PII: S0261-2194(97)00036-7

Crop Protection Vol. 16, No. 6, pp. 511–518, 1997

0261-2194/97 $17.00 + 0.00

Location and abundance of adult Colorado potato beetles (Coleoptera: Chrysomelidae) following potato harvest

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Colorado potato beetle, *Leptinotarsa decemlineata* (Say), population biology was investigated after Irish potatoes, *Solanum tuberosum* (L.), were harvested in eastern North Carolina. The abundance of adult Colorado potato beetles following potato harvest was estimated by taking more than 450 visual transects in 45 commercial potato fields in July and August, 1993 and 1994. Few second- and third-generation Colorado potato beetle egg masses and larvae, volunteer potato plants and wild hosts such as horsenettle, *S. carolinense* L., were encountered, suggesting that Colorado potato beetle generations produced after potatoes are harvested in June and early July do not contribute significantly to the overall overwintering population. Location and abundance of overwintering adult Colorado potato beetles within the soil in fields previously planted in potato were determined. Densities of overwintering adults in soil along field edges were greater than those within fields prior to emergence in the spring, suggesting that adults moved toward field edges to overwinter. However, given that the area within potato fields was much greater than the area along field edges, the estimated total number of overwintering adults within fields was greater than along the edges. In light of these results, tillage at different times between crop production seasons was evaluated for its effect on overwintering Colorado potato beetle survival, but was found to have little effect. © 1997 Elsevier Science Ltd

Keywords: *Leptinotarsa decemlineata*; Irish potato; overwintering; management

Introduction

The widespread occurrence of insecticide resistance has made the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), difficult and costly to manage in the eastern potato production areas of North America (Forgash, 1981; Heim *et al.*, 1990; Roush *et al.*, 1990). To address this problem, extensive effort has been directed toward the development of economical, non-chemical approaches to manage this pest. Recently, researchers have examined methods to increase overwinter adult mortality between crop production seasons (Kung *et al.*, 1992; Milner *et al.*, 1992), and to disrupt colonization of the crop in the spring (Lashomb and Ng, 1984; Wright, 1984; Zehnder and Linduska, 1987; Zehnder and Hough-Goldstein, 1990; Boiteau *et al.*, 1992, 1994; Moyer *et al.*, 1992; Weisz *et al.*, 1994; Weber *et al.*, 1994). However, the success of such measures requires knowledge of the overwintering sites of local Colorado potato beetle populations.

For example, previous research has found that most adult Colorado potato beetles overwinter in the upper $\approx$25 cm of soil (Ushatinskaya, 1978; Lashomb *et al.*, 1984; Milner *et al.*, 1992; Weber and Ferro, 1993). Therefore, disking soil prior to emergence of adult beetles in the spring may have the potential to increase mortality by direct injury. If tillage is to be effective in this regard, a large proportion of the local potato beetle population must overwinter within potato fields. In Massachusetts, many potato beetles overwinter along field margins near tree lines rather than within the fields (Weber and Ferro, 1993; Weber *et al.*, 1994), suggesting that efforts to control overwintering populations through tillage would be ineffective.

Boiteau *et al.* (1994) suggested that plastic-lined trenches used to trap overwintered adult potato beetles that colonize potato fields by walking should be placed between the crop and the location of the potato beetles' overwintering site to be most effective. If potato beetles overwintered within potato fields rather than along field edges near tree lines, trenches would not be likely to be effective in trapping these adults if the field was not rotated.

In North Carolina, most commercial potato fields are surrounded by drainage ditches, canals and other fields planted to potato, corn or small grain. The potato crop is typically planted in March and harvested in June or early July. Within a few days following harvest, most potato fields are planted to a second crop, usually soybean, but occasionally grain sorghum, and most growers rotate these fields with corn. Colorado potato beetle populations rarely complete more than a single generation in the potato crop before harvest. When provided with a continuous supply of potato foliage, potato beetle populations can complete three to four generations before entering the soil to overwinter in September (French, 1992). However, in the absence of suitable foliage after harvest, first-generation adult beetles that have fed on potato foliage for several days will enter the soil in July where most are likely to remain until the following spring (Nault *et al.*, 1996). In contrast, most first-generation adults that emerge after the potato crop has been harvested remain above the ground feeding on remnant tubers while searching for host plants. Unless they find suitable foliage to feed on for one to three days, most of these beetles die during the summer, without reproducing (Nault *et al.*, 1996).

In many potato production areas, wild solanaceous plants may serve as hosts for Colorado potato beetles (Hare, 1983; Hare and Kennedy, 1986; Horton and Capinera, 1990). In North Carolina, horsenettle, *S. carolinense* L., is the only wild host plant on which Colorado potato beetle populations are commonly observed (French, 1992). However, volunteer potato plants, produced from tubers left in the fields following harvest, are often present in August and September. Potato beetles developing on these hosts during the summer could potentially represent a significant portion of the overwintering population of potato beetles in North Carolina. This study was undertaken to determine if second- and third-generation adult potato beetles produced on horsenettle and volunteer potato plants during the summer contribute significantly to the overwintering population of potato beetles and to determine if beetle populations overwinter primarily along field edges or within potato fields. Information on the location of overwintering beetles is important to the development and use of procedures either to increase overwinter mortality or to disrupt the colonization of potato crops in the spring. An additional objective was to determine if different tillage practices affect the survival of beetles overwintering within potato fields.

Materials and methods

Second- and third-generation Colorado potato beetles on volunteer potatoes and horsenettle

The abundance of volunteer potato plants, horsenettle and second- and third-generation Colorado potato beetles was determined 4 to 8 weeks after the potato crop had been harvested by taking a total of 459 visual transects in a total of 45 fields in eastern North Carolina over 2 years. These fields, which were planted in potatoes earlier in the spring, were sampled during late July or August, 1993 or 1994. Fields were located in Pamlico, Pasquotank, Tyrell and Washington Counties, which are representative counties included in the major commercial potato production areas of eastern North Carolina. Many fields were selected for sampling based on previous knowledge of the occurrence of a substantial potato beetle population before potato harvest and the occurrence of horsenettle in past years. By sampling in these fields, the probability of encountering second- and third-generation potato beetles would be maximized.

Transects, perpendicular to the longest edge of the field, 1 m wide and equal in length to the width of the field, were searched visually for Colorado potato beetle lifestages, horsenettle and volunteer potato plants. The number of living and dead adult beetles, the number of adults feeding on remnant tubers on the soil surface and the numbers of horsenettle and volunteer potato plants in each transect were recorded. Depending on the size of the field, 4 to 12 transects per field were taken. In addition, at least one transect was taken along the longest edge of each field. Transect lengths in each field were measured and data were converted to a m^2 basis.

Above- and below-ground densities of first-generation adult Colorado potato beetles following potato harvest were compared in six fields. Data were taken at the same time the transects were taken. To determine the density of beetles in the soil, 10 soil samples were taken from randomly selected locations within the field and along field borders. Seven soil samples were taken within each field and three were taken adjacent to field borders. Each sampling unit was a $0.91 \times 0.25 \times 0.30$ m deep (0.07 m^3) section of soil. These and all other soil samples were sifted through 3 mm mesh screen to separate the beetles from the soil.

Location and abundance of overwintered adult Colorado potato beetles within fields

Portions of four commercial potato fields that had high Colorado potato beetle populations the previous year were sampled to determine location and abundance of overwintered adult potato beetles prior to their emergence in the spring. All fields were located in areas of intense potato production and bordered on at least two sides by other potato fields, as is typical for potato fields in eastern North Carolina. The fields designated as Hot Spot II, Hot Spot VI and Nutrina I were located in Washington County, whereas the field designated as R.E. James V was located in Pasquotank County.

Hot Spot II was planted in potato followed by soybean in 1992 and corn in 1993. Hot Spot II was bordered on the north and east by 2.5 m deep drainage canals and dirt roads, the other side of which were other fields planted to corn in 1992. It was bordered on the south by a 1 m deep drainage ditch, the other side of which was a field planted to potato in 1992. Sampling was restricted to an area of approximately 1.18 ha at the east end of Hot Spot II, which was heavily infested by potato beetles in 1992. The remainder of the field, which extended to the west, was only lightly infested and was not sampled. The soil in Hot Spot II was classified as Wasda muck.

Hot Spot VI was planted in potato followed by soybean in 1993 and corn in 1994. It was bordered on the north by a 2.5 m deep drainage canal across which was a large area of uncultivated land that had been clear cut several years earlier. The southern border of the field consisted of a dirt road across which was a 2.5 m deep drainage canal and Hot Spot II. Sampling was restricted to a 1.44 ha area in the southern half of the field. The soil type was also a Wasda muck.

Nutrina I was planted in potato followed by soybean in 1993 and corn in 1994. In 1993, it was separated from an adjacent field of potato on the west by a 1.5 m deep drainage ditch, and from a 2 ha soybean field on the east by a 0.5 m weed margin. The northern edge of Nutrina I was bordered by a 1.5 m deep drainage ditch, a paved road and several homes, all of which were surrounded by trees. The southern edge was bordered by a 4 ha sewage lagoon surrounded by mowed grass. A 1.13 ha portion of the northern half of Nutrina I was sampled. The soil type was classified as a Conetoe loamy fine sand.

R.E. James V was planted in potato followed by soybean in 1993 and corn in 1994. In 1993, it was separated from adjacent potato fields to the north and south by 1 m deep drainage ditches. The eastern border consisted of a 2 m deep drainage ditch across which was a field planted in soybean. To the west, a 1.5 m deep drainage ditch and a paved road separated R.E. James V from a field planted in potato. Sampling occurred in a 1.66 ha area in the western portion of R.E. James V. The soil type was classified as a Weeksville silt loam.

The location of overwintered adult Colorado potato beetles in these fields prior to emergence the following spring was determined by taking 40 soil samples per field on 2 March 1993 (Hot Spot II) and 1 March (Hot Spot VI), 5 March (Nutrina I) and 8 March 1994 (R.E. James V). Ten samples were taken from each of two field borders, which formed the intersection of tilled and untilled ground, and 20 samples were taken within the field. Sample locations were determined by a stratified random sampling plan. The sampling unit was a $0.6 \times 0.22 \times 0.3$ m deep (0.04 m^3) section of ground. Beetles were classified as either alive or dead. Because only elytra remained from some of the dead beetles recovered in a sample, one dead adult was recorded for every pair of elytrons encountered. Densities of overwintered adults in the soil along field edges and interiors were compared, as were the percentages of dead overwintered adults in each location, using the analysis of variance procedure PROC GLM of SAS at $P \leq 0.05$ (SAS Institute, 1990). The percentage of dead adults within each sampling unit was determined by dividing the number of dead adults in the soil by the total number of adults (alive plus dead) in the soil and then multiplying this quotient by 100. Neither living nor dead adults were encountered on the soil surface. There were two sampling locations (field edges and interior), each with 20 subsamples, arranged in a complete block design replicated four times (field = replicate). Data from the two edges of each field were not considered separately prior to this analysis. However, in an additional analysis data from each edge and the interior of each field were compared using analysis of variance (PROC GLM) and means were separated using LSMEANS at $P \leq 0.05$. Numerical data were transformed using a log function $(x+1)$, whereas percentage data were transformed using a square root function $(x+0.01)$ before analysis, but untransformed data are presented. Additionally, the overall number of living adult beetles overwintering along field edges and within fields was estimated by multiplying beetle densities in each location by the areas represented by field edge or field interior, as appropriate.

In a separate study in Hot Spot II, the number of adult Colorado potato beetles (alive and dead) in the soil in the fall of 1992 was compared with the number of adults in the soil before emergence in the spring of 1993 by taking 40 soil samples each year, half of which were along field edges and the remainder of which were within the field. The sampling unit was a $0.6 \times 0.22 \times 0.3$ m deep (0.04 m^3) section of ground. Samples were taken on 20 November 1992, immediately after soybeans were harvested, and again on 2 March 1993. Flags marked the specific locations of samples taken in November to ensure that corresponding samples taken in March were within ≈ 60 cm. This field was not tilled between sampling dates. The percentage of dead adults in the soil within field edges and the interior in November 1992 was compared with the percentage of dead adults in the soil in March 1993 using analysis of variance (PROC GLM; $P \leq 0.05$). Sampling location (field edges and interior) was considered as the main plot factor and sampling date (November and March) was considered as the subplot factor. The experiment was arranged as a split plot replicated 20 times. Data were transformed using a square root function $(x+0.01)$ prior to analysis, but untransformed data are presented.

To characterize the gradient of overwintered adult Colorado potato beetles extending from the field edge into the field, soil samples were taken along five transects perpendicular to the small drainage ditches bordering the south side of Hot Spot II. These samples were taken on each side of the ditch 0.15, 0.45, 0.75, 2.0, 3.2 and 7.75 m from the edge of the water in the ditch. The sampling unit was a $0.3 \times 0.22 \times 0.3$ m deep (0.02 m^3) portion of ground. Samples in Hot Spot II were taken on 3 December 1992.

The vertical location of adult beetles in the soil in Hot Spot II was determined on 15 December 1992. Soil samples were taken in incremental depths of 0–5, 6–10, 11–15, 16–20, 21–25 and 26–30 cm. Ten soil samples each were taken along the south edge and within the field (total = 20 samples). The sampling unit was a $25 \times 20 \times 5$ cm deep (0.0025 m^3) section of ground. The hardpan in this and all other fields in which soil samples were taken began approximately 30 cm below the soil surface, so most beetles should have been within 30 cm of the soil surface. The percentage of adults overwintering at various depths within a sample along the field edge was compared with the percentage of overwintering adults at these depths in the field interior using a repeated measures analysis of variance (PROC GLM and REPEATED statement) at $P \leq 0.05$. The experiment had two locations (edge and interior) and six depths arranged such that depth within each location was replicated 10 times. The percentage of adults at each depth within each sample was transformed using a square root function $(x+0.01)$ prior to analysis, but untransformed data are presented.

Effects of tillage on potato beetle survival

Several tillage regimens are common in commercial potato fields following potato harvest in North Carolina. To determine tillage effects on survival of overwintered potato beetles, an experiment was conducted in a field of Lynchburg sandy loam soil on the Peanut Belt Research Station near Lewiston, NC. All tillage practices were conducted using tractor-mounted equipment. Corn was harvested and the field tilled using a disc harrow in early September 1993, prior to the initiation of the experiment. On 17 September 1993, adult potato beetles were placed in groups of 50 in open-bottomed fiberglass screen cages in the field. These adults were obtained from a colony that had originated from individuals collected from a commercial potato field in May 1993 and maintained on actively growing potato plants in a greenhouse with a photoperiod of (15:9) (L:D) and day and night temperatures between 32.2 and 37.8°C and 21.2 and 26.7°C, respectively. These adults had access to potato foliage as food for one to two weeks following emergence as adults before they were released into field cages. Cut tubers were placed in each field cage as a food source for the beetles. The cages were $1.0 \times 0.5 \times 1.0$ m high. Soil was mounded around the base of each cage to prevent beetles from escaping. On 12 November, after beetles had entered the soil to overwinter, the number of dead beetles above the soil was recorded, the cages were removed and their locations carefully recorded. These data were used to estimate the initial number of diapausing adult potato beetles within each cage. In 1994, plots were subjected once to one of the following five commonly used tillage practices: winter bedding for potato on 9 February, spring bedding for potato on 22 March, spring bedding for corn on 6 April, disking for soybean on 3 May and no tillage. Each tillage practice disrupted the soil to a depth of ≈ 25 cm. All five treatments were arranged in a randomized complete block design replicated four times and there were two cages (subsamples) containing 50 beetles each per experimental unit. On 22 March, open-bottomed, fiberglass screen cages, $2.0 \times 0.5 \times 1.0$ m high, were placed as described above over the beetle-infested areas in each plot. Potato seed pieces, variety Atlantic, were planted in each cage on 25 March 1994. Cages were checked weekly for adults from 6 April through 12 May, and on 12 May the cages were removed and the soil under each cage sifted through 3 mm mesh screen. The percentage overwinter survival was computed by dividing the total number of living beetles recovered (i.e. emerged plus those in the soil on 12 May) by the quantity 50 minus the number of beetles that were dead on the soil surface at the time cages were removed the preceding November. Data were transformed using a square root function $(x+0.01)$ prior to analysis of variance for a randomized complete block design using PROC GLM at $P < 0.05$ (SAS Institute, 1990).

Results

Second- and third-generation Colorado potato beetles on volunteer potatoes and horsenettle

A total of 94 volunteer potato plants were observed in 17 of the 45 fields (38%) and a total of 759 horsenettle plants were observed along the edges of 13 of the 45 fields (29%). Rainfall and temperatures during the summers of 1993 and 1994 were normal for the region so it is unlikely that the densities of volunteer potato plants were unusually low. Over 700 live adult potato beetles were observed in 41 of the 45 fields (91%) even though volunteer potato or horsenettle plants were present in only 25 of the 45 fields (56%). Only 14 Colorado potato beetle egg masses and nine first instars were observed. One egg mass was on a volunteer potato plant, 11 were on horsenettle, and two were on soybean plants, while all nine larvae were on a single horsenettle plant. In addition, the volunteer potato plant with the egg mass also had on it an adult *Coleomegilla maculata* (DeGeer), one of the horsenettle plants with an egg mass also had on it an adult *Perillus bioculatus* (F.), and three of the egg masses on horsenettle had been preyed upon. *Coleomegilla maculata* and *P. bioculatus* have been shown to feed on Colorado potato beetle eggs and larvae in North Carolina (Hilbeck and Kennedy, 1996). Thus, only nine of the 14 egg masses might have hatched, but because larvae cannot survive on soybean, only seven of the egg masses might have produced larvae that could have survived.

Of the living adult Colorado potato beetles observed above the soil in the transect samples, 19 and 48% were feeding on remnant tubers in 1993 and 1994, respectively. The remaining living beetles were either on the soil surface or on volunteer potato, soybean or other plants. Thirty-seven ($n = 330$) and 84% ($n = 339$) of all adult potato beetles observed above the soil in the transects in which living and dead beetles were counted were alive in 1993 and 1994, respectively; the remainder were dead. In the six fields in which both above-ground transect and soil samples were taken in 1993, the mean number $\pm$ SEM of living beetles in the soil ($7.75 \pm 4.06/m^2$) was 86 times greater than above the soil ($0.08 \pm 0.03/m^2$). These data suggest that most adult potato beetles have either entered the soil, dispersed from the field or died during the first four to eight weeks after the potato harvest.

Location and abundance of Colorado potato beetles within fields

Overwintered adult Colorado potato beetles were more concentrated in the soil along field edges than in field interiors ($F = 13.87$; df = 1, 3; $P = 0.0337$). The densities (number/m^2) of overwintered adults were higher along at least one field edge than in the field interior of Hot Spot VI ($F = 8.08$; df = 2, 37; $P = 0.0012$), Nutrina I ($F = 3.72$; df = 2, 37; $P = 0.0337$) and R.E. James V ($F = 19.68$; df = 2, 37; $P = 0.0001$), whereas densities of adults were higher along both field edges than in the field interior in Hot Spot II ($F = 16.24$; df = 2, 37; $P = 0.0001$) (*Table 1*). Although the densities of overwintered Colorado potato beetles were greater along field edges than in field interiors, the estimated percentage of total living adults within field interiors was much greater than along field edges in each field (*Table 1*).

Overall mean percentage of dead (±SEM) overwintered adult potato beetles within the soil in field interiors (20.4±9.8%) was numerically greater than along field edges (5.3±2.8%), but the difference was not statistically significant ($P = 0.0833$). In Hot Spot II, Hot Spot VI and R.E. James, the mean percentage of dead adults within fields was greater than along field edges, but this difference was significant only in Hot Spot VI ($F = 7.49$; df = 2, 37; $P = 0.0019$) (*Table 1*).

In Hot Spot II, the mean (±SEM) percentage of dead overwintered potato beetles in the soil in November 1992 (field edges plus field center) and in March 1993 did not differ significantly ($P = 0.7927$), suggesting that mortality did not increase over winter (November = 12.7±3.5% and March = 12.5±3.9%). Similarly, the percentages of dead beetles in the soil along field edges (November and March) and in the field interior (November and March) did not differ ($P = 0.2517$), nor was the sampling location × sampling date interaction significant ($P = 0.0801$).

Steep gradients of living overwintered adult potato beetles within the soil were observed extending into two fields from a common field edge (*Figure 1*). The mean number of adults (±SEM) within the first 0.75 m of the south edge of Hot Spot II was 175.8±52.2 m^2, whereas the mean number of adults beyond this point up to 7.8 m was only 16.2±6.3 m^2. Similarly, the density of adults (±SEM) within the first 0.75 m of the northern edge of the adjacent field was 73.7±37.5 m^2, whereas the density of adults beyond this point up to 7.8 m was 26.3±15.7 m^2.

Nearly 75% of the adult potato beetles overwintered at a depth between 11 and 20 cm in Hot Spot II (*Table 2*). The vertical distribution of adults within soil samples between locations (i.e. field edge versus field center) did not differ ($P = 0.1448$), nor did the shape of this distribution (i.e. quadratic) differ between locations ($P = 0.3789$). The vertical distribution of adults within a soil sample pooled across locations was quadratic ($F = 9.10$; df = 2, 9; $P = 0.0069$) ($y = -18.93 + 6.30x - 0.20x^2$; $R^2 = 0.67$) (*Table 2*).

Effects of tillage on potato beetle survival

The mean percentage survival of overwintered Colorado potato beetles was not affected significantly by tillage at different times between growing seasons ($P = 0.2534$). Mean percentage survival (±SEM) values in the spring were 31.6±1.0, 37.9±2.8, 28.0±2.3, 34.9±3.7 and 37.4±6.2, after tillage on 9 February, 22 March, 6 April, 3 May or no tillage, respectively. Temperature and soil moisture conditions during the winter and spring of 1994 at this test site were typical.

Discussion

The low densities of Colorado potato beetle egg masses and larvae together with the low number of horsenettle and volunteer potato plants encountered in this survey indicate that second- and third-generation Colorado potato beetles produced after the potato crop is harvested contribute little to the overwintering potato beetle population that infests the potato crop in the spring in North Carolina. Thus, overwintered potato beetle populations in North Carolina consist primarily of first-generation adults, many of which enter the soil within or adjacent to potato fields after harvest.

The greater densities of first-generation adult Colorado potato beetles along one or more field edges than in the field interior indicates that adults

Table 1. Location and abundance of adult Colorado potato beetles in the soil prior to spring emergence in four commercial potato fields in eastern North Carolina

Field[a]	Location[b]	Mean (±SEM) number of adults/m^2 Alive[c]	Dead	% Dead adults (±SEM)[d]	Estimated total mean (±SEM) number alive[e]	Estimated % total alive
Hot Spot II	N edge	84.8±31.7 b	3.0±1.2	4.4±3.3% a	25,440±9510	8.2%
	Center	18.9±5.5 c	5.3±2.1	21.4±7.2% a	211,680±61,600	68.0%
	S edge	247.7±25.3 a	7.6±3.0	2.7±0.9% a	74,310±7590	23.9%
Hot Spot VI	E edge	105.3±21.7 a	9.8±5.1	9.1±4.1% b	21,100±4300	3.7%
	Center	39.4±10.3 b	11.4±2.4	29.0±6.4% a	551,600±144,200	95.9%
	W edge	12.9±2.8 b	0.8±0.8	3.3±3.3% b	2600±600	0.4%
Nutrina I	E edge	26.5±18.5 ab	1.5±1.5	0.7±0.7% a	7200±5000	10.9%
	Center	4.9±1.9 b	0.4±0.4	2.5±2.5% a	52,900±20,500	80.2%
	W edge	22.0±6.0 a	2.3±1.6	7.5±5.3% a	5900±1600	8.9%
R.E. James V	N edge	26.5±9.4 a	0.8±0.8	0.7±0.7% a	8000±2800	37.6%
	Center	0.8±0.5 b	0.4±0.4	4.9±4.9% a	12,800±8000	60.1%
	S edge	1.5±1.0 b	0.0±0.0	0.0% a	500±300	2.3%

[a]Hot Spot II, Hot Spot VI, Nutrina I and R.E. James V were sampled on the following dates: 2 March 1993, 1 March 1994, 5 March 1994 and 8 March 1994, respectively. [b]Numbers of soil samples taken after harvest along field edges and the center of the field were 10 and 20, respectively. [c,d]Means within a field followed by the same letter are not significantly different ($P<0.05$) (LSMEANS: SAS Institute, 1990). [e]Estimated number of living adult beetles within fields and along field edges determined by multiplying the mean number of adults per m^2 by either the total area of field center or field edge that was sampled. Total area of each field sampled is presented in the text.

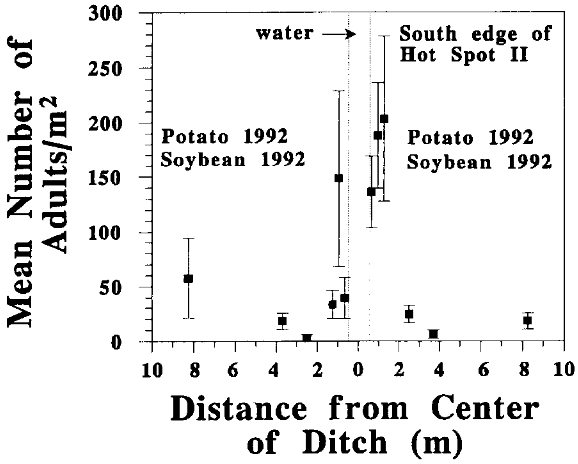

Figure 1. Density gradient (mean SEM) of overwintered adult Colorado potato beetles extending into two fields from a common field edge. Soil samples were taken 0.15, 0.45, 0.75, 2.0, 3.2 and 7.75 m from the edge of the water in the ditch into each field on 3 December 1992. Area to the right of 0 represents the south edge of Hot Spot II, whereas the area to the left of 0 represents the north edge of a field adjacent to Hot Spot II

tended to move from within the field to the intersection of field edges and field borders after harvest, where they remained until the following spring. This behavior may have been influenced by a combination of cultivation practices and the physiological state of the beetles. We offer two hypotheses that may explain this behavior late in the growing season.

In North Carolina, growers typically harvest fields beginning with the center rows, but often they may leave four to eight rows along each edge unharvested for up to one to two weeks. In this situation, adult beetles may move to edge rows after inner rows have been harvested. Nault *et al.* (1996) have shown that in field cages first-generation adult potato beetles that fed on non-senescent potato foliage for three to seven days entered the soil soon after foliage was removed in July. Because the availability of alternative hosts for potato beetles is limited after harvest, beetles are likely to enter the soil within field edges after these outer potato rows are harvested, provided that there are no unharvested potato fields nearby.

Alternatively, adult beetles may move towards field edges after potato harvest in June and July to diapause. Studies have shown that adult potato beetles can be stimulated, by either feeding on senescent foliage or by an interruption of feeding, to enter diapause even under long photoperiods (de Wilde *et al.*, 1959; de Wilde and Ferket, 1967). In

Table 2. Depth of overwintered Colorado potato beetles in the soil in Hot Spot II, a field planted in potato in 1992 near Roper, NC and sampled in December 1992

Depth (cm)	n	Mean ($\pm$ SEM) percentage of adults within a sample
0–5	20	0.3 ± 0.2
6–10	20	6.7 ± 2.1
11–15	20	29.3 ± 6.2
16–20	20	45.1 ± 7.0
21–25	20	7.6 ± 2.8
26–30	20	1.3 ± 0.8

Massachusetts, Voss and Ferro (1990) observed adult potato beetles dispersing from potato fields in August and early September in a 'diapause-mediated flight' towards surrounding woods. Weber and Ferro (1993) suggested that shrubs or tree-mimics adjacent to potato fields could be manipulated as 'diapause traps' late in the growing season to promote aggregation of adult potato beetles seeking overwintering sites. In contrast to the northeastern US where many potato fields are bordered by woods, many potato fields in North Carolina are bordered by weeds, which separate them from other fields, drainage ditches, canals and service roads. Weeds are often 1–2 m tall at the time potatoes are harvested and may provide a silhouette, similar to that of a distant tree line, that potato beetles may use as a visual cue for locating an overwintering site.

Overwintered adult Colorado potato beetle densities in the soil were higher within field edges than within field interiors. Weber and Ferro (1993) and Weber *et al.* (1994) also found overwintered potato beetles highly aggregated in the soil along the interface of potato fields and field borders. Similarly, our results and those of Weber and Ferro (1993) illustrate a dramatic decrease in the density of overwintered adult potato beetles in the soil within a short distance from the interface of potato fields and field borders. Although overwintered adult potato beetles were more concentrated (i.e. higher density) along edges than within fields, we estimated that the majority of the overwintering population was located within the field rather than along field edges (see *Table 1*). In contrast, Weber *et al.* (1994) estimated that only 14.9 and 44.4% of the total potato beetle population overwintered within a potato field in Hatfield and Whately, MA, respectively, while the remainder overwintered in habitats adjacent to fields, primarily woods. The differences in climate, size of potato fields and the habitat surrounding these fields in North Carolina and Massachusetts may be responsible for the differences in the overwintering location of the majority of adult potato beetles (see Introduction).

The percentages of dead overwintered potato beetles were generally greater within potato fields than along field edges, suggesting that the mortality rate was higher within the field than along field edges, but that the difference was rather small. Weber *et al.* (1994) reported similar results in two Massachusetts potato fields. In North Carolina, Nault *et al.* (1996) indicated that most of the mortality in the overwintering generation of potato beetles (i.e. first-generation adults) occurs during the summer following potato harvest, rather than during the winter.

In eastern North Carolina, French *et al.* (1993) observed more overwintered Colorado potato beetles colonizing potatoes in the spring along field edges than within fields in rotated and non-rotated fields. Overwintered adults clearly colonized rotated potato fields from the direction of the previous year's closest potato fields. An explanation for this same colonization pattern in non-rotated fields was less obvious. The authors presented two explanations for why colonization appeared to initiate from field edges in non-rotated fields: (1) density of overwintered adults was much greater along field edges than within fields, giving the impression that colonization initiated from the edge, or (2) adults had no preference in overwintering location, but mortality was significantly greater within fields than along undisturbed edges. Although we estimated that the percentage of dead adults was slightly higher within fields than along field edges, our results supported the first hypothesis. Additionally, the non-rotated potato fields examined by French *et al.* (1993) may have been close enough to fields rotated out of potatoes that overwintered beetles from these fields colonized the non-rotated fields from the field edge(s), which resulted in a greater number of adults (local plus immigrants) observed along edges than within the field.

Because a majority of potato beetles are likely to overwinter within potato fields in North Carolina, we hypothesized that tillage between growing seasons would disrupt these adults during diapause and result in increased mortality. However, results indicated that tillage had no effect on overwinter survival of Colorado potato beetles, despite the presence of a majority of adults in the tillage zone. Tilling prior to a change from mild to cold temperatures in the winter in order to lower soil temperatures and subject overwintering beetles to a thermal shock would not be likely to increase overwinter mortality in North Carolina. Soil temperatures would have to be lowered to $< -6°C$ for significant potato beetle mortality to occur (Kung *et al.*, 1992), but soil temperatures at or below this level are unlikely to occur in the major potato-producing regions in North Carolina. Based on the overwintering location of potato beetles, our results also suggest that plastic-lined trenches placed between a non-rotated potato field and the area immediately adjacent to the field will only minimally disrupt spring colonization by resident beetles in North Carolina.

Acknowledgements

We thank S. Barnes at the Peanut Belt Research Station, Lewiston, NC for cooperating with us on this project. Earlier reviews of this manuscript by F. Gould, R. Groves, K. Sorensen, J. Walgenbach (Department of Entomology) and D. Ferro (University of Massachusetts, Department of Entomology) were appreciated. We also thank D. Afra, T. Bacheler, B. Bumgarner, V. Covington, M. Etheridge and N. Robbins for their assistance in the field. This material was based on work supported by the US Department of Agriculture/Agricultural Research Service and the North Carolina Agricultural Research Service under Specific Cooperative Agreement No. 58-1275-3-034.

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Received 15 January 1997
Revised 3 April 1997
Accepted 4 April 1997