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MOVEMENT OF ADULT COLORADO POTATO BEETLES, *LEPTINOTARSA DECEMLINEATA* (COLEOPTERA: CHRYSOMELIDAE), IN RESPONSE TO ISOLATED POTATO PLOTSMichael A. Caprio^{1,2} and Edward J. Grafius¹

ABSTRACT

Mark recapture techniques were used to determine Colorado potato beetle movement in circular arenas with isolated plots of potatoes at each ordinal direction. Post-diapause beetles aggregated on one or a few of the plants in one of the plots for each release, but not on the same plants in different releases. Differences in plant attractiveness were therefore not likely responsible for the aggregatory behavior. Aggregations were probably a result of either coordinated movement from the release site to the plants or an aggregatory signal with a range of at least 15 m. Summer adults did not aggregate on plants. Correlations of summer beetle recapture distributions to wind direction showed that anemotactic behavior could not account for the major portion of variation in beetle orientation to the potato plots. Some positive attraction to the plots was indicated because more beetles were recaptured at the plots than would be expected from random motion. The number of beetles recaptured at plots covered by cheesecloth was not significantly different from recaptures on uncovered plots, indicating little reliance on visual cues specific to potatoes for location of the plants.

Complete reliance on insecticides for management of the Colorado potato beetle (*Leptinotarsa decemlineata* [Say]) has proven difficult as the beetle has become increasingly resistant to pesticides, and interest has developed in alternative methods of control (Hare 1990). Wright (1984) and Lashomb and Ng (1984) both reported that crop rotation was effective in retarding the build-up of Colorado potato beetle population in potato (*Solanum tuberosum*) fields. Since potato is most sensitive to defoliation during tuber initiation and bulking (Beresford 1967, Hare 1980), delays in the early build-up of beetle populations can be important in reducing insecticide applications on rotated fields.

The effectiveness of crop rotation as a management tool for the control of Colorado potato beetle depends upon the ability of beetles to find new patches of host plants. *Leptinotarsa decemlineata* used plant odors to locate plants in wind tunnel studies (Visser 1976, 1979; Visser and Ave 1978). Schanz (1953) reported that in olfactometers the odor-conditioned anemotactic response ceased when the terminal 4 segments of the antennae were amputated. In contrast, both Wegorek (1959) and Caprio (1987) were unable to demonstrate host-plant attraction by *L. decemlineata* in wind tunnel studies. The seem-

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ingly contradictory results from these studies could possibly be due to differences in the physiological state of the beetles examined. Ng and Lashomb (1983) reported that post-diapause beetles moved in a predominantly north-westerly direction after emergence. The authors hypothesized that oriented movement is an adaptation by beetles to move onto southerly mountain slopes where warmer temperatures would allow for early spring flight following emergence.

The objectives of this study were to determine if post-diapause and summer adult Colorado potato beetles moved randomly with respect to isolated potato plots, or if an extrinsic factor, such as wind or inter-plant variation in attractiveness, was important in host plant location. Secondly, we wished to determine if visual cues specific to potato plants (ie. color, shape), were important in host plant location, since color has been reported to be an important cue for flying Colorado potato beetles (Zehnder and Speese 1987). Finally, the effective use of traps crops to increase efficacy of crop rotation relies not only on how beetles locate the trap crops, but also on the overwintering location of the beetles and where they emerge in the spring. Our third objective was to determine the proportion of individually marked beetles which overwintered in the arenas.

MATERIALS AND METHODS

In 1985 and 1986, three 22 m diameter circular arenas were constructed, with plots of 16 potato plants (var. Atlantic) spaced 0.3 m apart in each of the four ordinal directions. In 1985, a circular pitfall trap was placed in the arc between plots to capture beetles which did not move to plots. Because we observed a small number of beetles moving along the pitfall trap rather than falling directly into it, the pitfall trap was replaced in 1986 by an outer, 30m diameter ring of potato plants spaced 2m apart. One arena in 1986 was destroyed by flooding, so results are reported for two arenas only. Beetles were released in the center of each arena. Releases were made before 1000 hr when temperatures were coolest to reduce beetle movement immediately following release.

Beetles were collected at the Michigan State University Montcalm Potato Research Farm (Entrican, MI) and stored at 5°C in 1 l containers filled with 750 ml of soil. Post-diapause beetles were either dug from the soil or collected from the surface prior to potato emergence. Tests were conducted with post-diapause and first generation (summer) adults. Releases were replicated over three arenas.

In 1985, a total of 1282 post-diapause beetles were released in 5 different releases on four different dates. The beetles were marked with Testor's® enamel paints. Two dots each of two colors were applied to the elytra, which was sufficient to identify beetles to the date and arena in which they were released. Caprio et al. (1990) found that 90% of beetles marked with four dots of enamel paint retained at least one mark for two weeks. The pitfall traps and potato plants were sampled once daily and recaptured beetles were removed from the arenas. In 1986, 301 post-diapause beetles marked with enamel paints were released in 3 releases on different dates, and 605 summer adults were released in 5 releases and marked using 1.5x2.5 mm paper labels which were glued to the left elytra (Caprio et al. 1990). These marks were unique to each individual, and beetles were allowed to remain in the field after sampling. All plants, both in the plots and the exterior border row, were sampled twice daily.

Weather parameters in 1986 were recorded using a Campbell Scientific

Inc. CR21 Micrologger. Hourly measurements of temperature, wind speed, wind direction and a calculated wind vector at 2 m were recorded.

Sampling for diapausing beetles was done in 1986 following plant senescence. Soil beneath half of the plants in each plot was excavated to a depth of 30 cm and sifted to check for marked potato beetles. Because it is possible that beetles may have moved away from the plants before diapausing, our estimate was a conservative estimate of the number of beetles which diapause in fields in Michigan.

In 1986 one randomly selected plot in each arena was surrounded by a single layer of cheese cloth (1 m high and raised 4–6 cm off the ground) to reduce visual cues specific to potato plants while minimally reducing olfactory cues. The cheese cloth covering would not, however, eliminate *L. decemlineata* movement in response to other visual cues such as standing objects. Five releases of summer adults were made in each arena. Results were analyzed by analysis of variance, treating each plot as a separate treatment and releases as replicates. Single df orthogonal contrasts were used to compare covered versus uncovered plots.

Statistical analysis. To determine if beetles were moving preferentially to upwind plots, we wanted to correlate the number of beetles moving to a plot with a relative measure of wind passing over that plot towards the beetle release point. In 1986, a wind index for each plot was calculated by taking hourly wind vectors for the previous 24 hr and weighting them with the cosine of the deviation of the vector from directly upwind of the plot. This wind index was negative for downwind plots and positive for upwind plots. Four wind indices were generated per sample date (1 for each plot), summed and converted into percentages of the total for each plot. Beetles captured at a plot were summed over the arena and individual plot totals converted into percentages which could then be correlated with the wind indices for the respective plot.

In 1986, captures were recorded on an individual plant basis, allowing us to determine if beetles were aggregating or were distributed randomly among the plants.

Because of the tendency of some individual beetles to move along pitfall traps rather than falling directly into them, the 1985 data cannot be used to directly determine the ability of beetles to locate the plots of potatoes. Comparisons of recapture distributions between arenas and between release dates using a hierarchical log-linear analysis can, however, discriminate between four important hypotheses. If beetles locate host plants by random movement, the first hypothesis, then the beetle distributions of recaptures at each plot should not be significantly different from each other. An alternative hypothesis is that variation in host plant quality (or the previous presence of beetles from earlier releases) made some plots more attractive than other plots. In this case, beetle recapture distributions would vary between arenas, but would remain the same between releases within an arena. A third hypothesis is that wind direction was of primary importance in determining the location of the plots by the beetles. In this case, there should be differences in the distribution of recaptures within arenas (more beetles should be caught in the upwind plot), but the distribution of recaptures between arenas should not be different because the same plot would be upwind in each plot. Releases made at different times should also have different distributions because of differences in wind direction over time. Finally, a fourth hypothesis is that beetles interact in the location of host plants. In this case, beetle recapture distributions would vary between releases with arenas as well as between arenas on the same release dates. The distributions of beetle captures at the four plots in each arena in 1985 were compared using both chi-square and hierarchical log-linear analysis. When more than 20% of the cells were sparse (fewer than 5

Table 1. Chi-square analysis of 1985 post-diapause beetle recapture distributions by release date.

Date of releases	# of releases	X ²	df	p ¹
6-14	3	35.19	6	<.01
6-17	2	32.16	3	<.01
7-01	3	39.30	6	<.01
7-02	3	28.94	6	<.01

¹Significant chi-square values indicate that replicates released on the same day do not have similar recapture distributions.

individuals), a small constant was added to each cell. This tends to homogenize cells, making the test to find differences in distributions more conservative.

RESULTS

1985. Of the 1282 beetles released, 830 (64.7%) were recaptured. 630 (75.9% of the recaptured beetles) were recaptured at the plots (either in the trap next to the plot or on the plants).

In the hierarchical log-linear analysis, only the complete model which included the interaction between date, release arena and recapture distribution could successfully predict beetle distributions (because the model is fully saturated, there is exact agreement between observed and predicted recapture distributions). In hierarchical log-linear analysis, inclusion of this three-way interaction automatically includes all lower order two-way interactions as well as the main effects. The model with only the three two-way interactions predicted a distribution significantly different from the observed (likelihood chi-square = 94.4, df = 16, $p < 0.001$). If the first hypothesis, that beetle movement and orientation to the plants is random, were correct, none of the higher order interaction terms would have been necessary to predict recapture distributions. In the case of the second two hypotheses, one of the two-way interaction terms should have been sufficient to predict beetle orientation to the plots. The second hypothesis, that movement was determined by host plant quality or previous beetle presence, was not supported because the release arena x recapture plot interaction did not predict beetle orientation. The third hypothesis, that a factor extrinsic to the arena (such as wind) was of primary importance in determining beetle orientation, was not supported because the date x recapture plot interaction was insufficient to predict beetle recapture distributions. A separate contingency table analysis of beetle recapture distributions over plots on different dates also did not support the third hypothesis, as releases made on the same date in different arenas had significantly different distributions (Table 1). Because the three-way interaction term was significant in the log-linear analysis, it was necessary to know both the arena and date of release in order to predict beetle movement. Interactions between beetles in locating or orienting to the potato plots (the fourth hypothesis) is the most likely explanation of this three-way interaction.

1986. Three hundred and one post-diapause beetles were released, and 43.9% were recaptured. Of the recaptured beetles, 47.5% were recaptured at the potato plots. Recapture rates were lower in 1986 than 1985. This was probably due to the aggregation of beetles on plants in the outer ring in 1986 (discussed below), which may have reduced beetle orientation to the plots. Of the 608 summer adults released in the arenas, 54% were recaptured and of

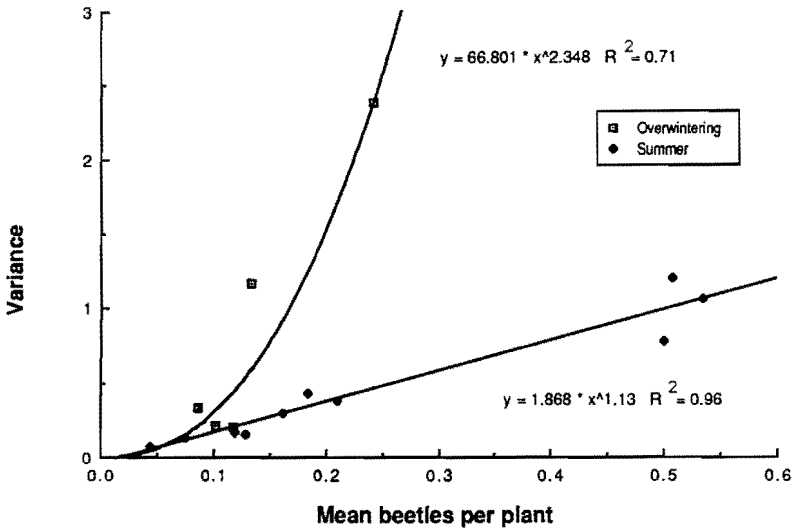


Figure 1. Aggregation of post-diapause and summer adult potato beetles on individual plants in circular arenas, 1986. The exponent of x is a measure of aggregation. A value of 1.0 corresponds to a poisson (random) distribution, while higher values indicate clumping.

these, 68.4% were recaptured at the plots. Despite the different techniques employed, these recapture rates are very similar to those found in 1985.

Differences in aggregation were observed between post-diapause and summer adults. The variance to mean ratios based on single plant samples and fit to Taylor's power law showed substantial differences (Figure 1). The exponent in the fitted equation is a measure of aggregation, with values near 1.0 indicating random dispersion and higher values indicating clumped distribution. The results establish that post-diapause beetles were more aggregated, while summer adults were dispersed more randomly among the plants.

Adult beetle recapture distributions (initial recaptures only) were generally not well correlated with wind indices (Figure 2). Summer adult correlations (those after julian date 225) tended to be higher, at least until JD 237, after which diapause effects may have become important. The low correlation for post-diapause beetles may be explained by the high aggregation of this generation, which may have masked any anemotactic response.

Analysis of variance of percent of total daily recapture for each plot showed no significant differences (arena 1, $F = 0.43$, $df = 3,12$, $P > 0.05$; arena 2, $F = 0.64$, $df = 3,12$, $P > 0.05$), indicating that over the course of the summer there was no reduction in adult movement towards the covered potato plots. While the plots covered with cheesecloth had the lowest average daily recapture rates in each arena (Table 2), the differences were not significant even when compared with single df orthogonal contrasts between covered and uncovered plots (arena 1, $F = 0.96$, $P > 0.05$; arena 2, $F = 1.48$, $P = 0.247$). These results indicate that visual cues specific to potato plants were not a major factor in host plant location in this study.

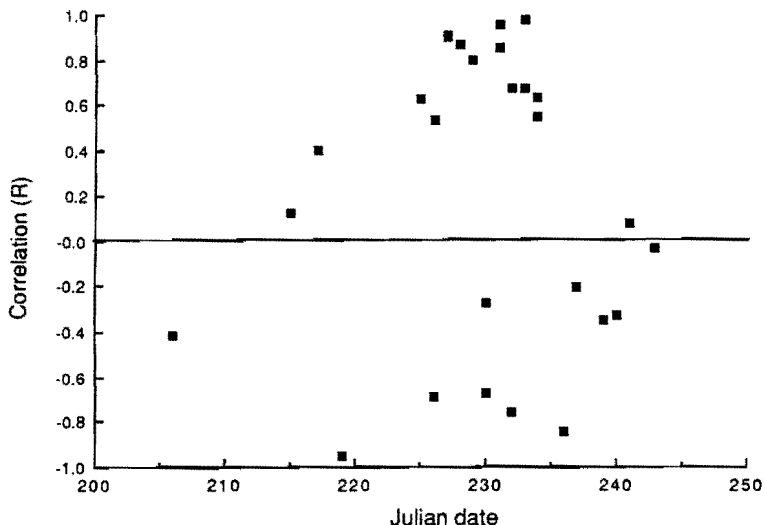


Figure 2. Correlation of wind indices to beetle orientation. Each point represents the correlation of four plots to four corresponding wind indices for a single release.

Sampling of soil under the plots showed that 43.8% of the beetles recaptured on the plots went into diapause directly below the plants. This is likely to be an underestimate because neither dispersal out of the arenas nor mortality were evaluated.

DISCUSSION

The results of this research clearly indicate that there are important differences in behavior between post-diapause and summer adult *L. decemlineata*. The data from 1986 show that post-diapause beetles tended to aggregate on host plants after short dispersal phases while summer adults showed no similar tendency. Post-diapause aggregations were very localized and in the most extreme cases, all the beetles recaptured in a plot were recaptured from a single plant. It is unlikely that these aggregations were due to qualities

Table 2. Average daily plot recapture (# of new adults recaptured/day) over 5 summer adult releases. Starred plots were covered by cheesecloth (reduced visual cues).

Plot	Average plot recapture (over 5 releases)	
	Arena 1	Arena 2
North	5.2	5.0*
East	5.8	7.0
South	4.6	6.0
West	3.6*	6.8
Pooled SD	6.4	4.1

of the particular plant since in other releases, other plants were sites for aggregations. This aggregatory behavior may be related to the patchy distribution of the original host plants of *L. decemlineata*. These results do not necessarily contradict those of Ng and Lashomb (1983), as beetles were immediately removed from an outer (1 m diameter) ring of potato slices in their experiment, eliminating the potential for beetle interactions. Jermy et al. (1988) also reported aggregations of beetles on plants in smaller (6 m diameter) arenas. Unfortunately, they did not report results from overwintering and laboratory reared adults separately, though in the field arena where no overwintering adults were released there were no reports of beetle aggregations. They also reported that the aggregations occurred on the same plants throughout the experiment, in contrast to our results. This may have been due to the fact that beetles were released every day, allowing for the perpetuation of the beetle interactions, while we allowed 3-5 days between releases in most cases. Aggregation in response to conspecifics (Bach and Carr 1990) and the presence of aggregation pheromones (Rowell-Rahier and Pasteels 1986) have been reported in other chrysomelid beetles.

The data from 1985 are also consistent with the aggregation of beetles on one or more plants. Successful prediction of beetle recapture distribution required a model incorporating the three-way interaction of release date, release arena and recapture distribution. This suggests that the recapture distribution in an arena depended upon which plot or plots the beetles aggregated at, and this varied between arenas on a release date as well as between release dates.

Trap cropping has been suggested as a method to enhance the efficiency of crop rotation in management of *L. decemlineata*. Management of resistance to transgenic crops, for example, could be assisted by trap cropping in association with crop rotation (Audubon Bt-resistance workshop 1992). Our results suggest that trap cropping could be an efficient means of attracting post-diapause beetles, but less efficient at attracting summer adults. The results also illustrate that there are significant differences in the behaviors of post-diapause and summer *L. decemlineata* adults, and extrapolating experimental results between the two generations is not advisable. Trap crops might also be effective in fields planted to potatoes the previous year, since our results indicate that at least in Michigan, a major proportion of the beetles overwinter in the field.

The anemotactic response of *L. decemlineata* noted in wind tunnel studies is not sufficient to explain a large part of the variation in summer beetle orientation to potato plots in the field. As each plot had similar daily recapture rates, a significant amount of *L. decemlineata* orientation behavior may be random, at least at distances 11 m or more from host plants. The chrysomelid beetle, *Altica subplicata* (LeConte), which has a similar gregarious behavior, also did not aggregate based on wind or magnetic direction (Bach and Carr 1990).

Directed orientation of the beetles when they are closer to the plants is not excluded by these results. Indeed, positive host plant attraction is indicated by the high proportion of recaptured beetles found near or in the plots (76% in 1985, 66% in 1986). These plots only accounted for 11.6% of the circumference of the arena. If the attraction cues were not active from 11m, the distance at the time of release, then beetles may be committed to a particular direction on a random basis, and only after covering some distance do they become attracted to nearby plants.

The results of this research indicate that olfactory and visual cues specific to potato plants are probably not active over distance of 11m, at least for plot sizes of 16 plants. In field situations, directed movement between and within fields has been noted (Gibson et al. 1925, Williams 1988), but it is not certain

what the causative factors were in those cases. There is also evidence that *L. decemlineata* overwinters in large numbers in Michigan potato fields and that placement of trap crops in fields planted to potatoes the previous year along with suitable control tactics could increase the efficacy of rotation in reducing infestations.

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