 exotic species *C. septempunctata* and *H. axyridis* when fed diets of the aphid *Myzus persicae* Sulzer, or *L. decemlineata* eggs, or a mixed diet of both. Results indicated that *C. septempunctata* had the highest survivorship compared with the other Coccinellidae species when fed the mixed diet. However, all 4 Coccinellidae species in this study had a significantly higher survivorship when fed *M. persicae* versus *L. decemlineata* eggs or a mix (Snyder and Clevenger 2004). Additional research has shown that *C. septempunctata* does not readily feed on *L. decemlineata* larvae or eggs (Heimpel and Hough-Goldstein 1992).

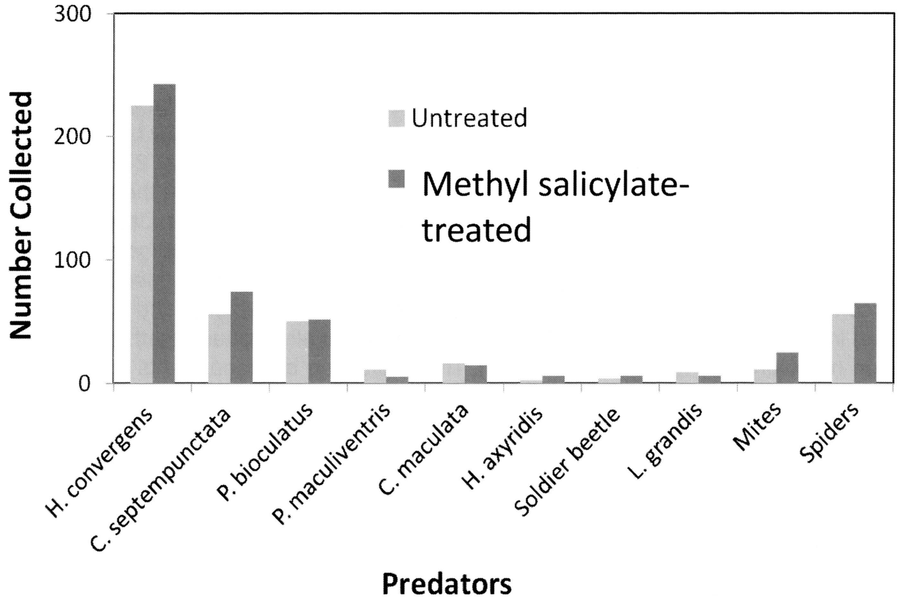

Fig. 3. Arthropod predators collected per 10 plants in potato plots with and without release packets of methyl salicylate in Painter, VA.

Thus, *L. decemlineata* egg and larval populations incur a tremendous amount of natural mortality and yet *L. decemlineata* remains a major pest of potato year after year. In our plots, over 50% of the potato foliage was consumed by *L. decemlineata*. The resilience of *L. decemlineata* has caused a heavy reliance on chemical control (Kuhar et al. 2013) and has created a cycle of continuously developing new insecticides with novel modes of action that are effective for a few years before *L. decemlineata* develops resistance and new chemistries are needed for their control (Alyokhin 2009). The high level of natural mortality should be taken into consideration when selecting an insecticide or deciding whether a spray is warranted. Methods to further enhance natural mortality could reduce that reliance on chemical control.

Use of chemical attractants to recruit natural enemies is one approach to do just that. Results from our experiments indicated that methyl salicylate release packets (Predalure) increased the number of *L. decemlineata* adults in treated plots. These results indicate methyl salicylate had attractant properties to *L. decemlineata*. As mentioned earlier, Dickens (2000, 2006) reported methyl salicylate to be a component of plant kairamones attractive to *L. decemlineata*. Our results also showed significantly greater mortality in the egg and small larvae stages in the untreated plots compared with the treated plots. There was also no effect of treatment on the abundance of arthropod predators. Although methyl salicylate did not significantly impact *L. decemlineata* cumulative mortality or increase the number of natural enemies within plots in this study, research evaluating the use of volatile compounds should not be abandoned for the management of *L. decemlineata*.

Synthetic or naturally-derived volatile compounds with attractant properties to natural enemies can play an important role in biological control of pests. Mallinger et al.

(2011) investigated the effects of methyl salicylate lures in organic soybean fields. Researchers found methyl salicylate treated plots had significantly less soybean aphids and significantly greater numbers of syrphid flies (Diptera: Syrphidae) and green lacewings adjacent to methyl salicylate lures compared with nontreated plots. When methyl salicylate lures were included in exclusion cage studies researchers saw no difference in numbers or population growth rates for soybean aphids (Mallinger et al. 2011). James and Price (2004) showed that slow-release methyl salicylate increased the number of natural enemies including *Chrysopa nigricornis* Burmeister (Neuroptera: Chrysopidae), *Hemerobius* sp., *Deraeocoris brevis* (Uhler) (Hemiptera: Miridae), *Stethorus punctum picipes* Casey (Coleoptera: Coccinellidae), and *Orius tristicolor* (White) (Hemiptera: Anthocoridae), and 4 insect families (Syrphidae, Braconidae, Empididae, and Sarcophagidae) in hop yards and grapes. Both of these crops naturally produce methyl salicylate upon herbivory (James and Price 2004). The interaction between plants and natural enemies is a complex relationship dependent on numerous factors.

Research by McCormick et al. (2012) describes the relationship between herbivore-induced plant volatiles and natural enemy responses as very specific and dependent on dose, blend of the volatiles produced, duration of release, and the type of predator receiving the signal. Research indicates a greater utilization of plant volatiles for specialist predators compared with generalist predators (McCormick et al. 2012). It is important to note that herbivore natural enemies are not exposed to just a single plant volatile compound in nature; but rather a mix of compounds produced by a plant in response to herbivory. For example, the predatory mite *Phytoseiulus persimilis* Athias-Henriot was attracted to methyl salicylate, one of 5 major herbivore-induced compounds of lima bean, *Phaseolus lunatus* L., but when presented with a blend of all the major herbivore-induced volatiles produced by lima bean there was a greater attraction compared with just methyl salicylate (Van Wijk et al. 2008, 2011). Therefore, incorporating a mixture of plant volatiles for attracting herbivore natural enemies may be more successful than just a single compound.

Plants produce a number of volatile compounds with the sole purpose of indirect defense, usually in the form of attracting predaceous insects and arthropods to disrupt the herbivorous insects feeding on these plants. *Leptinotarsa decemlineata* has many natural enemies that feed on its different life stages; manipulating this natural cycle to control *L. decemlineata* populations during oviposition and as eggs hatch could be an effective biological control strategy within an IPM program. However, from this research and the results found in other experiments it appears methyl salicylate alone may not be a useful tool for attracting predatory insects into *L. decemlineata* infested potato fields. Future research should focus on determining the different volatiles, concentrations of those volatiles, timing of when to apply, and ratios of the different volatile blends, that could be used to attract natural enemies of *L. decemlineata* in a potato field. Additional research should also determine which predators primarily feed on *L. decemlineata* and how each volatile as well as mixtures impact predator-prey interactions including type of damage and species specific volatile combinations.

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References

Alyokhin, A. 2009. Colorado potato beetle management on potatoes: Current challenges and future prospects. Fruit Veg. Cereal Sci. Biotech. 1: 10-19.

Alyokhin, A. V., M. Baker, D. Mota-Sanchez, G. Dively and E. Grafius. 2008. Colorado potato beetle resistance to insecticides. Am. J. Potato Res. 85: 395-413.

Biever, K. D. and R. L. Chauvin. 1992. Suppression of the Colorado potato beetle (Coleoptera: Chrysomelidae) with augmentative releases of predaceous stinkbugs (Hemiptera: Pentatomidae). J. Econ. Entomol. 85: 720-726.

Cappaert, D. L., F. A. Drummond and P. A. Logan. 1991a. Incidence of natural enemies of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera:Chrysomelidae) on a native host in Mexico. Entomophaga 36: 369-378.

Cappaert, D. L., F. A. Drummond and P. A. Logan. 1991b. Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae) on a native host in Mexico. Environ. Entomol. 20: 1549-1555.

Cassagrande, R. A. 1987. The Colorado potato beetle: 125 years of mismanagement. Bull. Entomol. Soc. Am. 33: 142-150.

Delahaut, K. A. 1997. Colorado potato beetle. University of Wisconsin-Extension, Cooperative Extension. A3678.

Dicke, M., T. A. v. Beek, M. A. Posthumus, N. B. Dom, H. v. Bokhoven and A. d. Groot. 1990. Isolation and identification of volatile kairomone that affects acarine predator–prey interactions. J. Chem. Ecol. 16: 381-396.

Dickens, J. C. 2000. Sexual maturation and temporal variation of neural responses in adult Colorado potato beetles to volatiles emitted by potato plants. J. Chem. Ecol. 26: 1265-1279.

Dickens, J. C. 2006. Plant volatiles moderate response to aggregation pheromone in Colorado potato beetle. J. Appl. Entomol. 130: 26-31.

Dively, G. P. 2005. Impact of transgenic VIP3A Cry1Ab lepidopteran-resistant field corn on the nontarget arthropod community. Environ. Entomol. 34: 1267-1291.

Drukker, B., J. Bruin and M. W. Sabelis. 2000. Anthocorid predators learn to associate herbivore induced plant volatiles with presence or absence of prey. Physiol. Entomol. 25: 260-265.

Glinwood, R. T. and J. Pettersson. 2000. Change in response of *Rhopalosiphum padi* spring migrants to the repellent winter host component methyl salicylate. Entomol. Exp. Appl. 94: 325-330.

Hare, J. D. 1980. Impact of defoliation by the Colorado potato beetle on potato yields. J. Econ. Entomol. 73: 69-73.

Hare, J. D. 1990. Ecology and management of the Colorado potato beetle. Annu. Rev. Entomol. 35: 81-100.

Hazzard, R. V., D. N. Ferro, R. G. V. Driesche and A. F. Tuttle. 1991. Mortality of eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) from predaction by *Coleomegilla maculata* (Coleoptera: Coccinellidae). Environ. Entomol. 20: 841-848.

Heimpel, G. E. and J. A. Hough-Goldstein. 1992. A survey of arthropod predators of *Leptinotarsa decemlineata* (Say) in Delaware potato fields. J. Agric. Entomol. 9: 137-142.

Hough-Goldstein, J. and D. McPherson. 1996. Comparison of *Perillus bioculatus* and *Podisus maculiventris* (Hemiptera: Pentatomidae) as potential control agents of the Colorado potato beetle (Coleoptera: Chrysomelidae). J. Econ. Entomol. 89: 1116-1123.

Hough-Goldstein, J. A., G. E. Heimpel, H. E. Bechmann and C. E. Mason. 1993. Arthropod natural enemies of the Colorado potato beetle. Crop Prot. 12: 324-334.

James, D. G. 2003. Synthetic herbivore-induced plant volatiles as field attractants for beneficial insects. Environ. Entomol. 32: 977-982.

James, D. G. and T. S. Price. 2004. Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. J. Chem. Ecol. 30: 1613-1628.

Kiritani, K. and F. Naksuji. 1967. Estimation of the stage-specific survival rate in the insect population with overlapping stages. Res. Popul. Ecol. (Kyoto) IX: 143-152.

Krebs, C. J. 1998. Ecological Methodology, Addison Wesley Longman, Inc.

Kuhar, T. P., K. Kamminga, C. Philips, A. Wallingford and A. Wimer. 2013. Chemical control of potato pests, pp. 375-397. *In* P. Giordanengo, C. Vincent and A. Alyokhin (eds.), Insect pets of potato: Global perspectives on biology and management. Elsevier, Waltham, MA.

Lashomb, J. H., Y. S. Ng, R. K. Jansson and R. Bullock. 1987. *Edovum puttleri* (Hymenoptera: Eulophidae), an egg parasitoid of Colorado potato beetle (Coleoptera: Chrysomelidae): development and parasitism on eggplant. J. Econ. Entomol. 80: 65-68.

Mallinger, R. E., D. B. Hogg and C. Gratton. 2011. Methyl salicylate attracts natural enemies and reduces populations of soybean aphids (Hemiptera: Aphididae) in soybean agroecosystems. J. Econ. Entomol. 104: 115-124.

Manly, B. F. J. 1976. Extensions to Kiritani and Nakasuji's method for analyzing insect stage-frequency data. Res. Popul. Ecol. (Kyoto) 17: 191-199.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology., Chapman and Hall.

McCormick, A. C., S. B. Unsicker and J. Gershenzon. 2012. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. Trends Plant Sci. 17: 303-310.

Mena-Covarrubias, J., F. A. Drummond and D. L. Haynes. 1996. Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae). Environ. Entomol. 25: 68-77.

Ott, R. L. and M. Longnecker. 2001. An introduction to statistical methods and data analysis., Duxbury, Thompson Learning, Inc., Pacific Grove, CA.

Ruberson, J. R., M. J. Tauber, C. A. Tauber and B. Gollands. 1991. Parasitization by *Edovum puttleri* (Hymenoptera: Eulophidae) in relation to host density in the field. Ecol. Entomol. 16: 81-89.

SAS. 2013. JMP version 10, SAS Institute, Cary, N.C.

Snyder, W. E. and G. M. Clevenger. 2004. Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles. Biol. Control 31: 353-361.

Tamaki, G. and B. A. Butt. 1978. Impact of *Perillus bioculatus* on the Colorado potato beetle and plant damage. U.S. Depart. Agric. Tech. Bull. 1581.

Van Driesche, R. G., D. N. Ferro, E. Carey and M. Maher. 1991. Assessing augmentative releases of parasitoids using the "recruitment method", with reference to *Edovum puttleri*, a parasitoid of the Colorado potato beetle (Coleoptera: Chrysomelidae). Entomophaga 36: 193-204.

Van Wijk, M., P. J. A. De Bruijn and M. W. Sabelis. 2008. Predatory mite attraction to herbivore-induced plant odors is not a consequence of attraction to individual herbivore-induced plant volatiles. J. Chem. Ecol. 34: 791-803.

Van Wijk, M., P. J. A. De Bruijn and M. W. Sabelis. 2011. Complex odor from plants under attack: Herbivore's enemies react to the whole, not its parts. PLoS ONE 6: 1-7.

Weber, D. C. 2013. Biological control of potato insect pests, pp. 399-437. *In* A. Alyokhin, P. Giordanengo and C. Vincent (eds.), Insect pests of potato: Biology and management. Elsevier. Waltham, MA.

Wilson, H. P., T. P. Kuhar, S. L. Rideout, J. H. Freeman, M. S. Reiter, R. A. Straw, T. E. Hines, C. M. Waldenmaier, H. P. Doughty and U. T. Deitch. 2012. Commercial Vegetable Production Recommendations - Virginia. Virginia Cooperative Extension, Blacksburg, VA.

Young, L. J. and J. H. Young. 1998. Statistical Ecology: A Population Perspective, Kluwer Academic Publishers.