

# Spatial and Temporal Dynamics of Colorado Potato Beetle (Coleoptera: Chrysomelidae) in Fields with Perimeter and Spatially Targeted Insecticides

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**ABSTRACT** Concern over insecticide resistance has led to the suggestion of spatially variable within-field management of Colorado potato beetle, *Leptinotarsa decemlineata* (Say). Here we compare *L. decemlineata* spatial and temporal dynamics, and potato yield, in fields treated with a narrow perimeter (5.5 m) of systemic imidacloprid supplemented with spatially targeted sprays to untreated fields and to fields where all rows received the systemic. The systemic targeted immigrating individuals which, having acquired the field through either flight or walking, first established themselves in the outer 5.5 m of the field. The perimeter treatment ( $\approx 25\%$  of field area) reduced mean densities with no effect on timing of peak densities. Immigrating adults established similar spatial trends in both perimeter and untreated fields. Although trends in  $F_1$  larval densities have been shown to follow the patterns established by immigrating adults, trends in the  $F_1$  larval densities of the perimeter treatments diverged from adult patterns and developed highest densities in field centers. Immigrating adults had little to no spatial dependence in the covariance structure in any treatments. Spatial dependence in the covariance structure of  $F_1$  larval and  $F_1$  adult populations developed as density increased in both perimeter and untreated fields, with a tendency for increasing spatial dependence in perimeter fields, though this was not statistically significant. Comparing the perimeter to untreated fields, yields increased at a proportion that was higher than the proportion of land area treated, but remained significantly lower than the whole-field treatment. These results suggest that the perimeter tactic has promise as a site-specific resistance management program, but that refinement of border width is needed to optimize trade-offs among yield, quality, and long-term maintenance of susceptibility.

**KEY WORDS** Colorado potato beetle, global positioning systems, insect spatial dynamics, population dynamics, potatoes, geostatistics

COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is a significant defoliator of potatoes (Hare 1980), and insecticidal control has been and remains a major part of management for this insect in potatoes. The magnitude of the resources required for this management approach in the United States alone was estimated at 2 million kilograms of raw product, 1 million barrels of oil, and 1.7 million kilograms of inert ingredients to make 2 million kilograms of formulated product in 180,000 containers (Magretta 1997).

Foliar insecticides have been the major tactic directed against *L. decemlineata* in potatoes (Ferro 2000b), but there have been dramatic changes in both insecticide classes and their method of delivery. By the mid-1990s, the nitroguanidine class had gained wide-scale adoption. In Massachusetts, for example, 77% of growers had switched to the nitroguanidine imidacloprid in the first year after introduction (Ferro 2000b). Imidacloprid can be applied as a systemic at planting or as a foliar spray, but is most commonly applied at

planting with rates designed to give residual control for multiple weeks. In addition to the nitroguanidine class, two types of microbial metabolites, abamectins (AgriMek), and spinosyns (SpinTor), have recently become available as a foliar spray. Use of a third microbial metabolite, a protein toxin produced by *Bacillus thuringiensis* subsp. *morrisoni* (Federici 2000), can be effective when timed properly, but its use as a foliar spray tended to be supplanted with the introduction of the systemic nitroguanidines (Ferro 2000b). However, this toxin is now presented to *L. decemlineata* as the Cry3A protein in NewLeaf transgenic potatoes.

The *L. decemlineata* has demonstrated a remarkable ability to rapidly develop resistance against most classes of toxins (Forgash 1985, Ferro 2000b) dating back to the 1940s (Gauthier et al. 1981). Resistance to some toxins was observed even before field registration (Ferro 2000b) and the *L. decemlineata* is capable of developing resistance to the newer, more selective toxins (Whalon et al. 1993, Zhao et al. 2000). Clearly, it is important that these toxins be deployed in a

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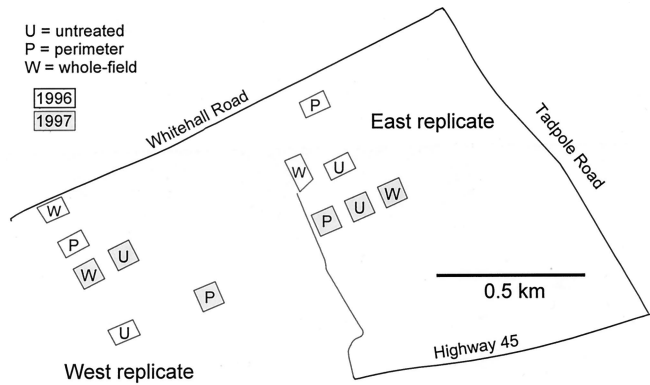


Fig. 1. Landscape position of 1996 and 1997 experimental potato fields and their field treatment assignments.

manner that helps delay the development of resistance. However, both the nitroguanidine (when applied as a systemic at planting) and the transgenic option result in presence of the toxin over long time frames, which increases selective pressure for resistance (Taylor et al. 1983) and requires resistance management actions to be deployed at planting. Although resistance management for foliar materials includes minimizing use to times when densities exceed thresholds, resistance management for transgenics that confer pest protection has involved influencing the spatial deployment of the transgenic genotype within the landscape.

Precision integrated pest management (IPM) uses knowledge about the spatial variation of the pest population to influence the spatial deployment of management inputs. For *L. decemlineata*, colonizing adults aggregate along field edges (French et al. 1993, Weisz et al. 1996), and plastic lined trenches at field edges (Boiteau and Osborn 1999) are examples of spatial variation of *L. decemlineata* management that have been deployed at or before planting. Blom and Fleischer (2001) explored spatial structuring of *L. decemlineata* populations in untreated fields and their results suggest a systemic perimeter treatment could be an important management tactic. Ferro (2000b) reported an average of 142, 10, and 4 dead beetles per imidacloprid-treated plant on the first, third, and fifth row in from the field edge, and suggested that insecticides could be limited to a 6-m perimeter of a field (Ferro 2000a). Dively et al. (1998) intermingled imidacloprid-treated and untreated rows and showed protection to untreated plants. Using foliar insecticides, a mapped-and-targeted management approach reduced sprays 30–40% comparable to sprays applied to whole fields when field means exceeded thresholds (Weisz et al. 1996), which resulted in temporally dynamic refugia for susceptible phenotypes, reduced rates of resistance, and conservation of biocontrols (Midgarden et al. 1997).

A resistance management approach could integrate systemics or transgenics applied at planting with foliar sprays of microbial metabolites. An example would be to limit at-planting treatments to field perimeters and

to map-and-target the foliar sprays. Our objective was to describe the temporal and spatial dynamics of *L. decemlineata* populations, along with potato yield and quality, subjected to this management approach which we called the "perimeter treatment." We compared the insect population dynamics and crop response in this perimeter treatment to both untreated fields and fields where all plants were treated at-planting.

## Materials and Methods

**Field Plots.** Six potato ('Katahdin') fields were established during each of two field seasons on a commercial farm adjacent to the Russell E. Larson Agricultural Research Center (40.715° N latitude and 77.938° W longitude), which was surrounded on all sides by field corn. All fields were rotated from field corn. Fields for 1996 were ≈0.5 ha in size, configured as roughly 60 by 90-m rectangles. The per field area was increased to 80 by 80 m (0.64 ha) in 1997, with a square configuration. Seed pieces were planted on 22–24 May 1996 and 5–7 May 1997 with 0.3-m plant spacing and 0.91-m furrow separation. Between and within year field locations were separated by distances >150 m but <1 km (Fig. 1). Each field was grided into 10 by 10-m blocks. The blocks encompassed 11 rows of potatoes, termed the block-row.

In each year the six fields were divided into east and west replicates (Fig. 1) and assigned to whole-field, perimeter, or untreated treatments for management of *L. decemlineata*. Whole-field consisted of 0.913 liter/hectare Admire 2 F/acre (Bayer, Kansas City, MO) incorporated throughout the field applied at planting. The perimeter treatment used imidacloprid at the same rate, though applied only in the six perimeter rows and ≈5.5 m on row ends (≈25% of the field area), and foliar application of abamectin 0.593 liter/hectare AgriMek 0.15 EC (Novartis, Greensboro, NC) targeted to within-field areas that had developed high *L. decemlineata* densities. Untreated fields received no insecticide at planting nor AgriMek over the course of the season. Over the 2-yr experiment, targeted foliar sprays occurred only once (on 7 July 1997, calendar

day 188) over 12.3 and 17.6% of the field areas of the east and west replicates, respectively. Management of potato leafhopper was with 0.280 liter/hectare Malathion 5 EC (MicroFlo, Lakeland, FL) applied to all treatments uniformly only on 10 July in 1997.

**Sampling and Data Management Protocols.** Weekly counts of *L. decemlineata* adults and instars were made with an above-canopy visual inspection and clipped into 1-row meter sampling units as described in Blom and Fleischer (2001). Geographic location of the counts was determined using a backpack GPS receiver (Trimble ProXL), and both location and beetle counts were recorded in the Trimble TDC-1 datapod. Early in the season the fields were exhaustively sampled by surveying the entire length of every other furrow. Due to labor constraints, the number of furrows was progressively reduced as the population increased, until finally a systematic pattern was used. In 1996 a stratified random design was used by sampling one of the 11 furrows from each of the six block-rows during each week. This stratified random design was used occasionally in 1997, but an hexagonal pattern of paired, ≈10-m furrow lengths was adopted most frequently. The exhaustive design resulted in >3,000 and the least intensive pattern ≈300 1-m samples per field.

In 1997, yield was determined using sampling units based on the 10 by 10-m blocks encompassing 11 potato rows. For each of the 36 central blocks, one of the rows was harvested. The outer blocks had to be subdivided in accordance with the pattern of imidacloprid application in the perimeter treatment (Fig. 2), with corner blocks giving rise to three yield blocks of 4.5 by 4.5 m, 4.5 by 5.5 m, and 5.5 by 10 m, and all others comprising two yield blocks of 4.5 × 10 and 5.5 × 10-m configuration. All treated blocks are termed “edge” and the remainder “internal” (untreated). This sampling design, based on the perimeter-treated fields, was applied to harvesting in all fields regardless of their field treatment. The potatoes were sorted into five size classes (1 ≤ 3.8 cm, 2 = 3.8–4.8 cm, 3 = 4.8–6.4 cm, 4 = 6.4–10.2 cm, and 5 ≥ 10.2 cm) using a Haines mechanical roller, and the yield (kg/m<sup>2</sup>) determined for each size class.

**Analyses.** For *L. decemlineata* density values, log<sub>e</sub> was the optimal transformation to best approximate normality. Spatial and temporal dynamics of *L. decemlineata* density were analyzed by field and week after transformation. Comparisons of mean density between field treatments were made for the adult and large larval stages within each sampling week using analysis of variance (ANOVA) (PROC GLM, SAS Institute 1999). Mean field density was plotted over calendar day, which provided the best coincidence of major phenological events across both years. Regression was used to model density as a function of percent of 1-m sample units that were infested with *L. decemlineata*, and a test for heterogeneity of slope (Littell et al. 1991) was used to compare this relationship among life stages.

Analysis of spatial patterns followed techniques developed for *L. decemlineata* in untreated fields (Blom and Fleischer 2001). Field-wide spatial trends of the

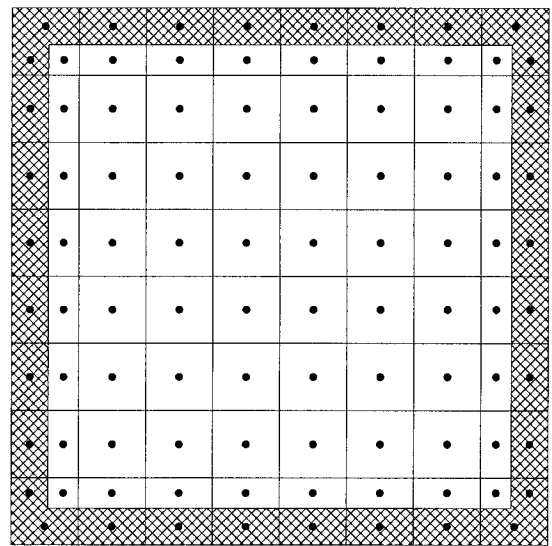


Fig. 2. Potato yield sampling design showing the perimeter (hatched) area and internal untreated area. Dots mark the center coordinate of each yield block. Major blocks are 10 by 10 m and correspond directly to internal yield blocks. These major blocks were subdivided along the field edge (4.5 by 10 and 5.5 by 10 m) and corners (4.5 by 4.5, 4.5 by 5.5, and 5.5 by 10 m) to create yield blocks distinguishing between imidacloprid-treated and untreated zones. Potato rows ran left to right.

mean were modeled using  $z_i = \beta_0 + \beta_1x_i + \beta_2y_i + \beta_3x_i^2 + \beta_4y_i^2 + \beta_5x_iy_i + \epsilon_i$  (Cressie 1993) and backward elimination (PROC REG, SAS Institute 1999), where  $z_i$  is the density and  $x_i$  and  $y_i$  are the field spatial coordinates of the sample in meters. Regression coefficients were retained and trend models were considered significant using the SAS default of  $P < 0.10$ . When a significant trend was found, geostatistical analyses were performed on trend residuals, otherwise the log<sub>e</sub> transformed data were used (Isaaks and Srivastava 1989, Sharov et al. 1996).

Spatial dependence was examined using estimates of the correlogram function,  $\rho_{(h)}$ , at specified lag intervals. These estimates were made with the S-PLUS S+SPATIALSTATS module (MathSoft 1997),

$$\rho_{(h)} = \frac{\frac{1}{N_{(h)}} \sum_{(ij)|h_{ij}=h} v_i \cdot v_j - M_{ih} \cdot M_{jh}}{S_{ih} \cdot S_{jh}}$$

where  $v_i$  and  $v_j$  are observation values at the head and tail, respectively, of a vector with a separating distance  $h$ . In the same way,  $m$  and  $s$  are the respective mean and standard deviations of the heads and tails of the  $h$  separation distance. Standardized correlograms,  $1 - \rho_{(h)}$ , were constructed from these estimates (Isaaks and Srivastava 1989, Rossi et al. 1992). Lag separation was 1 m with a 0.5-m tolerance. Lag vectors were omnidirectional with a 22.5-degree tolerance. Spherical, exponential and Gaussian models were fit to the

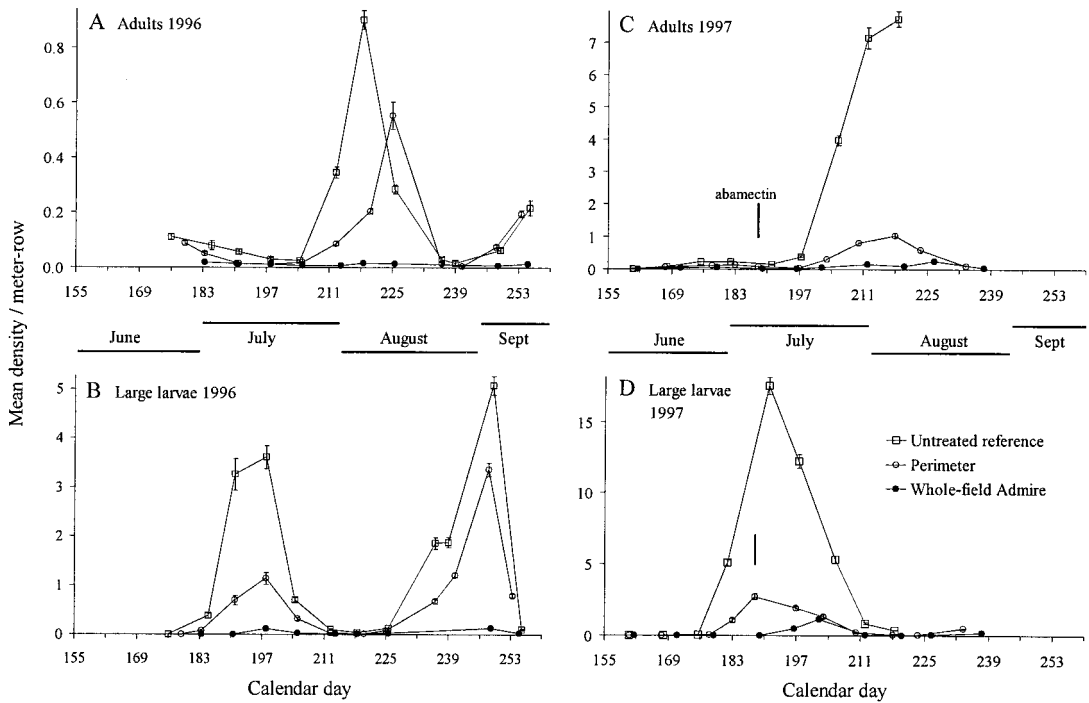


Fig. 3. Mean *Leptinotarsa decemlineata* density ( $\pm$ SEM) for adult and large larval life stages in three field treatments: untreated, perimeter, and whole-field, during two field seasons. Each panel is scaled to its maximum mean density + SEM.

correlograms using nonlinear regression (PROC NLIN, SAS Institute 1999) to obtain nugget and range estimates. Model selection for a given field and sampling time was chosen using the following criteria: (1) Estimating a nugget that best fits the estimates of  $1-\rho$  near the origin; (2) estimating a range closest to the correlogram's departure from the population variance; and (3) minimizing the squared residual error within the range of spatial dependence. Models were fit including lag distances out to 50 m, although lags with  $<30$  pairs were excluded. Nugget estimates from the correlogram models were treated as estimates of degree of spatial dependence (cf. Williams et al. 1992) and related to dynamics (density and life stage) of the *L. decemlineata* population. Those data sets showing no spatial structure were assigned a nugget of 1, range of 0, and sill of 1 in these relationships.

Mean yields were compared between treatments and locations within a field (edge versus interior) with ANOVA (PROC GLM, SAS Institute 1999). Proportions of total yield per size class were transformed using arcsine-square root, and a likelihood ratio chi-square test was used to examine differences in yield distribution among the five potato size classes (PROC FREQ, SAS Institute 1999). The chi-square was then partitioned for comparisons among the various size classes within treatments.

Voucher specimens have been deposited with the Frost Entomological Museum of the Pennsylvania State University.

## Results

**Field-Wide Seasonal Dynamics.** The seasonal progression of mean density was similar between all field treatments. In 1996, sampling began after immigration had initiated, but it appeared to have peaked by calendar day 176 in all fields (Fig. 3A), and the timing in rise and decline of  $F_1$  large larvae (calendar days around 183–211, Fig. 3B), was nearly identical in all fields. With the  $F_1$  adults there was a slight lag of peak density in the perimeter field treatment. Whole-field and untreated fields densities peaked around calendar day 218, whereas the greatest densities of  $F_1$  adults in the perimeter treatment were observed around calendar day 225 (Fig. 3A). As with the  $F_1$  large larvae, the  $F_2$  immatures followed nearly identical patterns of rise and decline in density among the treatments. In 1996 we monitored the initiation of the  $F_2$  adult population though we could not follow it to fruition. During our period of observation (calendar days around 239–255) the increase in density was similar across treatments.

Densities were higher in 1997 populations. Immigration began around calendar day 160 (Fig. 3C). Peak densities were observed first in the whole-field and untreated fields at about the same time (around calendar days 171 and 175, respectively), and were maintained in the untreated fields through calendar day 182. There was a steady increase in mean density of the perimeter treatment, but it did not achieve its peak until 1 wk after the other treatments (around calendar

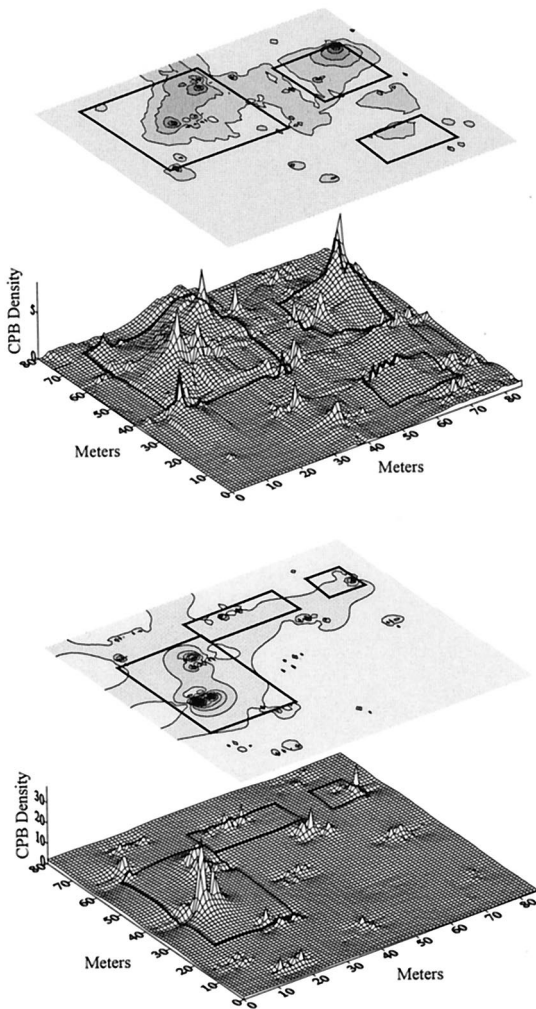


Fig. 4. Maps of *Leptinotarsa decemlineata* adult and large larval densities in the two perimeter treatment potato fields on 7 July 1997. Rectangular overlays on these surfaces show the areas treated with 0.593 liter/hectare AgriMek 0.15 EC on calendar day 188.

day 183).  $F_1$  large larvae densities showed a similar pattern of increase and decline in the untreated and perimeter fields (Fig. 3D), with peak densities at the same time (calendar days 188 and 191), although this observation is confounded by the spatially targeted intervention with abamectin immediately following observations on calendar day 188 in the perimeter treatment fields (12.3 and 17.6% of field areas, Fig. 4). Without this foliar application, peak densities in these perimeter fields may not have been reached until the following week. Rise and decline of the  $F_1$  larvae in the whole-field treatment lagged behind the other treatments by  $\approx 2$  wk. Patterns of increase for the  $F_1$  adult population appeared identical between untreated and perimeter fields (Fig. 3C), both achieving peak densities around calendar day 218. Having experienced high densities of large larvae and now  $F_1$  adults, the

untreated fields were nearly defoliated and observations terminated after this date. Density patterns of the  $F_1$  adults in the whole-field treatment were sporadic and difficult to contrast with those of the other treatments.

Overall, means for adult and large larval densities were reduced in the perimeter and whole-field treatments relative to the untreated reference (Fig. 3). Though appreciable populations developed in the perimeter treatment, adult mean density was significantly ( $P < 0.05$ ) lower than in the untreated fields for 70% of the sample weeks, and in 83% of the sample weeks for large larvae. Comparing the perimeter against the whole-field treatment, adult densities were significantly lower in the latter for 72% of the sample weeks, and the corresponding large larval densities significantly lower in 81% of the sample weeks.

**Spatial Structure. Incidence.** The percent of 1-m row sampling units that harbored at least one beetle (percent incidence) was a function of mean density for all life stages (Fig. 5). Field treatment did not influence this relationship. The relationship was linear for the immigrating adults, but only occurred over a low density range. The subsequent life stages displayed an asymptotic relationship of incidence with respect to mean density over a wider range. For the  $F_1$  large larvae an exponential saturation was fit to the relationship: percent infested =  $85.994 \cdot (1 - e^{-0.315 \cdot \text{mean density}})$  (Fig. 5B). For the  $F_1$  adults and  $F_2$  large larvae, hyperbolic saturation was used: percent infested =  $(108.179 \cdot \text{mean density}) / (1.040 + \text{mean density})$  and percent infested =  $(88.915 \cdot \text{mean density}) / (0.951 + \text{mean density})$ , respectively (Fig. 5 C and D).

Because the density range was very different between the immigrating adults and subsequent stages, we also compared the incidence-to-mean relationship among treatments restricted to a density of one per meter of row or less. Within this range the relationship was linear for all stages (Fig. 5E), and the regression for immigrating adults (percent infested =  $0.013 + [89.520 \cdot \text{mean density}]$ ,  $R^2 = 0.987$ ) had a significantly greater slope than those for the other life stages ( $F_1$  large larvae,  $F = 13.67$ ;  $df = 1, 57$ ;  $P < 0.0005$ ;  $F_1$  adults,  $F = 29.85$ ;  $df = 1, 48$ ;  $P < 0.0001$ ;  $F_2$  large larvae,  $F = 28.84$ ;  $df = 1, 37$ ;  $P < 0.0001$ ). The slopes for both the  $F_1$  and  $F_2$  large larvae (percent infested =  $0.625 + [41.051 \cdot \text{mean density}]$ ,  $R^2 = 0.743$ ; percent infested =  $2.654 + [49.846 \cdot \text{mean density}]$ ,  $R^2 = 0.912$ , respectively) were the lowest ( $F_1$  large larvae versus  $F_1$  adults,  $F = 16.75$ ;  $df = 1, 53$ ;  $P < 0.0001$ ;  $F_2$  large larvae versus  $F_1$  adults,  $F = 8.37$ ;  $df = 1, 33$ ;  $P < 0.0067$ ) and not significantly different ( $F = 1.57$ ;  $df = 1, 42$ ;  $P < 0.2167$ ). The slope for  $F_1$  adults (percent infested =  $2.329 + [61.657 \cdot \text{mean density}]$ ,  $R^2 = 0.980$ ) was intermediate and differed significantly from immigrants and large larvae.

**Trends in Mean Density.** Within-field changes in local means (trends) were significant in 88 and 83% of the 34–42 sampling dates for adults, and 97 and 84% of the 29–37 sampling dates for large larvae, in the untreated and perimeter fields, respectively. The pattern

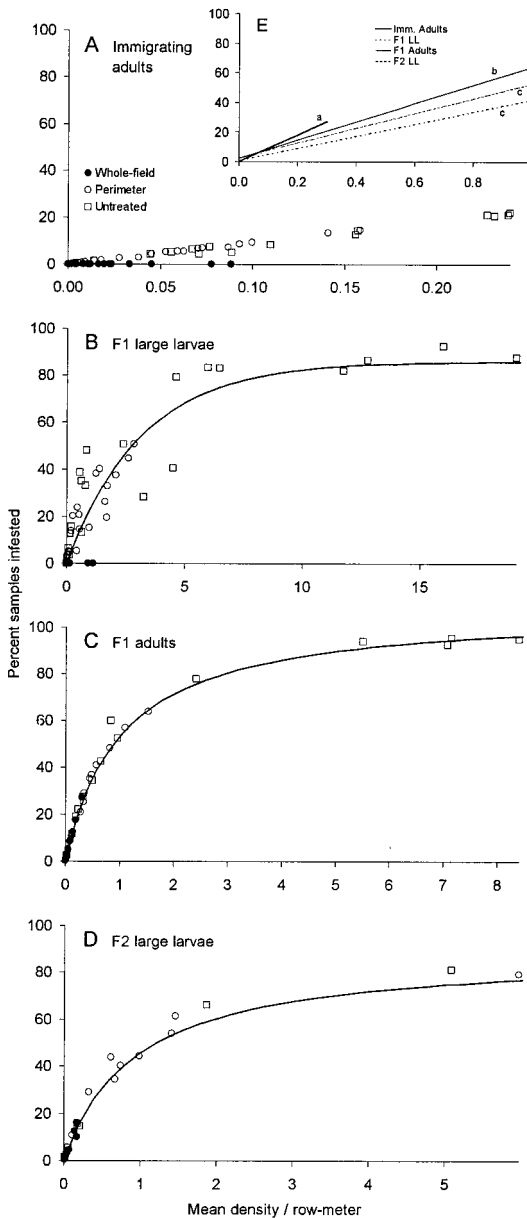


Fig. 5. Relationship between mean *Leptinotarsa decemlineata* density and incidence (percent of 1-m sample units infested) for four life stages over the three field treatments: untreated, perimeter, and whole-field. Insert (E) shows the linear regression model fit to each life stage within a density range of 0–1 beetle per meter.

of these trends in both untreated and perimeter fields was established with the immigrating adult populations that were highest along the field edge(s) oriented toward the most probable overwintering sites, and declined from there across the field. However, trend patterns in the perimeter fields departed from those in the untreated reference fields with the  $F_1$  large larvae. Whereas trends established by the im-

migrating adults persisted through the season in the untreated reference fields (e.g., Fig. 6 A and B), there tended to be a disjuncture between patterns of these two stages in the perimeter field treatment (e.g., Fig. 6 C and D). Trends in the  $F_1$  large larvae in the perimeter fields tended to be more centralized even when the pattern for the immigrating adults had a strong relationship to a single field edge. Trend patterns in the  $F_1$  adults continued with the structures established by the  $F_1$  large larvae, long after the efficacy of imidacloprid would have abated. Although the trends showed patterns over time, the models only explained a small proportion of the total variance, and the  $R^2$  values of the trend models in the untreated and perimeter fields ranged from 0.002 to 0.37. The low and uncharacteristic populations that established in the whole-field treatments failed to produce any consistent pattern of within-field trends.

**Point-to-Point Dependency.** Short-ranged spatial dependency developed only rarely with the immigrating adults (6 of 51, 11.8%, Fig. 7; see Blom and Fleischer 2001). However, this spatial dependency was found in the  $F_1$  life stages that followed immigration, with asymptotically increasing structure as the density of these life stages increased. Including all the field treatments within a life stage, the nugget declined (spatial dependency increased) with increasing density for both the  $F_1$  large larvae and  $F_1$  adults (Fig. 7 B and C; nugget =  $0.768 \cdot \text{mean}^{-0.045}$  and nugget =  $0.784 \cdot \text{mean}^{-0.056}$ , respectively). These models, which include data from all three field treatments, are very close to those used to describe the relationship in the untreated reference fields alone (Blom and Fleischer 2001).

For all three life stages there appeared to be no difference in the relationship of the nugget and mean density between the untreated reference and the perimeter treatment. To examine this in the  $F_1$  large larvae and  $F_1$  adults the data were linearized and the two field treatments compared using a test for heterogeneity of slope. Because the perimeter field treatment did not attain the densities experienced in the untreated reference fields the comparison was made only over the range of mean values up to the maximum obtained in the perimeter field treatment ( $F_1$  large larvae: <3 m of row;  $F_1$  adults: <1.5 m of row). The test showed no difference in either slope ( $F = 0.60$ ;  $df = 1, 37$ ;  $P < 0.44$ ) or intercept ( $F = 1.01$ ;  $df = 1, 37$ ;  $P < 0.32$ ) for the  $F_1$  large larvae, nor for the  $F_1$  adults ( $F = 1.28$ ;  $df = 1, 26$ ;  $P < 0.27$  and  $F = 0.00$ ;  $df = 1, 26$ ;  $P < 0.95$ ; respectively).

**Potato Yield.** There were significant differences ( $F = 318.38$ ;  $df = 2, 559$ ;  $P < 0.0001$ ) in field-wide yields between all field treatments (Fig. 8). The whole-field treatment had the greatest yield, which was followed by the perimeter field treatment. Yield in the untreated reference was the lowest.

Mean yields were not significantly different between internal and edge blocks in the untreated fields ( $F = 0.50$ ;  $df = 1, 177$ ;  $P < 0.48$ ; Fig. 9A). In contrast, mean yields in the edge blocks of the perimeter field treatment were significantly greater than those in cor-

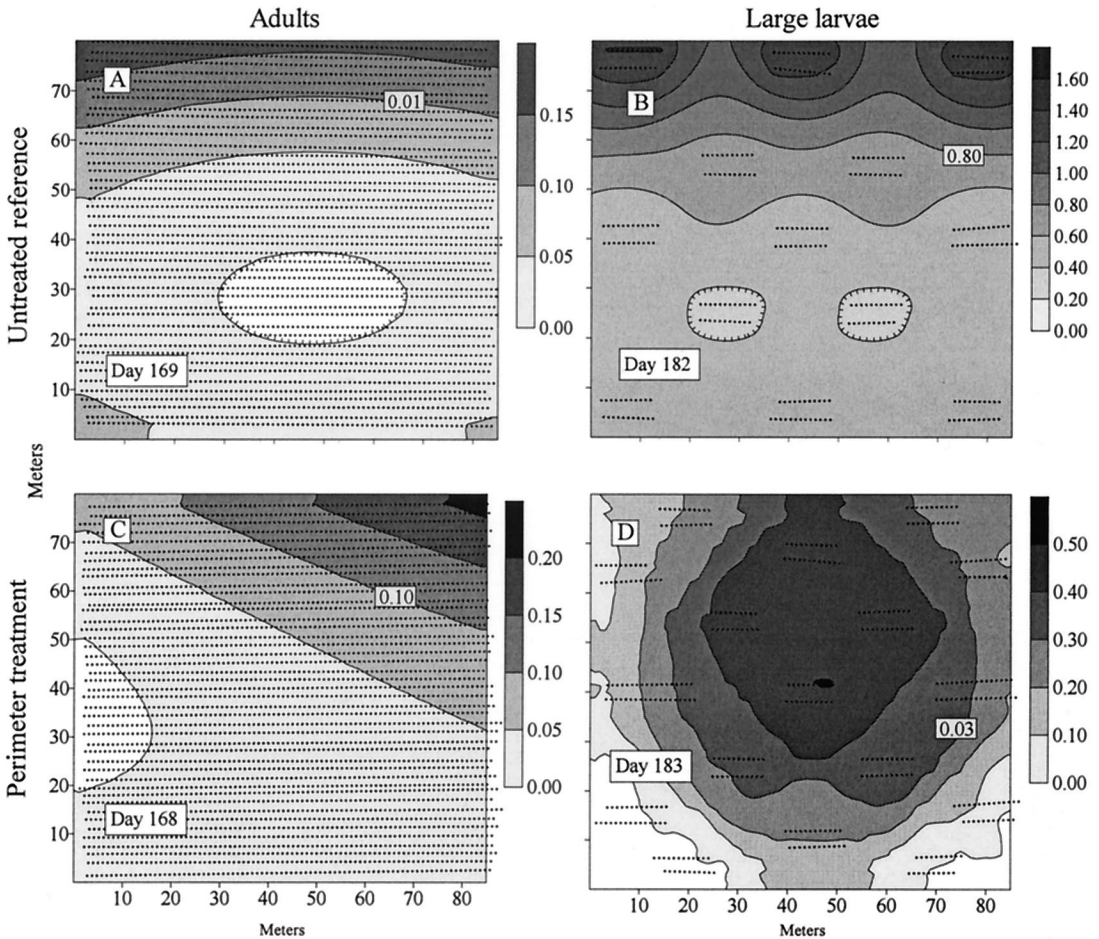


Fig. 6. Exemplary comparison of presence of trend fidelity between *Leptinotarsa decemlineata* adults and large larvae for the untreated (top), and lack of this fidelity in perimeter (bottom) field treatments. Trend models for the large larvae (right) are from sampling that occurred  $\approx 2$  wk after that of their corresponding (antecedent) adults (left). The Z-axis (local mean density/m of row,  $1/d^2$  interpolation of the trend model estimates) is scaled to each contour panel.

responding internal blocks ( $F = 10.62$ ;  $df = 1, 188$ ;  $P < 0.001$ ). The comparison of internal versus edge blocks was also significant in the whole-field field treatment, though inversely as the mean yield in the edge blocks was lower than internal blocks ( $F = 15.49$ ;  $df = 1, 189$ ;  $P < 0.0001$ ).

Comparison of internal plot areas revealed significant differences between all field treatments ( $F = 308.14$ ;  $df = 2, 369$ ;  $P < 0.0001$ ; Fig. 9B). Whole-field treatment had the greatest yield, followed by the perimeter field treatment and finally the untreated reference. When considering comparisons in only the edge area, no significant differences were found in mean yield between whole-field and perimeter treatments, but the mean yield in the internal area of the untreated fields was significantly lower than the other two field treatments ( $F = 72.74$ ;  $df = 2, 186$ ;  $P < 0.0001$ ).

Field treatment significantly altered the distribution of the yield among size classes ( $\chi^2 = 77.55$ ,  $df = 8$ ,  $P < 0.001$ ,  $n = 600$ ; Fig. 10). Additionally, all pairwise

comparisons between treatments were significant (untreated to perimeter,  $\chi^2 = 15.39$ ,  $df = 4$ ,  $P < 0.004$ ,  $n = 400$ ; untreated to whole-field,  $\chi^2 = 46.16$ ,  $df = 4$ ,  $P < 0.001$ ,  $n = 400$ ; perimeter to whole-field,  $\chi^2 = 51.79$ ,  $df = 4$ ,  $P < 0.001$ ,  $n = 400$ ). Size class 3 composed the largest yield proportion in all three field treatments, significantly higher than all other size classes in the untreated reference (63.6%) and perimeter (47.5%) field treatments. In the whole-field treatment, size classes 3 and 4 were not significantly different and collectively account for 91.0% of the yield.

Discussion

In some situations, overwintered *L. decemlineata* adults locate and invade rotated fields by walking (Lashomb and Ng 1984, French et al. 1993), thus entering through field edge. The beetles may also locate a field through flight (Weber and Ferro 1994, Ferro et al. 1999) but still have first contact within the perimeter. Given the position of our fields and their

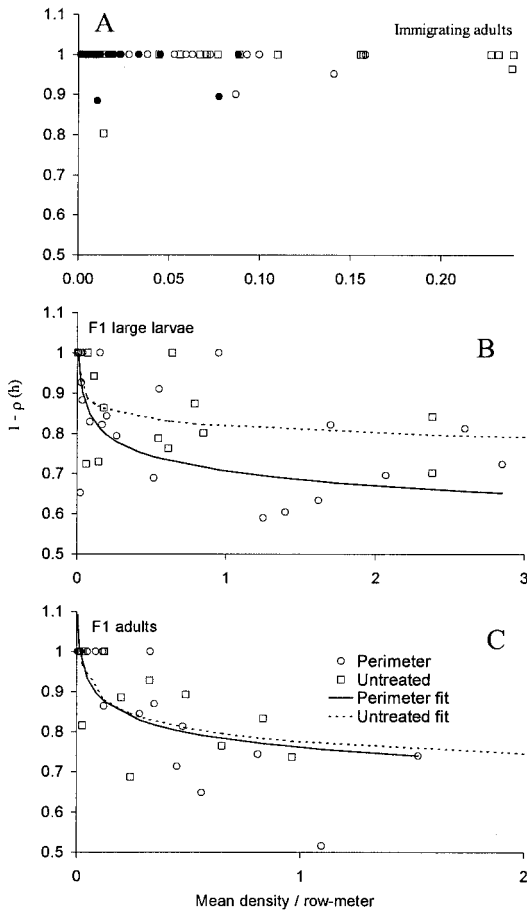


Fig. 7. Relationship between mean *Leptinotarsa decemlineata* density and spatial dependency (estimated by the modeled nugget of standardized correlograms) for three life stages and three treatments: untreated, perimeter, and whole-field.

separation distances, we presume that the majority of the immigrating adults fit into the latter category. Under either of these scenarios, use of a border systemic or transgenic may serve as an efficient control

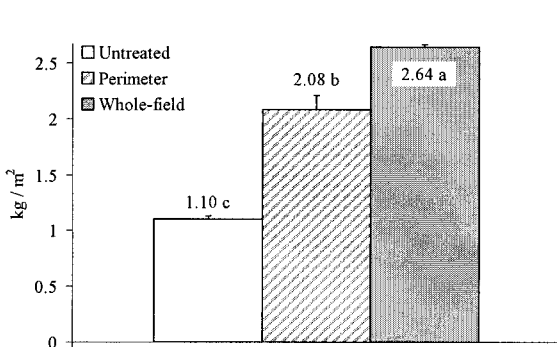


Fig. 8. Mean potato yield (kg/m<sup>2</sup> + SEM) for three field treatments, untreated, perimeter, and whole-field. All means are significantly different (LSMeans *t*-tests,  $P < 0.0001$ ).

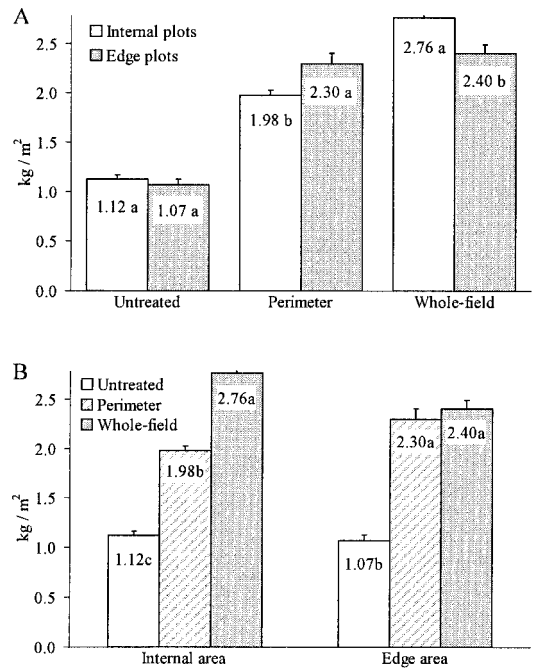


Fig. 9. Mean potato yield (kg/m<sup>2</sup> + SEM) in the internal and edge areas of three field treatments: untreated, perimeter, and whole-field. (A) Mean comparison of internal and edge areas within each field treatment. (B) Mean comparison of field treatments for each area of the field. Shared letters indicate no significant difference (LSMeans *t*-test,  $P < 0.05$ ).

measure and a tactic consonant with resistance management. Our data suggest that even a narrow ( $\approx 5\text{--}6$  m) perimeter application of imidacloprid can significantly curtail growth of the within-field *L. decemlineata* population. As expected, the perimeter treatment was intermediate between untreated and whole-field treated fields, both in *L. decemlineata* population density (Fig. 3) and yield (Fig. 8). However, with only 25% of the area treated, these effects were closer to the efficacy of the whole-field treatment than might be expected given a simple 1:1 relationship between area

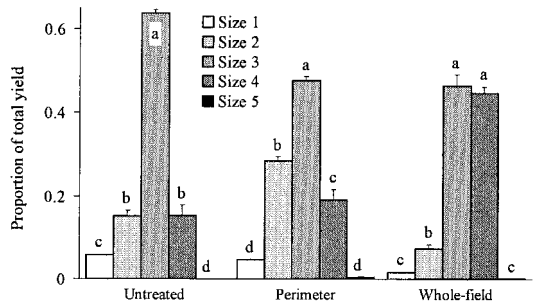


Fig. 10. Proportion of total potato yield sorted into five size classes. Distribution of size classes differed significantly among field treatments ( $P < 0.05$ , likelihood ratio chi-squared). Shared letters within a field treatment are not significantly different (LSMeans *t*-test,  $P \leq 0.05$ ).



treated and pest or yield response. Dively et al. (1998) found similar results using systemic imidacloprid in an alternating row configuration. The amount of benefit was disproportionately higher than the percentage of land treated. When using a narrow perimeter it is reasonable to hypothesize that the relative benefit could increase in larger fields because a smaller proportion of the field would be treated.

It is important to note that our perimeter treatment allowed for in-field targeted sprays of microbials. The foliar spray occurred on only one date over the 2-yr study, and only on 12.3 and 17.6% of the land area (Fig. 4). We therefore attributed most of the effect of the perimeter treatment to the systemic applied within the 5- to 6-m field perimeter. Further experiments would need to fully separate the influence of the perimeter systemic from the targeted microbial spray. Our experiments also assume little to no effect to the *L. decemlineata* populations from the Malathion directed against potato leafhopper, which would be consistent with the lack of *L. decemlineata* response to the same compound in this geographic area during 1994 (Midgarden et al. 1997).

The perimeter treatment, while reducing the within-field density, did not affect the timing of population events (Fig. 3). Only in a few instances did population development lag behind the timing in untreated fields. Thus, the perimeter treatment will not likely affect the predictability of the dynamics in population phenology.

The effect of treatment on spatial structure was variable. We consider incidence (or percent infestation) a crude indicator of the percent of the field occupied. Within a life stage, treatment had little effect on the relationship between mean density and incidence (Fig. 5), and we presume that potential biological processes driving this relationship (Blom and Fleischer 2001) are unaffected by the treatment. Immigrating adults, when analyzing data across all treatment fields, still appear to have the role of primary dispersers, establishing spatial extents of the population's within-field occupation (Fig. 5E). This is useful for management, because it suggests that the perimeter tactic will have little impact on predictability of the density-incidence relationship.

We could find no significant influence of treatment on the spatial covariance structure (Fig. 7). As had been discussed for the untreated fields alone (Blom and Fleischer 2001), the immigrating adults failed to develop point-to-point dependency (Fig. 7A). Spatial structure did emerge with the  $F_1$  large larvae and  $F_1$  adults and no statistical difference between the treatments could be detected. However, there was an inclination for spatial dependence to increase in the perimeter treatment over the untreated (Fig. 7B). If this tendency reflects reality it would be an added benefit of a perimeter tactic, informing decisions about the number and placement of samples and optimizing the efficacy of targeted sprays (principally by improving the quality of map interpolation).

The most pronounced effect of treatment on spatial structure occurred with trends in the local mean with-

in-field. Although trend models had low  $R^2$ , the patterns defined by the trend models over time were consistent with biological processes discussed for the untreated fields in Blom and Fleischer (2001). Although trends in the mean structure appeared to be established by the immigrating adults in both untreated and perimeter fields (Blom and Fleischer 2001), with the perimeter treatment there was a tendency to disrupt continuity between immigrants and the subsequent within-field, established population (e.g., Fig. 6). As might be expected in a border treatment, the population mean density became more centralized, sometimes leaving little indication of orientation of the original immigration. In a management context, this disruption of the trend pattern would influence optimum deployment of sampling locations within the field and methods accounting for the trend in map generation.

There are effects of the perimeter treatment on yields. Consistent with the impact on *L. decemlineata* densities, ungraded yields from the perimeter treatment were much higher than in the untreated fields, but significantly lower than the whole-field treatments (Fig. 8). Although this increase in total yield from the perimeter treatment was proportionately greater than the percentage of land area treated, failing to achieve the yields obtained in the whole-field treatment suggests there is a cost associated with letting a moderate-sized population develop internally. This disparity between the whole-field and perimeter treatment appears to be a consequence of yield reductions in the internal blocks. Significantly lower yields in the edge blocks of whole-field treatment are probably due to within-field edge effects (Fig. 9A), because there is no difference in edge area yields between whole-field and perimeter treatments (Fig. 9B). The presence of an established *L. decemlineata* population internally, however, reversed the pattern of yield rank between internal and edge areas in the perimeter treatment (Fig. 9A).

When yield quality (sizing) is considered, the perimeter treatment provides little benefit over the untreated field in size-class distribution (Fig. 10). Although the size-class distribution of proportion of total yield was significantly different among all treatments, the proportions in both the untreated and perimeter-treated fields were centered on the middle size class and only the whole-field treatment had a distribution skewed toward a larger potato.

Despite its benefit over the untreated condition, perimeter total yield and quality (size-class distribution) were still significantly lower than the whole-field scenario and may be unacceptable to growers. However, it may be possible to manipulate several factors and push yields under a perimeter treatment toward those obtained with whole-field application. For example, one might adjust the width of a border application. Records of high perimeter mortality (e.g., Ferro 2000a) suggested that a narrow border (e.g.,  $\approx 6$  m) would cause extensive mortality among immigrating adults. We have data documenting immigration locations (unpublished data) that suggest a wider

border treatment (roughly 20–30 m) may be necessary. Of course, the absolute size and geometry of the field may also affect the breadth of a perimeter treatment necessary to maintain the *L. decemlineata* population at a desired density. Manipulation of perimeter size becomes more complex when we consider the goal of resistance management. A better understanding of the optimal population characteristics for the maintenance of susceptibility is needed and could recommend population levels greater than optimal for yield and quality. Some immediate cost through yield reduction may be required to gain the benefits of a long-term resistance management program.

Our data help quantify the influence of narrow perimeter treatments of a systemic on *L. decemlineata* spatio-temporal dynamics, suggesting how these treatments could be further developed for both population and resistance management.

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