Habitat manipulation in potato affects Colorado potato beetle dispersal

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Abstract

Increased habitat complexity in agricultural fields can alter the movement of pests into or within a field. Using a mark–release–recapture method with Colorado potato beetle [*Leptinotarsa decemlineata* (Say)], we compared the tenure time and dispersal of marked insects released within experimental potato fields to those released at the field borders in three trials in summer 2006. Plots within fields had rye, vetch or no plant residues. Movement of marked Colorado potato beetles into the tilled plots was significantly higher than into vetch or rye cover treatments. The abundance of naturally occurring beetles in the three cover treatments followed the general patterns of the number of marked immigrants over all releases. Marked beetles released inside the potato field tended to move along the release row rather than across rows; this pattern was stronger for the tilled treatment than for the two mulch cover treatments. Marked beetles disappeared from within the potato fields differently, depending on the cover crop treatment, but the patterns were not consistent over the season. Incorporation of dispersal patterns into pest management strategies should improve methods of pest population regulation, especially for the initial colonization of fields.

Introduction

The Colorado potato beetle [*Leptinotarsa decemlineata* (Say); Coleoptera: Chrysomelidae] is a significant pest of potatoes in North America and Eurasia and can cause severe defoliation and yield loss (Ferro 1985; Weber and Ferro 1994b). Managing the Colorado potato beetle with intensive pesticide applications has led to resistant populations (Forgash 1985; Ioannidis et al. 1991; Stewart et al. 1997) which make alternative methods of control imperative. Habitat manipulation of agricultural fields is a potentially viable ecologically based approach for Colorado potato beetle management that could provide a non-chemical preventative strategy for population regulation of this pest (Weber and Ferro 1994a; Schmera et al. 2007).

In a previous study, increasing host plant density and diversity reduced all stages of the Colorado potato beetles in potato fields (Horton and Capinera 1987); the authors suggested that increased time and energy costs of movement in a high plant diversity potato plot could be responsible. Physical plant characteristics were important in reducing walking speeds of the Colorado potato beetle in turf or tall wheat-crops compared with bare ground (Ng and Lashomb 1983; Lashomb and Ng 1984; Schmera et al. 2007). Reduced colonization rates by Colorado potato beetles were found in the presence of non-host plants (Bach 1982; Zehnder and Hough-Goldstein 1990) and tenure time was reduced in non-host habitats (Weber and Ferro 1994a). Colorado potato beetle populations are negatively affected in the presence of mulch in potato and

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711

tomato fields (Zehnder and Hough-Goldstein 1990, Brust 1994; Stoner et al. 1996; Hunt 1998; Teasdale et al. 2004), though the underlying mechanism for this is unclear.

In Maryland, Colorado potato beetles have at least two full generations, overwintering as adults and emerging in April and May to locate and feed on plants. Colorado potato beetles colonize rotated fields in the spring by arriving from the field margins or other nearby areas. Once settled, they spread throughout the field and complete their lifecycles, usually without leaving it until the potatoes senesce.

Growing two or more plant species in the same agricultural field simultaneously can reduce the yield of the cash crop because of plant competition; this raises questions about the applicability of this method as a pest management strategy in agricultural production (Andow 1991; Bottenberg et al. 1997). The current study investigated the effects of plant residues, as this approach is more likely to be incorporated into growers' management strategies. While plant competition is mitigated if plant residues are used, these may have a different range of effective stimuli for managing pests when compared to live plants.

The first goal of this study was to determine the beetles' dispersal responses to habitat differences, by comparing movement within a field with hosts present nearby with movement from near the field border into the field. The second goal of this study was to investigate the effects of two types of plant residues in the row middles of potato fields on tenure time and dispersal of the Colorado potato beetles and compare them with a conventionally tilled control.

Materials and Methods

Experimental plots

Moor et al. (1994) described a cover crop mulch system resulting from planting a winter hardy cover crop in the autumn, killing the cover crop with an herbicide the following spring and mowing the cover crop to form the mulch on the soil surface before planting. We modified this method by leaving the cover crop standing and planting the potatoes into the living cover crops, followed by the application of a pre-emergent herbicide to reduce the plant–plant competition for the potatoes. Cover crops were seeded on 2 September, 2005 in 12 × 49 m plots in a 1.2 ha experimental field that was fallow in the previous year. The two cover crops tested in this study

were winter rye (*Secale cereale* L., 100 kg/ha) and hairy vetch (*Vicia villosa* Roth, 56 kg/ha). Tilled plots received crimson clover (*Trifolium incarnatum* L., 49 kg/ha) in the autumn which was treated with herbicide (glyphosate, 1.2 L/ha) on April 6, 2006 and cultivated a week thereafter to remove the cover crop. Potatoes (*Solanum tuberosum* L. 'Kennebec', 2027 kg/ha) were planted on 27 April 2006 in a 73.5 × 30 cm spacing. Rye and tilled plots were treated with herbicide (paraquat dichloride, 2.4 l/ha) on 1 May, 2006, and vetch plots were treated on 16 May, 2006. Vetch was not included in the first sampling, because the emerging potatoes were slightly affected by the herbicide application, but plants overcame this effect by the second release. The three cover treatments were randomized with two replications in an experimental field located in Beltsville, Maryland, USA (fig. 1). The potato field was not treated with herbicides during the experiment, but insecticide (73 ml/ha of SpinTor 2SC, equivalent to 17.5 g AI/ha of spinosad, corresponding to 1/6th–1/3rd of the labelled rate for Colorado potato beetle on potato) was applied to the release area 1 week
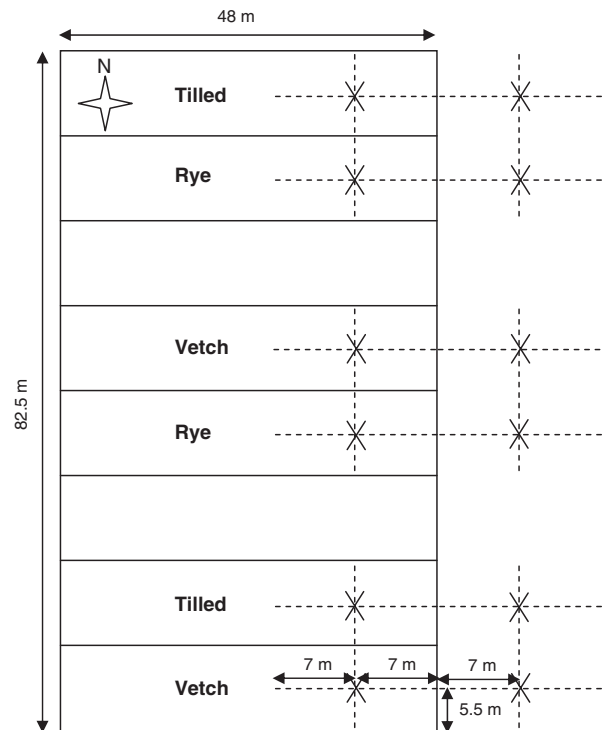
Fig. 1 Map of the potato field used for the mark–release experiment with Colorado potato beetles adults on 26 May, 6 June and 7 July, 2006 within or near a 1.2 ha potato field in Beltsville, Maryland, USA. 'X's mark release points and dashed lines represent transects for subsequent sampling to enumerate marked beetles.

after the first and second releases to avoid excessive damage by the marked beetles to the potato plants near the release point. As the same area of the field was used for subsequent releases, spinosad was chosen to minimize any potentially harmful chemical effects on released insects. Spinosad is a biologically derived insecticide that is classified as an organic substance by the USDA National Organic Standards Board (Anonymous 2002). Spinosad residues degrade quickly in the field, with little residual toxicity at 3–7 days post-application (Williams et al. 2003).

Mark–release methods

Colorado potato beetles for marking were collected by hand from a potato field located 1.6 km from the experimental field. Beetles were collected 24 h before the releases and were held in groups of 100 individuals per plastic container (5 l). Containers were lined with moist paper towels to provide beetles with water during handling. Marking was performed in the laboratory by puncturing the outer surface of the elytra (Unruh and Chauvin 1993) using a #7 insect pin (Bioquip, Rancho Dominguez, CA, USA). Such marks are permanent and do not alter beetle behaviour (Unruh and Chauvin 1993). Marks were coded for treatment, date of release and location of release using the specific location of one mark in one of the long three cream coloured bands of the elytra. Beetles were held overnight in an environmental chamber (25 ± 1°C, 50 ± 10%RH, 16 : 8 L : D), and released in the field between 07:30 and 08:00 h on 26 May, 6 June and 7 July, 2006. A total of 7200 beetles were released over the three dates by releasing 200 beetles at 12 locations on each of the three dates (fig. 1). In the grassy border, two containers with beetles were placed adjacent to each other on the grass; inside the potato field two containers were placed in the row middle on either side of a focal potato plant. Beetles were released by gently placing the container on the ground and removing the lid. Beetles were relocated on focal plants with minimal disturbance at 6, 24, 72 and 168 h after the release. The focal plants were located along two transects forming a cross, one parallel and the other perpendicular to the edge of the potato field, with the release point at the intersection of the two lines (fig. 1). All plants along the two transects were checked for the presence of beetles within 7 m of the release point. In the field border the same relocation pattern was used; vegetation was checked every 30 cm. The location coordinate, number of marked and naturally occurring beetles per location, and the origin of the beetle was recorded at the time of relocation, but the beetles were not otherwise disturbed.

Statistical analyses

We determined that our count data followed a Poisson distribution, thus we used a standard contingency table/log-linear analysis. One property of a Poisson distribution is that the mean equals the variance, therefore approximate standard errors for estimated means or total counts are the square root of the estimates.

We used chi-squared tests to compare differences in the total numbers of beetles between the two spatial replications (Sokal and Rohlf 1995). Chi-squared tests were also used to compare the numbers of marked beetles found inside and outside the potato field, to determine whether beetles released at the perimeter differentially preferred entering fields with particular treatments and to compare the number of naturally occurring unmarked beetles between treatments. Comparison of numbers of beetles moving along vs. across rows was done with continuity adjusted G^2-tests (Sokal and Rohlf 1995).

As fewer beetles moved across the rows and we hypothesized that patterns of movement might differ across rows vs. along rows, we analysed in detail only the number of marked beetles that moved along a row of potato plants among those that were released inside the field. Movement patterns of these beetles were first summarized using histograms that charted the frequency distributions of distances moved. Based on these histograms, we created five distance classes that grouped beetles according to their distance from the release point. We used log-linear modelling (R Statistical Software, 2008), separately for each release date, to determine the relationship among treatments, distance classes and relocation times. An important subset of this analysis was to determine whether the change in the total number of marked beetles over time differed among treatments, which may indicate treatment suitability to the beetles when released in a particular environment.

Results

Perimeter release and endemic population

The total number of beetles found in the spatial replicates was not significantly different for marked ($\chi^2 = 0.49$, d.f. = 1, P = 0.48) or for unmarked

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713

beetles ($\chi^2 = 0.11$, d.f. = 1, P = 0.74), therefore data for all subsequent analyses were collapsed over the two spatial replicates. Few perimeter released beetles remained in the border of the field (976 individuals found in the border vs. 3659 in the potato field, $\chi^2 = 41.46$, d.f. = 1, P < 0.01, summing over the three releases). Significantly more marked beetles moved from the field perimeter into the tilled plots than into plots with rye cover crop in the second ($\chi^2 = 13.04$, d.f. = 1, P < 0.01) and third releases ($\chi^2 = 4.06$, d.f. = 1, P = 0.04) (fig. 2a). Beetle movement into plots with rye compared with vetch cover crop was significantly lower only in the second release ($\chi^2 = 4.92$, d.f. = 1, P = 0.03) and the total numbers were not significantly different between tilled and vetch treatments in any of the releases

(fig. 2a). The abundance of naturally occurring beetles' response to treatments differed significantly for the second and third releases (release 1: $\chi^2 = 2.25$, d.f. = 1, P = 0.13; release 2: $\chi^2 = 22.51$, d.f. = P < 0.01; release 3: $\chi^2 = 52.95$, d.f. = 2, P < 0.01) with the highest abundance in tilled plots and the lowest in rye, with a consistent pattern over the three release dates (fig. 2b).
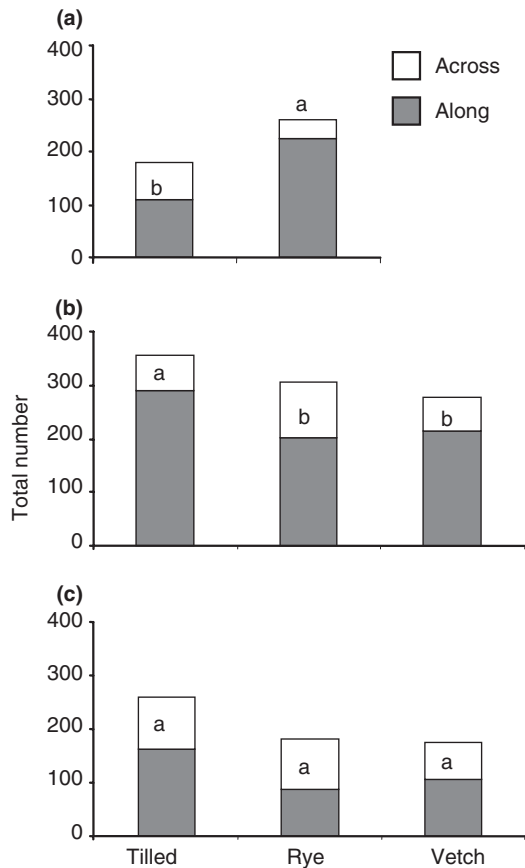
Inside release

The total number of relocated marked beetles inside the field was not significantly different ($\chi^2 = 0.41$, d.f. = 2, P = 0.81) among the three cover treatments in any of the releases (fig. 2c). Overall, beetles moved away from the release point within the release row rather than across the rows in all three releases ($G^2 = 36.67$, $G^2 = 19.57$, $G^2 = 9.71$ for the three releases respectively, all d.f. = 1, and P < 0.01). Examining cover treatments individually, we found inconsistent effects (fig. 3). For example, in the first release, significantly fewer beetles moved across the rows in rye than in tilled treatment ($G^2 = 11.05$, d.f. = 1, P < 0.01). In the second release, this trend was reversed; more beetles moved across rows in rye cover crop than in tilled ($G^2 = 11.67$, d.f. = 1, P < 0.01). In the third release, there were no significant differences among the three cover treatments ($G^2 = 5.77$, d.f. = 2, P > 0.05).

The analysis of beetle counts in the five distance classes (defined in fig. 4) from the release points yielded a log-linear model with all two-way interactions as the highest-order terms required to describe our empirical data (table 1, fig. 4). The significant interaction between distance class and time after release occurs because as beetles disperse over time, more beetles will accumulate in the distance classes further away from the release point (fig. 4). The significant interaction between relocation time and treatment indicates that beetles disappeared at different rates from the treatments; the declines were more gradual in the second and third releases. The significant interaction between distance class and treatment implies that beetles did not move at the same rate among treatments or, for the same distance class, beetles disappeared at different rates among treatments or some combination of these two factors (fig. 5). Regardless of the type of row middle treatment, less than half of the released individuals were found 6 h after the second and third releases (fig. 5) and they disappeared more rapidly from the two releases later in the growing season.
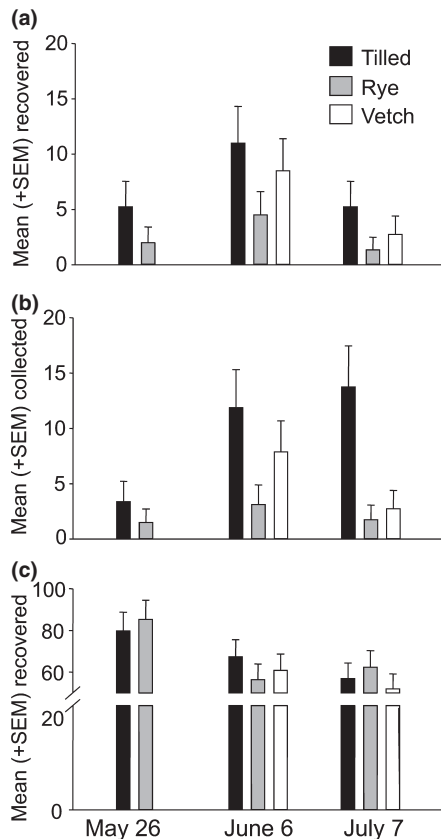
Fig. 2 Response of marked and released or naturally occurring Colorado potato beetle adults to habitat manipulation. Mean (+SEM) per block (a) marked Colorado potato beetles released on the field perimeter and recovered inside the experimental potato plots; (b) naturally occurring Colorado potato beetles collected in the experimental potato plots and (c) marked Colorado potato beetles released and recovered inside the experimental potato plots for three cover treatments and three releases.

Fig. 3 Total numbers of marked Colorado potato beetles released and relocated inside the experimental potato field, moving along and across rows of potato plants for the three releases (Release 1: 26 May; Release 2: 6 June and Release 3: 7 July, 2006). Letters on bars within a graph denote significant differences among the numbers of beetles moving across the rows in three types of cover treatments (P < 0.05).

Discussion

The purpose of this study was to investigate the role of habitat complexity on dispersal of Colorado potato beetle. The experiment provided information on insect movement into the field and insect redistribution within the field in the presence of variable plant residues. As potatoes are often grown in rotation (as in our experimental field), the main source of beetle infestation is typically from outside the focal field. Once the beetles are established in the potato field, their spread to uninfested parts of the field is undesirable, thus, the role of both dispersal processes is important to pest managers.

Field colonization

Our releases of marked beetles on the field perimeter and the surveys of the endemic (naturally occurring)

beetle populations yielded similar beetle distributions among the treatments. Both data sets indicated that significantly more beetles moved from the field perimeter into tilled compared to plots with cover crops. In previous studies, endemic Colorado potato beetle populations were also significantly reduced in crop fields with straw mulch (Zehnder and Hough-Goldstein 1990; Brust 1996; Stoner et al. 1996; Stoner 1997). The similarity of the distribution of marked beetles arriving from the field border (fig. 2a) and of naturally occurring beetles (fig. 2b), suggests that the natural population levels are the result of a similar colonization pattern. This result was consistent for all three releases, thus beetle behaviour in our experiments did not vary with the age of beetles or the day of release. Our finding is important because it reveals that plant residues interfere with beetle behaviour during the process of field colonization.

These results, however, do not provide an explanation for the mechanism of the reduced colonization in the presence of cover crop mulches, and this will be the focus of future investigations. Habitat diversification could provide long-range cues such as olfactory orientation to host plants: Colorado potato beetles are attracted by host odours but this may be disrupted when non-host plant odours are mixed into the odour blend (Thiery and Visser 1986). In experiments, Colorado potato beetles have been preferentially attracted to the colour that had the same peak reflectance wavelength as that of the potato leaf (Zehnder and Speese 1987), thus the addition of non-hosts could visually disrupt long-range host finding behaviour. Microclimate differs in straw-mulched and tilled plots; soil temperature is lower and soil moisture is higher (Zehnder and Hough-Goldstein 1990). Adults are highly responsive to temperature and solar radiation, which influences their behaviour and movement within the habitat as well as tendency to take to flight (May 1982; Boiteau et al. 2003). Alyokhin et al. (2005) found substantially lower Colorado potato beetle populations in manure amended potato plots, and beneficial direct effects of the cover crops on the potatoes may have contributed to lower Colorado potato beetle pressure in our experiments as well.

Of the three mulch treatments, the overall differences between the effects of rye and tilled treatments were more pronounced than the differences between vetch and the other two treatments. The total biomass per hectare of rye and vetch treatments was similar at planting, and typical for the growing area and region, approximately 5 tonnes/ha
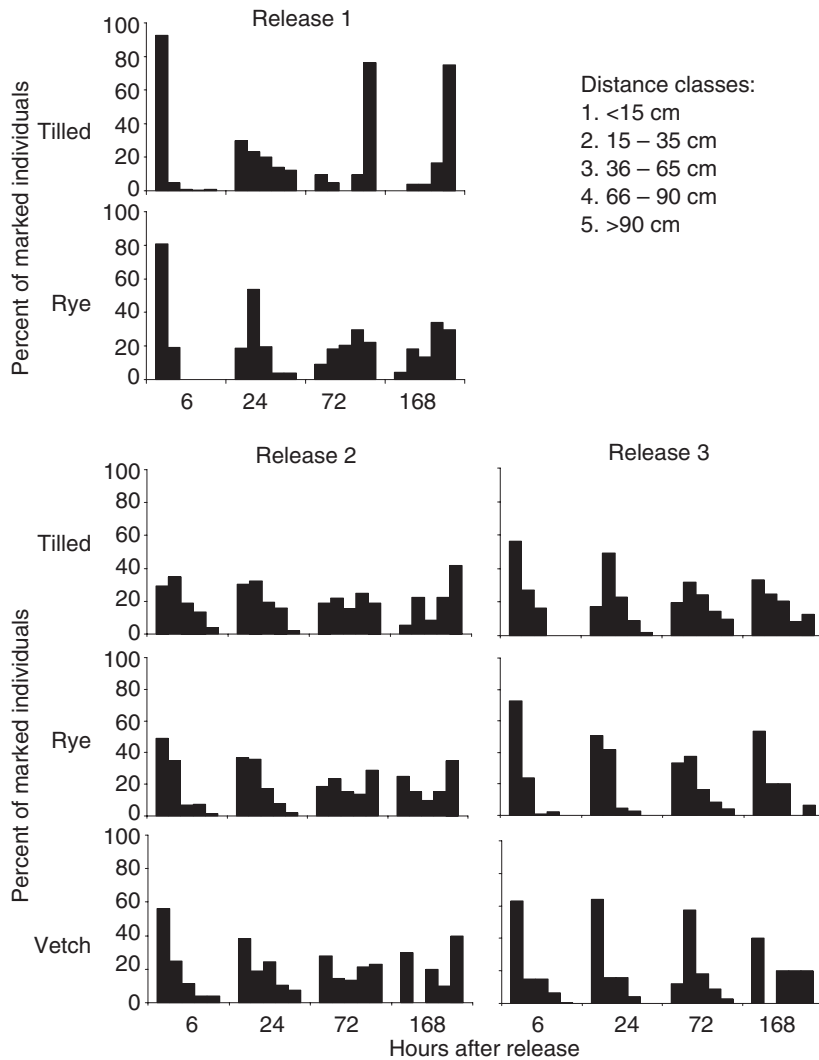
Fig. 4 Marked Colorado potato beetle dispersal in an experimental potato field in Beltsville, MD with three ground cover treatments. Bars represent the proportion of beetles in different distance classes from the release point 6, 24, 72 and 168 h after release for three releases (Release 1: 26 May, Release 2: 6 June and Release 3: 7 July, 2006).

Distance classes:
1. <15 cm
2. 15 – 35 cm
3. 36 – 65 cm
4. 66 – 90 cm
5. >90 cm

Table 1 Chi-square values from log-linear analyses for three releases; all values shown are significantly different from zero ($\alpha = 0.01$)

Source	Release 1	Release 2	Release 3
Time × treatment	26.57	17.77	21.16
Distance class × treatment	77.92	46.58	46.58
Distance class × time	639.55	181.79	97.45

including <16% non-cover crop weeds (D. Weber, unpublished data). One of the obvious physical differences between the two mulch treatments was that the rye residue was as tall as the mature potato plants, whereas the vetch mulch was only *c.* 5 cm tall. Thus, the structure of rye, perhaps appearing as greater non-host vegetation biomass or presenting a stronger visual or chemical deterrence

and/or physical barrier, may discourage beetle colonization.

Dispersal within the field

Our results indicate that once beetles find themselves within a patch of suitable resources, row middle treatment does not affect residency time. In contrast to our results, when marked Colorado potato beetles were released on potato plants located in a wheat field, the recovery rate was significantly higher and the movement distance was significantly smaller in the wheat than in a fallow field (Schmera et al. 2007). Increased vegetation density negatively influenced Colorado potato beetle movement in other cropping systems (Ng and Lashomb 1983; Weisz et al. 1994; Schmera et al. 2007), thus it is likely that certain vegetation traits are important in
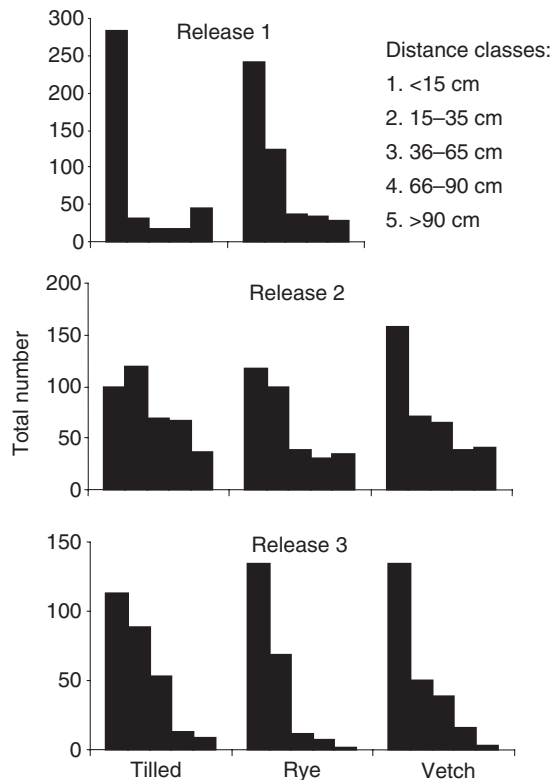
Fig. 5 The total number of marked Colorado potato beetles recovered at different distances from the release point in the three ground cover treatments and three releases (Release 1: 26 May, Release 2: 6 June and Release 3: 7 July, 2006) in an experimental potato field in Beltsville, MD. Total numbers are sums of insects recovered 6, 24, 72, 168 h after release.

determining the outcome of using non-hosts to reduce pest pressure.

Our log-linear model of the distances moved by beetles from the release points indicated significant differences among treatments, but the patterns of movement and disappearance were not consistent for the three releases. We relocated an increasingly smaller fraction of the beetles over time after release, so beetles actively moved around inside or moved out of the area regardless of the vicinity of suitable hosts. A steep reduction during the first 24 h after release was followed by a levelling off in the numbers of relocated marked individuals. In a mark–release study with grasshoppers, patch depletion was identified as a potential cause for the tendency to initiate movement (Bailey et al. 2003). In our case, this is also a potential explanation, because 200 beetles were released on either side of a focal plant which led to the consumption of potato plants near the release point, triggering dispersal. The sharp drop in numbers within the first 24 h after release could

also be attributed to the activity of predators (Brust 1994), that may aggregate in areas of high prey density. For example, we observed marked adults that were pursued by *Perillus bioculatus* (Fabricius), Hemiptera: Pentatomidae (Z. Szendrei, personal observation).

The variation in dispersal patterns among the three release dates was expected, as the beetles in the first two releases were from the overwintered generation (therefore the beetles in the first two releases were the same generation but different ages), while in the third release beetles were from the second generation. In our study, the majority of marked insects were relocated 6 h after the first release, and this may be due to the fact that early overwintered adults are recruited to the field in high numbers (Weber et al. 1995) and that post-diapausing individuals end the long-distance flight to the field with settling down to feed and reproduce. Subsequently, a portion of this population migrates to locate potential new hosts to allocate reproduction over space (Voss and Ferro 1990).

While in the first release the number of recovered marked insects stayed relatively unchanged between 72 and 168 h, in the second and third releases we found a slight decrease in the numbers of marked individuals as time from release increased. In the case of the third release, this may be the result of pre-diapausing adults' dispersal that comprises short-distance movements to reach the borders of the field to locate overwintering sites (Voss and Ferro 1990). In addition to this, cover crop mulches were biodegrading and potato plants were growing as the summer was progressing, creating a gradual reversal in the relative biomass of the two plants. In this experiment, the cover crops may have provided beetles with a more suitable microclimate during certain parts of the summer, but may have hindered them in mate finding, or increased the chances of predation in other parts of the season.

In summary, the greatest effect of increasing habitat complexity for Colorado potato beetle pest management was to reduce colonization. For beetles remaining in the area following colonization, subsequent dispersal was mainly within rows, especially for the tilled treatment, but was not otherwise affected by row middle residues in a systematic way.

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717

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719