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THE INFLUENCE OF PLANT DISPERSION ON MOVEMENT PATTERNS OF THE COLORADO POTATO BEETLE, *LEPTINOTARSA DECEMLINEATA* (COLEOPTERA: CHRYSOMELIDAE)

Catherine E. Bach[1]

ABSTRACT

The influence of plant dispersion on movements of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), was studied with mark-recapture techniques. Beetles released between potato monocultures, polycultures with two additional non-host plant species, and polycultures with five additional non-host species, randomly colonized the three types of plots. Releases between different arrangements of potted host and non-host plants showed (1) greater beetle colonization and greater length of time spent on potato plants growing alone than on potato plants surrounded by non-host vegetation, and (2) no effect of potato plant density on colonization or tenure time. Overall, there was a 65% recapture rate; beetles consistently stayed on the same plants they originally colonized, often for at least five days after release.

Much recent attention in the field of herbivore-plant interactions has been focused on the relationship between various aspects of host plant dispersion (plant density and plant species diversity) and the population dynamics of specialist herbivores (see review by Kareiva, in press). In particular, specialist herbivores are more abundant in monocultures or habitats with low plant diversity than in habitats with higher plant diversity (Root 1973, Bach 1980a, Risch 1980). Several recent studies have determined the mechanisms underlying these abundance patterns. Greater population densities in simpler habitats result from differences in herbivore movement patterns, rather than from differences in colonization, reproduction, or predation, at least for cucumber beetles, *Acalymma* spp. (Chrysomelidae: Galerucinae) (Bach 1980b, Risch 1981).

The purpose of the present study was to determine if another specialist herbivore species (the Colorado potato beetle, *Leptinotarsa decemlineata* (Say)) responds to diversity in a similar manner. And if so, what role do herbivore movement patterns and tenure time (length of time remaining in an area) play in the relationship between plant dispersion and herbivore abundance? *Leptinotarsa decemlineata* (Chrysomelidae: Chrysomelinae) feeds exclusively on plants in the family Solanaceae, especially on *Solanum* species (Radcliffe 1982). This study will enable comparison between specialist chrysomelid beetles which have different life cycles, since eggs, larvae, and adults of the Colorado potato beetle occur on host plant leaves, whereas only adults of cucumber beetles (rootworms) occur on leaves.

MATERIALS AND METHODS

Mark-recapture techniques were utilized to study the influence of plant dispersion on the movement patterns of the Colorado potato beetle, *Leptinotarsa decemlineata*. Beetles were collected in vegetable gardens in Ann Arbor, Michigan, individually marked with Testor's paint (maximum of two dots per elytron), and released at the study site at the Matthaei Botanical Gardens, The University of Michigan, Washtenaw County, Michigan.

Two basic types of releases were conducted: (1) releases between experimental plots, and (2) releases between potted plants arranged in different spatial configurations. Thirty beetles

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were released equidistant from experimental plots in a mowed rye and clover field on 12 August 1981 (Fig. 1). These plots were initially set up to study how natural colonization by Colorado potato beetles is affected by plant dispersion, but only one beetle naturally colonized the plots, thus necessitating releases of beetles. There were three replicates of each of four treatments: (1) potato (*Solanum tuberosum*) monoculture, (2) melon monoculture, (3) potato, melon, and bean polyculture and (4) potato, melon, bean, corn, tomato, and broccoli polyculture. (Melon monocultures were utilized in a concurrent study of *Acalymma vittatum*.) The position of the four treatments was randomized and plots had been planted on 26–29 May 1981.

In the first set of releases between experimental plots, *L. decemlineata* appeared to be very stationary. Thus, it was necessary to create smaller experimental plots. The use of greenhouse grown potted plants allowed a more controlled experimental design and ensured homogeneous plant quality. Potato plants were placed on the mowed rye and clover field in different arrangements. Plants were grown in an unsprayed greenhouse at the Matthaei Botanical Gardens in 20-cm-diameter pots with a standard potting mixture soil. Potato plants (variety Katahdin) utilized in the experiments were at the flowering stage and were about 0.5 m high. Melon plants (variety Hale's Best Jumbo) had vines up to 1.5 m long.

Experiments were conducted to answer the following questions:

(1) Does the presence of a non-host plant species (melon) near a host plant influence colonization of host plants? This question was investigated with two different experiments. The first involved releasing 15 beetles on 7 September equidistant from a potato plant by itself and a potato plant growing next to a melon plant (Fig. 2A). The second experiment involved releasing 11 beetles on 8 September equidistant from two replicates of each of two treatments: a single potato plant and a potato plant with a melon plant on either side, with melon vegetation completely surrounding the potato plant (Fig. 2B).

(2) Is there a difference in tenure time on host plants (potatoes) and non-host plants (melons)? On 7 September, five beetles were placed on a potato plant growing by itself, a potato plant growing next to a melon, and a melon growing next to a potato plant (Fig. 2A).

(3) Does plant density influence colonization of host plants? Fifteen beetles were released on 9 September equidistant from two replicates of each of two treatments: one potato plant and three potato plants in separate pots, but touching each other (Fig. 2C).

For each of these sets of experiments, all potato plants were searched for beetles for at least five days (six days for experiment 3 and seven days for experiment 1b) after the releases. The identification of each beetle and the particular plant and location were recorded.

RESULTS

Of the 30 beetles released between the large experimental plots, 16 (53%) were later found. There were large differences in which plots were colonized by beetles, after being released equidistant from four plots (one potato monoculture, one three-species polyculture, and two six-species polycultures). As shown in Table 1, the majority of beetles (10 out of 16) were later found in one of the six-species polycultures. However, the pattern of colonization was not significantly different from what would be expected given random colonization of the three types of plots ($\chi^2 = 4.6$, $P > 0.05$). Only one individual was ever found in a

Table 1. Number of beetles found in four experimental plots after being released equidistant from the four plots.

	Days after release				Number of different individuals found
	1	2	3	9	
Potato monoculture	0	3	3	0	3
3-spp. polyculture	0	1	1	0	1
6-spp. polyculture	6	7	7	2	10
6-spp. polyculture	1	1	1	0	1

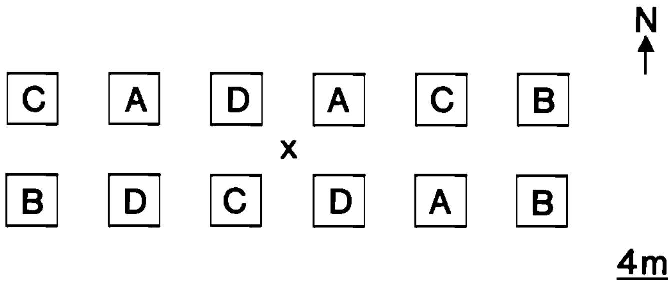

Fig. 1. Spatial arrangement of experimental plots. Each plot contained 36 plants; polycultures contained equal numbers of each plant species present. A = potato monoculture, B = melon monoculture, C = potato-melon-bean-polyculture, and D = potato-melon-bean-corn-tomato-broccoli polyculture. X = release site for mark-recapture study.

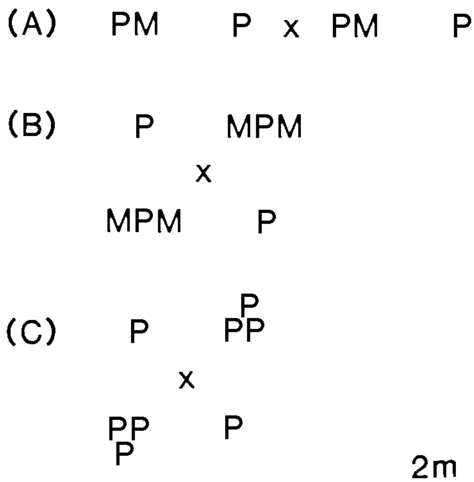

Fig. 2. Spatial arrangements of potted host and non-host plants for three experiments on host plant colonization: (A) the influence of a nearby non-host plant, (B) the influence of surrounding non-host vegetation, and (C) the influence of host plant density. P = potted potato plant. M = potted melon plant. X = release points for mark-recapture studies.

different plot other than the four plots at the center of which the beetles were released; this individual was found in a nearby potato monoculture.

Fourteen of the 16 beetles found were found more than once: eight were found on two of the four sampling days after release, five were found on three days, and one was found on all four sampling days. All of these individuals were found on the same plant on the different sampling days except one individual, which was found on a neighboring plant in the same plot. None of the individuals were found 19 days after release. Thus, maximum lengths of tenure on the same plant were eight days (n = 1) and nine days (n = 2). However, these represent low estimates since the plants were not sampled between 9 and 19 days after release.

Results from this release indicate that beetles are very stationary and do not appear to discriminate between host plants growing under different conditions, since they remained on whatever plant they first colonized. Thus, it was necessary to conduct experiments on a smaller scale with potted plants placed close together.

INFLUENCE OF NEIGHBORING NON-HOST PLANTS

When beetles were released equidistant from one potted potato plant and one potted potato plant growing next to a potted melon plant, seven out of the 15 beetles were found at least once on the potato growing next to the melon and two of the 15 were found on the potato growing by itself (Table 2A). No individuals were found on other potato plants in the area and none ever transferred from plant to plant.

In addition to greater colonization of the potato growing next to a non-host, individual beetles stayed in that treatment for a longer period of time. Three of the five individuals which originally colonized the potato next to a melon were still there five days later, whereas the two individuals which colonized the potato by itself stayed only until two days after release. Although statistics are not justified with such small sample sizes, the trends are consistent with results from the releases between large experimental plots. Again, there is no support for the prediction that the presence of non-host plants decreases colonization and tenure time.

A second experiment testing the effect of non-host neighbors was conducted to determine if the results of the first experiment were simply an artifact of the experimental set-up (i.e., because the potato was the first plant with which the beetles had contact and because only one replicate of each treatment was used) or if the beetles were actually unaffected by the presence of non-host plant neighbors. When beetles were given a choice of potato alone or potato surrounded by non-host vegetation, a very different pattern of colonization resulted. Seven out of 11 beetles released (64%) colonized the potato alone, whereas only two (18%) colonized the potato with surrounding non-host vegetation (Table 2B). No individuals were ever found on a different plant from the one on which they were originally found. Again, there appeared to be a difference in how long individuals remained on plants in the two treatments, but the results were opposite to those found in the first experiment. In this case, more individuals went to potato growing alone and they were also found for a longer period of time (over three times as long) on the potato growing alone (Table 2B).

To understand more about the response of the beetles to non-host plants, beetles were placed on non-host plants and host plants growing alone and near non-hosts. No beetles placed on melon were ever found on melon, even one day after release. In contrast, all five individuals placed on potato plants (both growing alone and growing next to a melon) were found at some time on the same potato plant on which they were originally placed (and none were found on a different potato plant). There was clearly no difference in the number of beetles remaining on potatoes growing alone (5,5,4, and 2, on 1,2,3, and 5 days after release, respectively) versus potatoes growing next to melon (4,4,4, and 2 on 1,2,3, and 5 days after release, respectively) or in the length of time remaining (potato alone, $n = 5$, $\bar{x} = 3.6$ days; potato next to melon, $n = 5$, $\bar{x} = 3.6$ days).

Of the beetles placed on melon, four were later found (three on the potato next to the melon and one on the potato growing alone 2 m away). These four individuals spent an

Table 2. Results of experiments testing the influence of neighboring non-host plants on colonization of potato plants by Colorado potato beetles. Number of beetles found on potato plants after being released between two different spatial arrangements of host and non-host plants: (A) potato growing by itself (P) versus potato growing next to melon (PM); (B) potato growing by itself (P) versus potato growing surrounded by melon vegetation (MPM).

		Days after release			
		1	2	3	5
(A)	P	2	2	0	0
	PM	5	7	3	3
		1	2	4	7
(B)	P	6	4	4	2
	MPM	2	2	0	0

average of 3.2 days on the potato to which they moved. Again, there were no plant to plant movements once beetles originally located a host plant.

INFLUENCE OF HOST PLANT DENSITY

Results from the final experiment on response to plant density indicate that beetles do not discriminate between areas which differ in the amount of host plant resource. There was no difference in the number of beetles found over time in areas with one potato plant (3,3, and 2 beetles on 1,3, and 6 days after release) versus three potato plants (3,3, and 1 beetle on 1,3, and 6 days after release), although five different individuals were found in the single potato treatments versus three different individuals found in the triple potato treatments. Thus, the three times as much plant biomass in the high density potato treatment did not attract more beetles, not did beetles stay longer in that treatment.

DISCUSSION

Results from this study indicate that the Colorado potato beetle does not appear to be negatively affected by plant diversity (either in terms of colonization or tenure time) when neighboring non-host plants are growing near host plants (as in the releases between experimental plots and the releases between single potato plants growing alone and growing near melon). Beetles did not preferentially colonize monocultures, nor did they have greater tenure times in less diverse habitats (as found for cucumber beetles, *Acalymma* spp., by Bach 1980a, 1980b; Risch 1981). Instead, beetles appeared to randomly colonize potato plants and remain on whatever plant they colonized, irrespective of the type of plot in which it was growing.

However, beetles did show less colonization and shorter tenure time when non-host plants were surrounding and physically touching the host plants; this presumably resulted from the beetles immediately leaving non-host plants after coming into contact with them (as shown by the releases on melons). Thus, beetles do not seem to be affected by visual or chemical stimuli from non-host plants (as reported for flea beetles in Tahvanainen and Root 1972), but only by direct physical contact. The presence of non-host vegetation similarly reduced colonization in a lepidopteran herbivore on *Aristolochia* (Rausher 1981) and reduced both colonization and tenure time in a tropical cucurbit specialist, *Acalymma innubum*.

Differences in plant quality have been implicated in many studies of the effects of plant dispersion on herbivores (see review by Kareiva, in press). However, the differences in colonization and tenure time in treatments which differed in plant dispersion reported in this study could not have resulted from differences in plant quality, since this was controlled for in the experiments with potted plants. In fact, part of the reason for the lack of a response to the amount of host plant resource, even when manipulations of host dispersion were done on a very small scale, may have been because the plants were all approximately the same quality.

The high recapture rates reported in this study indicate that Colorado potato beetles appear to be much more stationary than other insects for which mark-recapture studies have been done. Even when beetles were marked (which presumably disturbs them to some extent) and placed on non-host plants, they did not leave the study area, but simply moved to the closest host plant. In the experiments with potted plants, a total of 40 beetles (or 71%) were later found, and 12 of these were found at least five days after release. Moreover, none of these 40 beetles ever were found on more than one plant.

These high recapture rates definitely do not result from less herbivore movement caused by the marking technique. A separate experiment was conducted which compared the recapture rates over time of 13 marked beetles and nine umarked beetles. These beetles were released and recaptured in a potato-melon-bean polyculture with no Colorado potato beetles present. There was no difference in the proportion found of marked beetles versus unmarked beetles on any of the four sampling days after release (½ day, $\chi^2 = 1.8$; 1 day, $\chi^2 = 0.3$; 3 days, $\chi^2 = 0.3$; and 5 days, $\chi^2 = 0.001$; $P > 0.05$ for all).

Few studies have individually marked herbivorous beetles, thus making cross-species comparisons difficult. However, these results on Colorado potato beetles can be directly contrasted with results from a similar study of another specialist chrysomelid, the striped cucumber beetle, *Acalymma vittatum* (= *A. vittata* [Munroe and Smith 1980]) When individuals of *A. vittatum* were released between small experimental plots (cucumber monocultures, cucumber-corn polycultures, and cucumber-tomato polycultures, see Bach 1981 for experimental design), there was a much lower percentage recapture (22%). Eight out of the 10 beetles found went to monocultures, in direct contrast to the random colonization of plots by Colorado potato beetles. Only two individuals of *A. vittatum* stayed on the same plant for more than two days, again emphasizing the relative lack of movement in *Leptinotarsa decemlineata*. Finally, 30% of *A. vittatum* which were found transferred plants (two to other plots, one to another plant in the same plot), whereas only one Colorado potato beetle out of a total of 56 beetles later found, ever was found on more than one plant.

Although the sample sizes for the studies reported in this paper are small, the trends certainly suggest that specialist chrysomelids can respond very differently to plant dispersion, and these different responses appear to result primarily from differences in movement behavior. Clearly, the weak flying ability of *Leptinotarsa decemlineata* (Radcliffe 1982) and its "feigning death" response to disturbance contribute to the lack of discrimination between different host plant densities, as well as between host plants alone and hosts near non-hosts. This study emphasizes the important role of herbivore movement patterns in understanding and predicting how a particular herbivore species will respond to plant dispersion and the subsequent effects on host plant population dynamics.

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