

DISPERSAL AND SPATIAL PATTERN OF THE COLORADO POTATO BEETLE,
Leptinotarsa decemlineata (SAY), ON POTATOES

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The University of Manitoba

by

Heather M. Morris

In partial fulfilment of the

Requirements for the Degree

of

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BY

HEATHER M. MORRIS

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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TABLE OF CONTENTS

	Page
LIST OF TABLES	v
LIST OF FIGURES	vii
ABSTRACT	viii
CHAPTER 1	1
INTRODUCTION	1
CHAPTER 2	4
LITERATURE REVIEW	4
Life cycle of the Colorado potato beetle	4
Spatial Distribution of the Colorado Potato Beetle	6
Migration and Dispersal of Colorado Potato Beetles	7
Incidence of Migratory Flight	8
Extrinsic Factors Affecting Flight	8
Intrinsic Factors Affecting Flight	10
Host Plant Relationships	13
Sensory Cues Involved in Host Location	14
Effect of Plant Communities	16
Environmental Effects on Host Plant Location	17
CHAPTER 3	19
PART 1: WITHIN-FIELD DISTRIBUTION OF COLORADO POTATO BEETLE, <i>LEPTINOTARSA DECEMLINEATA</i> (COLEOPTERA: CHRYSOMELIDAE), IN MANITOBA: EFFECTS OF FIELD CHARACTERISTICS, AND APPLICATION TO MONITORING METHODS	19
Abstract	20
Introduction	21
Methods	22
Results	26
Edge Effects	26

Effect of Field Characteristics	28
Using Edge Effects in Monitoring	29
Discussion	30
PART 2: DISPERSAL OF COLORADO POTATO BEETLES, <i>LEPTINOTARSA</i>	
<i>DECEMLINEATA</i> (SAY) (COLEOPTERA: CHRYSOMELIDAE),	
IN POTATO PLOTS	48
Abstract	49
Introduction	50
Materials and Methods	51
Results	53
Incidence of Beetle Movement	53
Direction of Movement	56
Discussion	56
Incidence of Movement	56
Direction of Movement	59
PART 3: DISPERSAL BEHAVIOUR OF THE COLORADO POTATO BEETLE	
(<i>LEPTINOTARSA DECEMLINEATA</i> SAY) ON CAGED POTATO PLANTS	76
Abstract	77
Introduction	78
Materials and Methods	79
Results	82
Larvae	82
Adults	84
Differences between Larvae and Adults	86
Discussion	86
CHAPTER 4	99
GENERAL DISCUSSION	99
LITERATURE CITED	103

LIST OF TABLES

	Page
TABLE 1. Characteristics of Fields Sampled	40
TABLE 2. Mean (\pm SEM) numbers per plant and variance/mean ratio (s^2/m) of different stages of Colorado potato beetles before insecticide applications in commercial fields	41
TABLE 3. Density of larvae per plant in third week of sampling and relationship with distance to field edge	42
TABLE 4. Analyses of covariance for $Z = X^{0.25}$ transformed densities of larvae in third week of sampling	43
TABLE 5. Comparison of methods of assessing which areas of fields have larval densities above or below a threshold density of 1 larva per plant (in the third week of sampling). Regression models were used to predict zones above and below the threshold; the table compares these predictions with the actual larval populations in the zones, as indicated by 1408 individual plant samples	44
TABLE 6. Potential reduction in sprayed area of applying the pooled regression model of untransformed larval density on \log_e distance from the edge of the field. The economic threshold is assumed to be 1 larva per plant in the third week of sampling	45
TABLE 7. Comparison of location of centrally-released overwintered and newly emerged Colorado potato beetle adults	62
TABLE 8. Effect of initial beetle density on location of overwintered beetles on the day of release	63
TABLE 9. Location of centrally released newly emerged Colorado potato beetles in a rectangular plot (2 x 8m) and a square plot (5 x 5m)	64
TABLE 10. Compass direction of movement of Colorado potato beetles	65
TABLE 11. Direction of movement of Colorado potato beetle in relation to wind direction	66
TABLE 12. Location of larvae in the cage 31 h after release	92

TABLE 13. Effect of initial density on the percentage of larvae moving from the middle plant. Note that N for percentages is the initial density on the middle plant 93

TABLE 14. Effect of initial density on the percentage of larvae moving from the middle plant 94

TABLE 15. Location of adult beetles in the cage 31 h after release 95

TABLE 16. Effect of initial density on the percentage of adults moving from the middle plant. Note N for percentages is the initial density on the middle plant. 96

TABLE 17. Effect of density at release site and adult stage and defoliation status of the release site on the percentage of adults which moved to another plant or moved but did not go to another plant 97

TABLE 18. Comparison of movement of adults and larvae at initial densities of 30 - 35 insects on the middle plant. Note that adults from defoliated release sites were newly-emerged, whereas those from undefoliated sites had overwintered 98

APPENDIX TABLE 1. Hourly weather conditions and location of centrally released overwintered and newly emerged Colorado potato beetle adults in 1984 experiment 67

APPENDIX TABLE 2. Hourly weather conditions and location of centrally released overwintered and newly emerged Colorado potato beetle adults in 1985 experiment 68

APPENDIX TABLE 3. Location of overwintered adult Colorado potato beetles released either singly on plants, or from a single central plant. The experiment was performed in 1984 69

APPENDIX TABLE 4. Location of centrally released newly emerged Colorado potato beetle adults in square and rectangular plots in 1984 . . 70

LIST OF FIGURES

Page

- Fig. 1. Diagram of potato field showing region from which transects were randomly selected, and zones of different sample intervals along transects. Samples were taken 1 m apart in zone E, 2 m apart in zone I, and 10 m apart in zone M 46
- Fig. 2. Examples of half-transects in their week of sampling. A. Field 910 North side, B. Field 910 South side, C. Field 210 East side, D. Field 210 West side. Note differing horizontal and vertical scales 47
- Fig. 3. Plans of plots used in mark release experiments. Dots represent individual potato plants. (a) 1984 Square plot; (b) 1984 Rectangular plot; (c) 1985 plot 71
- Fig. 4. Percentage of adult Colorado potato beetles moving in each compass direction in four mark release trials: overwintered beetles 1984, overwintered beetles 1985, newly emerged beetles 1984, and newly emerged beetles 1985. The height of bars represents the percentage of all movement steps within a trial which were in the indicated direction 72
- Fig. 5. Percentage of adult Colorado potato beetles moving in each compass direction in two mark release trials conducted in 1984: the scattered release method, and release in the rectangular plot The height of bars represents the percentage of all movement steps within a trial which were in the indicated direction 73
- Fig. 6. Percentage of adult Colorado potato beetles moving in each quadrant relative to the wind direction in four mark release trials: overwintered beetles 1984, overwintered beetles 1985, newly emerged beetles 1984 and newly emerged beetles 1985. The height of bars represents the percentage of movement steps within a trial which were in the indicated direction relative to the wind. Only movement steps during periods when wind direction was constant are included . . 74
- Fig. 7. Percentage of adult Colorado potato beetles moving in each quadrant relative to the wind direction in two mark release trials conducted in 1984: the scattered release method, and release in the rectangular plot The height of bars represents the percentage of movement steps within a trial which were in the indicated direction relative to the wind. Only movement steps during periods when wind direction was constant are included. 75

ABSTRACT

Morris, Heather, M. M.Sc., The University of Manitoba, June 1990. Dispersal and Spatial Pattern of the Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say), on Potatoes. Major Professor: N. J. Holliday.

The patterns of spatial distribution of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), were studied in commercial fields of potatoes in Manitoba in 1984 and 1985. At weekly intervals, plants were inspected at predetermined points along randomly selected north-south and east-west transects through each field. Data for larval abundance in the third week after plant emergence were most completely analyzed because this was the week in which insects were most abundant and is the week in which producers make their decisions on whether to control the insect. Except in one small field, all half-transects in which there were abundant larvae had the highest numbers at the edge of the field and low numbers in the middle of the field. The abundance of larvae was affected by potato cultivar, and the nature of this edge effect was influenced by proximity and size of windbreaks; neither were consistently affected by the distance of the nearest site of potatoes in the previous year. It is concluded that edge effects must be considered in sampling, and that in many fields insecticide application to the middle of the field may not be justified; a preliminary method of assessing what portion of the field should be sprayed is investigated.

The processes of dispersal which may affect distribution of Colorado potato beetles in fields were investigated by mark-release experiments of adults in field plots, and by studies of adults and larvae in a large cage in the laboratory. In both situations, adults and larvae tended to

disperse more rapidly if there were high densities at the release site than if there were low densities. In the field, adults tended to move most frequently to the northeast, less frequently to the south west, and infrequently in other directions; this pattern is attributed to the direction of rows in the plots, which were from northeast to southwest. Wind direction did not appear to be important in the field. In the laboratory cage, larvae did not orient in response to wind, newly-emerged adults moved downwind, and overwintered adults moved upwind. In the cage, plants did not intermingle in rows, but in the field, foliage did intermingle and insects could pass from one plant to another within a row without descending to the ground. This might account for the anemotactic responses of adults in the cage, but for their absence in the field plots. In the field, overwintered adults moved more readily than newly emerged adults.

It is concluded that the patterns of Colorado potato beetle distribution in Manitoba potato fields should be utilized in pest management by continuing to rotate crops, by planting fields in large blocks to reduce the proportion which is edge, and by developing sampling and insecticide application techniques which accommodate the edge effect.

Further work is needed to develop appropriate sampling schemes as distribution is dependent upon the proportions of colonizing insects which fly and walk, and this is dependent on weather. Sampling schemes and other management practices might also take into account the propensity of insects to move along rows, and the effect of insect density and degree of defoliation of patterns on dispersal.

CHAPTER 1
INTRODUCTION

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) is thought to have originated in Mexico, and was collected on the border between Iowa and Nebraska in 1811 (Casagrande 1985) where it was apparently feeding on buffalo bur, *Solanum rostratum* Dunal. It was first reported as a pest on cultivated potato, *Solanum tuberosum* L., during 1859 in Nebraska (Walsh 1865), and has since spread to all the major potato growing regions of the world with the exception of the United Kingdom, Denmark and Sweden (Hurst 1975). The Colorado potato beetle was first reported in Canada in south western Ontario in 1870 (Bethune 1870). In Canada, intensive study of the insect began in 1919 and its subsequent spread in Canada has been well documented (Gibson et al. 1925). Currently, this pest occurs in all provinces except Newfoundland and Labrador (Atlantic Provinces Agricultural Services Coordinating Committee 1984).

The Colorado potato beetle has been one of the most destructive crop pests during the past 100 years. Although there are areas in which populations may be low for a number of years, these populations can increase rapidly if weather and biological circumstances are favourable and so vigilance is essential in all areas in which Colorado potato beetles are found. The Colorado potato beetle is still constantly moving and adapting to new geographic areas (Hsiao 1978), and resistance to a wide range of insecticides has developed in some populations (Forgash 1981, Harris and Svec 1981). The history of control of the insect in North America has recently been reviewed (Gauthier et al. 1981, Casagrande

1987). Both reviews advocate the integration of biological and cultural control measures with insecticide control, and indicate that successful management of the insect depends, in part, on the ability to anticipate infestations of the insect in relation to the development of its host plant.

Crop rotation is a cultural control method which has been shown to have great potential for reducing Colorado potato beetle populations (Lashomb and Ng 1984, Wright 1984, Casagrande 1987). Rotation ensures that the initial density of Colorado potato beetles in a newly-planted potato field is low and that the insect must colonize the field from outside; this reduces population density and delays the appearance of larvae (Lashomb and Ng 1984). Despite this, rotation is seldom practised in many major potato production regions. In contrast, in Manitoba, crop rotation is the norm; often a 2-year rotation plan is used in which potatoes are alternated with crops such as wheat and corn.

Although rotation ensures that initial densities are low in potato fields in Manitoba, almost all fields would suffer economic losses in the absence of insecticides because of immigration of beetles from overwintering habitats. Although the initial number of migrants may be low, the high fecundity of the female and the large amount of foliage consumed by each of her offspring, can result in crop loss. Since larvae do not move very far unless starved (Gibson et al. 1925), the location of ovipositing females in fields determines where defoliation will occur. In some circumstances, densities of adults, egg masses and larvae are highest near the edge of rotated potato fields (Skuhravy et al. 1968). It is hypothesized that beetles colonize rotated and non-rotated fields in

different patterns (Hollingsworth and Ferro 1984), however the colonization of fields by adult beetles is still not clearly understood.

These studies were initiated to investigate the dispersal of overwintered adults from overwintering sites to potato fields, the distribution and spread within fields, the long- and short-range orientation to host plants, and the influence of environmental factors on the dispersal behaviour of the larvae and adults. The information gained is intended to augment current information on economic injury levels and application of control methods and so improve Colorado potato beetle management in Manitoba.

The thesis is written in a paper style. Following this introduction is a literature review. The methods of research, and the research results and discussion are presented in Chapter 3 as three papers written in a form suitable for publication. Chapter 4 contains an overall discussion of the research in the context of the literature.

CHAPTER 2

LITERATURE REVIEW

My research is concerned with the patterns of spatial distribution of Colorado potato beetles (*Leptinotarsa decemlineata* Say) in potato (*Solanum tuberosum* L.) fields, and the mechanisms which result in the observed distribution patterns. These mechanisms include migration and dispersal and processes involved in host plant location. In this literature review, after a brief overview of the life cycle of the Colorado potato beetle, I will present a detailed review of spatial distribution patterns of the Colorado potato beetle, migration and related processes, and of factors involved in host plant location and selection.

Life Cycle of the Colorado Potato Beetle

In temperate regions, Colorado potato beetle adults overwinter buried in the soil. In early spring, the overwintered adults emerge in response to increasing soil temperatures (Lashomb et al. 1984). In Canada, beetles usually first appear during the last week of May or in early June (Gibson et al. 1925). Hurst (1975) summarized 9 years of first emergence dates gathered in the Netherlands and found that this event varied by as much as 71 days.

The adult beetles locate host plants, mate, and then females lay eggs in masses on the underside of potato leaves. Oviposition may continue for several weeks, during which females may move from plant to plant (Boiteau 1986). Each egg mass contains an average of about 30 eggs (Gibson et al. 1925). Larvae hatch within 5 to 10 days and feed mostly on the young leaves. Larvae remain on the same plant unless complete defoliation occurs (Gibson et al. 1925) There are four larval instars.

Depending upon temperature, larval development is completed within 2 - 3 weeks. If defoliation occurs, or if larvae fall off the plant, the larvae crawl to other plants; but eventually die if they fail to locate another host plant (Harcourt and Leroux 1967).

Pupation occurs in the soil after completion of feeding, and new adults emerge one to two weeks later (Gibson et al. 1925). Adults emerging from pupation feed for a while, then they either immediately begin reproduction, or enter overwintering diapause.

Overwintering diapause is induced by short photoperiod, low temperature, and changes in host plant quality (Norris 1964, de Wilde and Hsiao 1981). In the Netherlands, diapause induction occurs when day length falls below 15 hours, and temperature has little influence on this critical photoperiod (de Wilde 1962). The quality of foliage influences whether adults will reproduce or diapause. Young potato leaves contain lecithin, which matures the ovaries and allows oviposition to commence (Grison 1957). However, feeding on senescent potato leaves induces changes in the endocrine system which result in beetles entering diapause (de Wilde and Ferket 1967).

The overwintering site is often close to the final host plant of the season, and diapausing beetles may be found in the fall when potatoes are harvested or in spring by following the plough in old potato fields (Gibson et al. 1925). In loose soil, overwintering adults have been found at a depth of 43 cm, but they are much closer to the surface in heavy soils (Minder 1967).

Spatial Distribution of the Colorado Potato Beetle

Most insect populations exhibit an aggregated spatial distribution

(Southwood 1978), and the Colorado potato beetle is no exception to this general rule. Harcourt (1963), using single potato stems as the sample unit, found that populations of adults, egg masses, eggs, and larvae of each of the four instars are all significantly aggregated. Martel et al. (1986) used the whole potato plant as the sample unit, and found that "early larvae" (instars I and II), "late larvae" (instars III and IV) and adults are aggregated. Early larvae are most strongly aggregated, presumably because the eggs are laid in clusters; late larvae and adults are more strongly aggregated at the beginning of the season (Martel et al. 1986).

The aggregated distributions of Colorado potato beetles have been fitted to a number of theoretical models. Evans (1953) proposed the use of the negative binomial distribution for describing the distribution of adult beetles and for the counts of larvae originally published by Beall (1940). However, Harcourt (1963) criticized the fit of the negative binomial to Beall's data on the grounds that the population was composed of several different instars. Harcourt's own work (1963) confirmed that the negative binomial distribution can be fitted to the distribution pattern of each stage of the insect, but he noted that the value of k , the dispersion parameter of the distribution, is not independent of the mean density. Harcourt (1963) successfully fitted his data to Taylor's (1961) power law relationship. Martel et al. (1986), in preparation for constructing a sequential sampling scheme, fitted their data to Iwao's (1968) patchiness regression.

In addition to aggregation on individual plants in areas of uniform density, Colorado potato beetle populations are often more dense near the

edge of fields (e.g. Wegorek 1955). This phenomenon is most frequently observed when a potato crop is grown in a field in which the previous crop was not potatoes, i.e. a "rotated field". In a Czechoslovakian study of the distribution of larvae in rotated fields, only a small number of larvae were more than 120 m from the edge of a field which was adjacent to the site of the potato crop in the previous year. However, when rotated fields were 300 - 800 m from the site of previous crops, larvae were found up to 360 m from the edge of the fields, and densities were lower (Skuhravy et al. 1968). Unless plants become completely defoliated, larvae seldom move far from the plant on which they hatch (Gibson et al. 1925); therefore the larval distribution patterns observed by Skuhravy et al. are indicative of a similar distribution of ovipositing females. Le Berre (1950) suggested that females walk to the new crop when the overwintering site is close to it, but that they fly when the new crop is more distant; this would account for the more even distribution in crops which are remote from the sites of previous potato crops. In a rotated field in New Jersey, egg mass densities were highest at the edge of the field which was adjacent to the site of a previous potato crop, however this trend was less pronounced for the distribution of larvae (Lashomb and Ng 1984). In Massachusetts, a study of rotated and non-rotated potato fields revealed differences in the pattern of distribution of egg masses which were attributed to differences in the way beetles colonize rotated and non-rotated fields (Hollingsworth and Ferro 1984).

Migration and Dispersal of Colorado Potato Beetles

Adult Colorado potato beetles may undergo relatively long-range migratory flights and may also disperse short distances either by flight

or by walking. Migratory flights occur only at specific times in the development of the adult, whereas dispersal can occur at any time. Larval dispersal is relatively unimportant, but when larvae are short of food they may walk in search of host plants.

Incidence of Migratory Flight

There is considerable individual variation in the amount of flight that occurs; some beetles fly little if at all, but others undergo extended migratory flight (Johnson 1969). Where the insect is multivoltine, there are also differences in migratory tendency among the generations. In many parts of North America, and in southern and central Europe, the longest and most obvious migrations of Colorado potato beetles occur before hibernation in late summer, and shorter dispersal flights occur after emergence from diapause (Tower 1906, Trouvelot et al. 1950, de Wilde 1962). This migration pattern also occurs in parts of Germany (de Wilde 1962). However, in northern Europe, migrations are most obvious in the spring and early summer (Le Berre 1950, Johnson 1969).

Extrinsic Factors Affecting Flight

Wind. Colorado potato beetles are weak fliers, and long-range dispersal and migratory flights are the result of wind-assisted flight (Tower 1906, Johnson 1969). Tower (1906) observed that when mature beetles are allowed to disperse in calm air, they fly in all directions; however, when a steady breeze is blowing, the beetles start out in all directions but those beetles initially flying against the wind soon begin to drift downwind. Beetles have been observed to fly against breezes of 2m/second (7.2 km/h) and probably a limiting wind velocity determines whether beetles will fly with or against the wind (Wiluz 1958, de Wilde 1976). In

calm air, adult Colorado potato beetles fly at about 8 km/h (Feytaud 1930). Only in relatively calm weather are winds less than 8 km/h near ground level, and this speed is commonly exceeded a few metres above the ground; thus beetles would not be able to make headway upwind except on calm days.

An insect, flying forward and seeing the ground pattern below, experiences a flow of images that moves from front to back across the retina of the eyes. However, when a forward flying insect is blown backward by a strong wind, the images flow from back to front of the retina. This reverse flow is not tolerated, and the insect either alights, turns and flies with the wind or flies nearer the ground where it can make headway in the reduced wind velocity. Wind borne migrants are presumed to fly at a height at which the ground images cease to influence direction of flight (Johnson 1969). The layer of air above the ground within which an insect can control its track is called the boundary layer. The thickness of this layer varies with the particular species, the amount of shelter and wind speed. Whether Colorado potato beetles fly downwind or upwind is probably determined by these factors.

Temperature. Temperature during the day influences flight activity; however temperatures at night appear to have little influence (Wiluz 1958). Maximum flight activity of Colorado potato beetles occurs in hot, clear weather (Le Berre 1952) and mass migrations are usually seen on bright sunny days (Johnson 1969). Beetles which have emerged from hibernation require a period of exposure to insolation for mass take-off to occur; this seems to be more important than a high ambient temperature (Johnson 1969). For newly emerged adults, the optimum ambient temperature

for take-off is 25°C, provided there has been at least 6 h of intense insolation (Le Berre 1950). At lower temperatures, the proportion of beetles taking off depends on the duration of insolation (Le Berre 1962). The duration of flight is short at high temperatures (Gimingham 1950), and the existence of an upper threshold for flight has been suggested but not proven (Trouvelot et al. 1950).

Temperature is not only important in controlling flight behaviour of the beetle directly, but is also significant in determining the seasonal occurrence of flight activity: the number of generations, time of emergence from hibernation, amount of oviposition, duration of the larval stage and winter survival are all influenced by temperature (Hurst 1975).

Intrinsic Factors Affecting Flight

Sustained migratory flights only occur at specific times in the development of adult Colorado potato beetles. At other times, adults may undertake short local dispersal flights.

When migration occurs, it normally begins as soon as the beetle becomes flight mature (Johnson 1969). Thus migratory flight may begin about 10 days after emergence from the pupa (Le Berre 1950), or shortly after emergence from diapause (Johnson 1969). Migratory flights by females normally do not occur after the commencement of oviposition (Johnson 1969); this may be due to the weight of egg-laden females (Tower 1906).

Feeding. The beetles which emerge from hibernation in spring take flight in search of food almost at once, if environmental conditions permit (Gibson et al. 1925). Beetles which have emerged from hibernation but have not fed, contain enough glycogen for take-off during the first 9 days

after emergence, but for repeated take-offs thereafter they require food to replenish their glycogen store (Johnson 1969). Emerged adults need to feed before sustained flight and before mating (Gibson et al. 1925).

In early summer, shortage of food may trigger migrations of adults. This is not so in late summer or autumn when food shortages induce diapause (Wiluz et al. 1958).

Mating Status. When environmental conditions are favourable for flight, adult Colorado potato beetles may fly in search of mates. The search of males for mates is quite obvious in the fields. The males fly slowly over the plants from row to row. The females, when in flight, are more direct and move from one plant to another. The females alight on the highest point of a plant where males can easily find them (Gibson et al. 1925).

Flight Muscles. Flight muscles of Colorado potato beetles are subject to reversible degeneration, and episodes of migratory flight coincide with periods in which flight muscles are well developed (Johnson 1969). Flight muscle mass is related to diapause and other developmental states of the adult, and is regulated by the endocrine system (Stegwee et al. 1963).

Six weeks after the beginning of diapause, the flight muscles show extreme degeneration with very thin muscle fibres. The sarcosomes and the respiratory system of the flight muscles almost completely disappear and this may be the reason why diapausing beetles have a slow respiration rate (Johnson 1969). Flight muscles begin to regenerate towards the end of diapause. At emergence from diapause, muscles are completely regenerated and sarcosomes show almost normal respiration. In the laboratory, complete regeneration can occur within 5 days of the appropriate hormonal cue (Stegwee et al. 1963).

Developmental Status. Johnson (1969) suggested that the amount and timing of migratory activity is a consequence of differing temperature thresholds for flight and emergence. Thus beetles could emerge from pupation and enter the pre-reproductive stage during which migration normally occurs (Tower 1906), but might be unable to fly because it is too cool. Johnson (1969) hypothesized that migration would not occur if the pre-oviposition period were completed without the temperature exceeding the lower threshold for flight; however temperatures above the flight threshold during the pre-oviposition period would result in migration. He also suggested that the greater importance of spring migration in the northern part of the range is the result of diapause interrupting the pre-oviposition period; therefore adults emerging from diapause are not yet in reproductive condition and can migrate. In more southerly regions diapause induction does not occur until the pre-oviposition period is complete, and so adults emerging from diapause immediately begin reproduction.

Walking by Larvae and Adults

Larvae of the Colorado potato beetle do not normally leave the host plant on which they are feeding unless threatened with starvation, or dislodged by wind, rain, or other physical disturbance (Gibson et al. 1925). When potato plants are defoliated, larvae must die or leave the plants in search of another host plant (Hurst 1975). Later instar larvae can move farther after leaving defoliated plants than can earlier instar larvae: in one set of field observations, second instar larvae moved up to 15 m, third instar larvae up to 30 m, and fourth instar larvae up to 75 m (Cass 1957).

Adult beetles also walk along the ground, and this may be the primary means of dispersal when temperatures are relatively low (Lashomb and Ng 1984), or when beetles emerging from hibernation are close to a potato field (Le Berre 1950). When released in an unfamiliar habitat within a 3.04 m radius circle of potato slice baits, beetles showed a strong preference for movement towards the north west (Ng and Lashomb 1983). Beetles in this trial took 5 - 150 min to reach the baits on bare soil, 43 - 300 min on grass turf, and 82 - 480 min in wheat (Ng and Lashomb 1983).

Host Plant Relationships

The Colorado potato beetle was, until recently, thought to have been indigenous to the foot hills of the Rocky Mountains, where it fed on *S. rostratum* (Neck 1983). The insect transferred to *S. tuberosum* by 1859 (Casagrande 1985), and is an outstanding example of a native insect that reached pest status through widening of its host range to an introduced cultivated plant (Hsiao 1978). In North America, there is evidence of localized adaptation to different host species, however such divergence has not yet been detected in Europe (de Wilde and Hsiao 1981).

The Colorado potato beetle, is an oligophagous insect which feeds exclusively on Solanaceae, and its physiology and behaviour is now highly adapted to *S. tuberosum* (May and Ahmad 1983). The term oligophagous was proposed by Dethier (1947) for insects which are attracted by a few specific and different chemicals and are capable of distinguishing one from the other. But experiments conducted with Colorado potato beetles show that acceptance of a host plant depends mainly on the presence of "acceptant chemicals" and absence of deterrent chemicals (Jermy 1961).

The combination and amount of the acceptants seems to be of decisive importance. From this, Jermy (1961) concluded that Dethier's (1947) definition of oligophagy is not applicable to the Colorado potato beetle.

Sensory Cues Involved in Host Location

In general, the host plant selection of phytophagous insects depends mainly on visual and olfactory stimuli. The role of visual cues in location of hosts has not been extensively investigated for Colorado potato beetles. Larvae can discriminate between shades of grey and show preference for green over red or ochre, but these responses are only evident at short range (de Wilde & Pet 1957). Research on the role of vision in adult host-seeking behaviour has not been reported.

Most investigators of host-plant location in Colorado potato beetles have examined olfactory stimuli, and have worked with larvae or walking adults. It has been assumed that responses of beetles in flight are similar to those of walking adults on the ground.

In wind tunnel experiments, adult beetles walk upwind in the absence and presence of host odours (de Wilde et al. 1969, de Wilde 1976, Visser & Nielsen 1977, Visser 1976). The odour of potato plants enhances this positive anemotactic response of adult beetles (de Wilde 1976, Visser and Avé 1978). The effect of the potato foliage is enhanced by addition of odours of a variety of other *Solanum* species, but is reduced by the odour of some non-host plants (de Wilde 1976). These findings are concordant with field observations of beetles which, after emerging from the soil in spring, move against the wind to trap fields located at a distance of about 30 meters (Wegorek 1955).

The chemicals responsible for the chemo-anemotactic response are

known as the "green leaf volatiles"; individual components of the volatiles do not elicit the response, a complex of the volatiles is necessary (Visser and Avé 1978). Fully grown potato plants are more attractive than young plants. The volatiles are formed by oxidative degradation of leaf lipids and, due to plant aging and injury, are continuously released (Visser & Avé 1978). Removal of the terminal four antennal segments of the Colorado potato beetle eliminates both anemotactic and chemo-anemotactic responses (de Wilde 1976). De Wilde (1976) suggested that the green leaf volatiles are both attractants and feeding stimulants for adult beetles.

Larvae may also use olfactory cues to detect host plants. Cass (1957) observed that 58% of larvae leaving defoliated plants in a field moved upwind towards another potato field. However, wind tunnel experiments have not revealed an anemotactic response in larvae (de Wilde et al. 1969). When larvae move within a field in which potatoes surround them, they move in an apparently aimless manner (Gibson et al. 1925, de Wilde 1958). Larvae may be attracted to host plants by short range olfactory cues (Chin 1950), or olfaction may be unimportant until a potential food item has been located by the process of "random biting" (de Wilde 1958). These host-location mechanisms appear to function differently to those involved in host acceptance. For example, the odour of *S. demissum* Lindl. is as attractive to the larvae as that of *S. tuberosum*, yet larvae feed continuously on *S. tuberosum* but reject *S. demissum* as food (de Wilde 1958).

In nature, host plant selection is primarily carried out by adult female Colorado potato beetles because the selection of larval host plants is usually determined by where the female lays eggs. It is therefore not

surprising that although the chemical characteristics of the host influence behaviour in adults and larvae, adults are more selective than the larvae (Visser and de Wilde 1980).

Effect of Plant Communities

The texture of the plant community can influence both the rate at which host plant patches are discovered, and the intensity with which discovered patches are exploited by phytophagous insects (Stanton 1983). Larger patches will be discovered more often than smaller patches because the probability that a herbivore will immigrate into any host plant area is directly related to the peripheral distance around that patch (Stanton 1983).

The host-finding adaptations of the Colorado potato beetle probably evolved in response to the characteristics of the plants on which it originally fed. *S. rostratum* is found in open, semiarid grassland, or on roadsides and waste ground (Whalen 1979) where vegetation is sparse and species diversity is either low or moderate. It is adapted to opportunistic exploitation of shifting habitats, and has become a weed throughout large areas of North America and on other continents (Hsiao 1981). Thus the local distribution is likely to be patchy but the patches can be large. The other natural food plants of Colorado potato beetle are also weedy and occur in open habitats, often in groups. For example, *S. carolinense* L. and *S. eleagnifolium* Cav. are perennial weeds of sparsely vegetated areas, and spread vegetatively, giving rise to fairly large but often widely dispersed patches (May, M.L. unpublished).

The influence of plant dispersion on movements of the Colorado potato beetle has been studied with mark-recapture techniques by Bach

(1982). In her studies, beetles released between plots containing potato monocultures, polycultures with two additional non-host plant species, and polycultures with five additional non-host species, did not exhibit preference for a particular type of plot. When potted plants were used, colonization rate and time spent on plants were higher on potato plants growing alone than on plants surrounded by non-host vegetation. No effects of plant density were observed. Beetles usually remained on the first plant they colonised (Bach 1982); this, and the sedentary behaviour of the larvae (Gibson et al. 1925), may be adaptations to avoid straying from the widely dispersed patches of host plants.

Environmental Effects on Host Plant Location

The open habitats of *S. rostratum* and other host plants on which Colorado potato beetles evolved, may still influence the way in which beetles locate host plants. Wind speeds are higher in open habitats and the boundary layer, in which beetle flight speed is greater than the wind speed, is very small. Obstructions such as vegetation reduce wind velocity, increase turbulence, increase the thickness of the boundary layer, and may reduce anemotaxis and so impede host-finding by adults (Visser 1976). Walking beetles sometimes climb into regions of higher wind velocity on small hills and projections (Visser 1976). It is likely that despite these apparent attempts to get above the region of turbulence, walking beetles can only orient to plants over distances of a metre or less (Jermy 1958); flying beetles are likely to orient over longer ranges (May and Ahmad 1983).

Perhaps the difficulties of orientation in habitats which impede wind flow are responsible for the observation that Colorado potato beetles

are less abundant in fields with barriers such as hills, mountains, forests and windbreaks (Wiluz et al. 1958). Infestation rates of the insect are higher in fields situated in open spaces. Windbreaks therefore may be useful in reducing the number of Colorado potato beetles in fields; however the numbers of aphids and other small airborne insects may be increased by the presence of a windbreak (Lewis 1969).

CHAPTER 3 PART 1

Within-field distribution of Colorado potato beetle,
Leptinotarsa decemlineata (Coleoptera: Chrysomelidae), in
Manitoba: effects of field characteristics, and application to
monitoring methods

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Abstract

In 1984 and 1985, the pattern of distribution of Colorado potato beetles in commercial fields of potatoes was investigated. In each year four fields, two of cv. Norland and two of cv. Russet Burbank, were sampled at weekly intervals by visual examination of plants at predetermined points along north-south and east-west transects. For each half transect from the edge of the field to the centre, the type, size and distance of windbreaks, and the distance to the nearest field which had been potatoes the previous year, were recorded.

Adults, egg masses and larvae tended to be aggregated; their numbers varied among fields and over time. In each field the number of larvae reached a peak in the third week after plant emergence; all fields were sprayed during the following week, and few Colorado potato beetles were found after spraying. Numbers of larvae per plant in the third week after emergence were analyzed. Except in one unusually small field, numbers were either low throughout the half transect, or were high at the field margin and declined with increasing distance from the field edge. In both years, the edge effect was modified by the height and distance of the nearest windbreak. Larval numbers per plant were consistently higher on Russet Burbank plants than on those of the smaller cultivar, Norland. Distance to previous potato crops did not consistently affect distribution of larvae. Methods of incorporating the edge effects into a sampling scheme were investigated. The best of the methods tested, if applied to an economic threshold of 1 larva/plant, would have reduced the area sprayed by 27% in 1984 and 66% in 1985.

Introduction

In temperate regions, Colorado potato beetles *Leptinotarsa decemlineata* (Say), overwinter as adults in the soil (Hurst 1975). The hibernation site is frequently close to the last feeding site of the season (Gibson et al. 1925). Therefore, typically, potato crops are colonized in spring by adult beetles migrating from the sites of the previous year's crop. When potatoes are not grown continuously in a field, colonization is by beetles walking or flying into the field. Skuhravy et al. (1968) observed that, when such fields are adjacent to previous crops of potatoes, beetles are abundant only near the edge of the field, but that when fields are distant from the previous crops, the distribution of insects is far more uniform. Since beetles do not readily walk through vegetation (Ng and Lashomb 1983), it is likely that the edge effect observed by Skuhravy et al. (1968) is the result of beetles walking into the fields, and the uniform distribution is the result of immigration by flight.

In Manitoba, potatoes are normally not grown in the same field in successive years, but often close to the site of previous potato crops. Furthermore, air temperatures at the time beetles emerge from hibernation are frequently below the 25°C threshold (Johnson 1969) for flight. Thus pronounced edge effects might be expected. The immigrant females oviposit on the potato plants, and the larvae seldom move far (Gibson et al. 1925), therefore it is likely that such edge effects persist at least until the time insecticides are applied for control of the Colorado potato beetles. For growers to use economic thresholds in deciding on control measures for

Colorado potato beetle, it is essential that the nature of the within-field distribution be known.

The current study was undertaken to investigate the within-field distribution of Colorado potato beetles in Manitoba, to examine factors influencing the abundance and distribution of the insects, and to examine methods of incorporating the results into a monitoring scheme for Colorado potato beetles.

Methods

Fields used in the study were commercial fields in the areas of intensive potato production in southern Manitoba; all fields were subject to the normal production procedures of the grower concerned. In 1984 and 1985, two fields of cv. Norland and two fields of cv. Russet Burbank potatoes were sampled. In 1984 all fields were near Morden, Manitoba (49°10'N, 98°4'W). In 1985, one field of each cultivar was located near Morden and one field of each cultivar was near Portage la Prairie (49°55'N, 98°18'W). All fields were approximately rectangular and oriented with sides north-south and east-west. All fields were sprayed against Colorado potato beetle in early-mid July.

For each field, the approximate area was determined by counting rows and plants in rows. The nature of windbreaks around each field was recorded; the distance from the edge of the crop to each windbreak was measured and the height of windbreaks was estimated trigonometrically. The distance from the sampled field to the nearest potato field of the previous year was obtained by consulting growers' records, plotting the results on large scale maps, and measuring the scale distances with a ruler.

Sampling began as soon as plants emerged in the spring, and continued at weekly intervals thereafter. Sampling was carried out by counting all the Colorado potato beetle adults, larvae and egg masses on selected plants along transects. On each sample occasion, two transects were sampled in each field, one from the north edge to the south edge of the field, the other from east to west. Each transect was randomly selected from a 100 m wide band centred on the side of the field (Fig. 1); where the field was less than 100 m in extent, all of the field was included in the band from which transects were selected. Once the transect was selected, the observer moved along it through the field and sampled plants at 1 m intervals in the edge zone (Zone E, Fig. 1), at 2 m intervals in the intermediate zone (Zone I, Fig. 1), and at 10 m intervals in the middle zone (Zone M, Fig. 1). Zone E was 10 m wide, zone I was 30 m wide, and zone M occupied the remainder of the transect. Thus, except in very small fields, a sampler moving along a transect would take 10 samples from zone E, then 15 samples from zone I, then an indefinite number from zone M, before encountering the zone I of the far side of the field where a further 15 samples would be taken; finally, 10 samples would be taken in the zone E of the far side of the field. In all fields the distance between rows was approximately 1 m. In fields of cv. Russet Burbank there were ca. two plants/m along the rows, in fields of cv. Norland there were ca. three plants/m along the rows. These between-row and within-row spacings were used to determine selection of plants, as this was much simpler than direct measurement. The scheme resulted in samples which were at corresponding distances from the field edge along each transect, but all distances were approximate because they depended

upon the precision of the planting equipment.

Transects were divided into two at the centre point, and data for each half-transect were analyzed separately. In preliminary analyses, attempts were made to describe the relationship of density with distance from the field edge by fitting the relationship (Taylor 1978):

$$\text{Density} = \exp (a + b (\text{distance}^c))$$

to the untransformed data using an iterative least squares method (Wilkinson 1988); in this relationship a, b, and c are coefficients of the non-linear regression. However, it was often not possible to obtain a satisfactory fit to this model and the method was discarded, in favour of a linear regression model.

To minimize heteroscedasticity, insect densities were transformed, based upon the relationship of the mean and variance (Taylor 1970):

$$\text{Variance} = a (\text{Mean})^b$$

by performing least squares regression on the logarithmic transformations of the mean and variance of subsamples of the data; in this relationship a and b are coefficients of the regression. The constant, b, was used in a transformation of the form:

$$Z = X^{(1 - 0.5b)}$$

(Taylor 1970), where X was the original value and Z was the transformed value.

Preliminary analysis indicated that the numbers on plants 1 m from the edge of the field were very different from those on other plants in zone E, and so these plants were not included in any of the analyses. Thus results of only nine samples from zone E are reported.

Regression analysis of the transformed insect densities in the half-

transects was conducted in three phases. Firstly, regressions were calculated for each individual half-transect, to define the nature of the relationship between density and distance from the edge of the field.

The second phase of the regression analysis was a comparison of regressions among half-transects to determine whether characteristics of the field influenced the regression line. Candidate characteristics were cultivar, the nature of windbreaks, and the distance to previous potato crops. Preliminary analysis indicated that the type of windbreak (tree species or road) had no significant effect on the regression relationship, so attention was focused on the size and proximity of the windbreak. A single variable was used to represent windbreak size and distance. This was the tangent of the angle subtended by the windbreak when viewed from the edge of the crop, and was calculated as the windbreak height divided by its distance from the edge of the potato crop. The straight-line distance to the site of the nearest previous potato crop from the edge of the sample field was determined for each half-transect. A log transformation of this value was used in the analysis. When the distance to the previous crop was more than 1 km it proved impossible to contact all the landowners involved and a value of 3 km was substituted in such cases.

The third phase of the regression analysis was an examination of the most reliable way of predicting areas in which larval densities exceeded a chosen threshold value. The threshold chosen for this analysis was 1 larva per plant in the third week of sampling. This value was chosen because it is within the range of economic injury estimates obtained by Senanayake and Holliday (in press) and Lactin (personal communication).

Four regression models, using three possible combinations of transformed or untransformed variables were assessed for their effectiveness in predicting which areas of fields required spraying. Effectiveness was determined by examining the observed mean densities of larvae in the samples in those areas identified by the model as above or below the threshold, and by examining the percentage of samples which were misclassified by the model.

Results

Information on the characteristics of fields is shown in Table 1. The fields from the Portage la Prairie area were fields 3 and 910; all the other fields were in the Morden area.

In both years, all fields were sprayed with insecticides in the fourth week after sampling began. Spraying had a profound effect on the numbers of Colorado potato beetles, and the numbers found after spraying were too small for analysis. The numbers of adults, egg masses and larvae found in the first three weeks of sampling are shown in Table 2. Initially only adults and egg masses were found, but larvae appeared in the second or third week of sampling. All stages were more abundant in 1984 than in 1985 (Table 2).

The variance/mean ratio is 1 when organisms are randomly distributed (Southwood 1978), and values greater than this indicate aggregation. All stages exhibited significantly aggregated distributions at some point in sampling (Table 2), and larvae were much more strongly aggregated than other stages.

Edge Effects

There was no clear edge effect at some field margins (e.g. North

edge of field 910, Fig. 2A), while others showed a strong edge effect (e.g. South edge of the same field Fig. 2B). The east - west transect of field 210 did not show a reduction in density at the middle of the field (Figs. 2C and D). With the exception of field 210, sides of fields where larvae were abundant did exhibit an edge effect similar to that in Fig. 2B.

The analysis of edge effects was restricted to the third week of sampling and to the larvae. For other stages, and in other weeks, the numbers were too small for analysis. The third week corresponded to the time when control decisions would be made. Because of the strongly aggregated distribution of larvae (Table 2), the transformation $Z = X^{0.25}$ was used before regression analysis; examination of residuals from the regression analysis confirmed the adequacy of this transformation.

A linear relationship between the number of larvae/plant and log_e distance from the field edge gave a satisfactory fit in many cases (Table 3). The transformation of distance was employed because the untransformed plot showed marked curvilinearity. Of the total of 32 half-transects, seven had no larvae in any samples (Table 3). Of the 25 half-transects with larvae, 11 showed significant regressions, all of which had positive intercepts and negative slopes. All but four of the remaining non-significant lines also exhibited the trend of a positive intercept and negative slope. Of the exceptions, one was a half-transect in field 210, in which it has already been noted that there was no reduction of numbers in the centre of the field. The remaining half-transects with non-significant slopes had low numbers of larvae.

It is noticeable (Table 3) that the proportion of the variance

explained by the regression model (r^2) is positively correlated with the number of larvae found in zone E ($r = 0.612$, d.f. = 23, $P < 0.01$). Thus, when the number of larvae near the edge of the field is high it is more likely that there will be a significant regression. Also, the slopes of the regressions in Table 3 are negatively correlated with the total number of larvae in zone E ($r = -.608$ d.f. = 23 $P < 0.01$).

Effect of Field Characteristics

The consistency of the regressions of transformed larval density on \log_e distance from the field edge, indicated that this type of regression could be adopted as the best model for analysis of covariance to examine the effects of field characteristics on the regressions.

The analysis of covariance was carried out for each year separately. Preliminary analysis indicated that in both years there was significant variation among the half-transects, and among the interaction of half-transects with distance from the field edge (Table 4A and 4C). This indicates that the characteristics of the half-transect affect not only the mean number of larvae per plant in that group of samples, but also the slope of the relationship of larval density with distance from the edge of the field.

An analysis of covariance model incorporating distance from the field edge, cultivar, the tangent of the angle subtended by windbreaks, and \log_e distance to previous crops was fitted to each year's data (Table 4B and 4D). In both years, cultivar, tangent of windbreak, and the interaction of tangent of windbreak with distance from the edge of the field were significant. Distance from the field edge was significant in 1984 only, distance to the previous year's crop was significant only in

1985. The coefficients indicate that larval densities were higher on Russet Burbank than on Norland, and that larger tangents of windbreak are associated with higher larval densities and with steeper regressions of density on distance from the field margin.

The analysis among half-transects (Table 4A and 4C) was the most complete analysis of covariance model fitted, the residual variance from this model represents scatter about the individual regressions for half-transects. Models which fit the effects of a limited number of field characteristics as independent or treatment variables to the data, cannot explain more variance than the among half-transects model. Thus the model reported in Table 4B explains 45% of the maximum possible variance among half-transects in 1984; in 1985, the model in Table 4D explains 74% of the maximum possible variance among half-transects in 1985.

Using Edge Effects in Monitoring

Although models with transformations of both distance from the field edge and larval density gave the best fit to the data (Table 5), models with these transformations tended to classify areas as not requiring spraying where densities were, in fact, above 1 larva/plant. The "individual" model used the regressions shown in Table 3 to predict where the mean density of larvae would be one or less. In areas predicted by this model to be below or equal to the threshold, observed mean larval densities were greater than 1 larva/plant in 1984, and the lower density calculated over both years (Table 5), was the result of better discrimination in 1985. In the "edge" model, in addition to the individual regressions, half transects with total numbers of larvae in zone E of less than 10 were considered to be below the threshold. This

model was a slight improvement over the individual model, but still the larval density in 1984 was above 1 larva/plant in the areas predicted to be below the threshold. In the "pooled" model, the data from 1984 and 1985 were pooled, and larval density was predicted by the distance from the field edge, the total number of larvae in samples from zone E, and their interaction. The ANCOVA model (Table 5), was similar to the pooled model but took into account the effect of the two years on the larval density and on the coefficients of the independent variables. Neither the pooled nor the ANCOVA model successfully predicted areas of the field with densities of larvae below the threshold.

There was little to choose between the two sets of models in which untransformed larval density was used as the dependent variable. Both sets discriminated well between areas with high and low larval densities, and the percentage of samples classified as requiring spraying was similar in each case (Table 5).

Discussion

Larvae were the most abundant stage during the period before spraying of the commercial fields, and their numbers peaked during the third week of sampling (Table 2). This was the week in which growers might have assessed the abundance of larvae before making a decision on spraying. The high degree of larval aggregation is typical for Colorado potato beetles (Harcourt 1963, Martel et al. 1986). This aggregation is responsible for the relatively poor fit of even the best fitting regression models: even in areas of high density there are many plants with no larvae, also in low density areas of the field deposition of a single egg mass on a plant can result in 30 or more larvae on that plant.

With the exception of field 210, the edge effect was consistently present in half-transects with abundant larvae. This effect is characterised by higher numbers at the edge of the field, and lower numbers as the distance from the edge of the field increases (Fig. 2B). The absence of this pattern in field 210 is probably because of the small size of this field, which resulted in the high edge densities of the east and west sides (Fig. 2 C and D) meeting in the middle.

The semi-logarithmic relationship of density with distance from the field edge (Table 3) suggests that density is related to distance in a multiplicative way; thus a doubling of distance results in a constant decrement in density. This type of relationship was also apparent (although the fit was poorer) when untransformed values of the larval density are used. Such a relationship would be consistent with random dispersal of insects from a source outside the field (Southwood 1978). However, interpretation of the regressions in terms of the dispersal behaviour of the insects must be tentative. This is because firstly, the larvae are not the dispersing stage and their distribution is dependent upon both the dispersal and oviposition behaviour of females, and secondly, without large amounts of data obtained under controlled conditions it is difficult to distinguish the most appropriate curve for fitting the fall-off of insect density with distance from their source (Taylor 1978).

In both years, individual characteristics of half-transects affected both the mean number of larvae per plant, and the rate of decline of larval density with increasing distance from the field edge (Table 4A and 4C). Substantial parts of this variation could be attributed to readily

measurable characteristics of the field (Table 4B and 4D). The influence of cultivar on larval density is probably related to plant size. Russet Burbank plants are larger than Norland plants and are more widely spaced within the row (Manitoba Agriculture 1988). When the sample unit is the plant, larger more widely spaced plants will support more larvae per plant even when the density per unit area is the same on both cultivars.

The other consistent effects were those associated with the tangent of the angle subtended by windbreaks. This measure combines windbreak height and distance in a single variable so that low close windbreaks are equivalent to distant tall windbreaks. Windbreaks which had high tangent values increased the density of larvae in the half transects, and increased the steepness of the slope of the regression of larval density on distance from the field edge. This effect is consistent with the findings of Lewis (1970) with regard to flying or drifting airborne insects on the lee side of windbreaks. However, for flight, adult Colorado potato beetles require temperatures exceeding 25°C, and several hours of sunshine (Johnson 1969). During June, when those females which resulted in the larvae sampled in week 3 would have been dispersing before oviposition, there were six sunny days with temperatures above 25°C in 1984 and only one such day in 1985 (Environment Canada 1984, 1985). Therefore it seems that at least in 1985, a substantial proportion of the adults must have walked to the field. It is not clear whether the windbreak effect is operating only on that portion of the population which flew to the field, or whether there is also an effect of windbreaks directly on walking beetles.

In 1984, distance from the field edge was a significant covariate

(Table 4B), but in 1985 (Table 4D) this was not so. However, the influence of distance to the field edge remained important in 1985 because of the significant interaction between it and windbreak. In addition to the effect of windbreaks on the pattern of distribution, the distance from last year's potato field to the present growing field should be considered. The effect of distance to the previous year's crop was significant in 1985 but not in 1984; moreover, the coefficient for 1985 (Table 4D) indicates that half-transects close to last year's field had reduced populations of larvae. The lack of consistency, and the reversal of the sign of the coefficient from that expected, could indicate that the significance of this variable is an artifact. This is always a possibility in studies such as this, in which the system cannot be manipulated or controlled.

Previous studies revealed that infestations are higher along field margins when a new potato field is adjacent to a previous field (Wegorek 1955, Wiluz et al. 1958). If the distance between the fields is more than 400 m, then the dispersion of adults and larvae in the new plot is uniform (Skuhravy et al. 1968). Wiluz (1958) proposed that this is because fields close to previous fields are invaded by walking beetles, and this causes edge effects; if previous fields are more distant, new fields are invaded by flying beetles, which causes a uniform dispersion pattern.

In my findings, fields which were >1000 m away from previous potato fields, and which would be expected to be colonized by flying beetles, showed evident edge effects. Fields which were 3 m from previous fields and would be expected to be colonized by walking beetles did not show edge effects. The difference between my results and those in the literature

may be because of different environmental conditions. In published studies, conditions may favour beetles walking to the new potato crop. In my study, flight or movement in late summer, just before hibernation, may be important and could modify distribution the following year. Migratory flights may occur in late summer (Tower 1906, de Wilde 1962). So, dispersal of adults in late summer may occur from senescing potato fields. If adults fly from early senescing fields in late summer, these fields would have less overwintered beetles emerging in early spring next year. Hence adjacent fields would not have high infestations along field margins the next year. However, even when plants senesce, hibernation of part of the adult beetle population may occur without dispersal to other fields. Newly emerged beetles may not have time to develop flight worthiness and may enter the soil for hibernation.

Whether beetles fly from fields in summer, or diapause and overwinter there, will depend upon the developmental stage of the beetles at the time potato plants senesce. Developmental stage, and diapause induction is dependent upon temperature and photoperiod (Hurst 1975). Time of plant senescence is also dependent upon environmental conditions (Dwelle 1985) but is affected by date of planting and cultivar. Date of planting also directly affects Colorado potato beetles because adults show a preference for younger plants rather than older plants (Boiteau 1986). Therefore later planted plots are attractive to beetles and may serve as diapausing sites for them.

Cultivar plays a major role in the time of plant senescence. Norland is an early maturing variety, while Russet Burbank matures much later. If fields of Norland senesce early and the beetles in those fields

are flight worthy, and temperatures are suitable for flight, then dispersal flights would surely occur from these fields. Only beetles whose flight muscles degenerated before they could be used would enter diapause. Therefore fewer beetles would emerge from Norland fields the following year. The later maturing cultivars such as Russett Burbank are harvested in September and October. The day length and temperature prevailing at that time induce beetles to enter diapause rather than disperse. A proportion of the beetle population from senescing Norland fields may migrate into Russet Burbank fields, and enter diapause. High emergence of beetles from these sites can be expected the following year.

In my study, even at a distance from previous fields of >1000 m, there is sometimes an evident edge effect. This could be because beetles flying below the boundary layer might arrest flight at the edge of a field in response to the odour of potato plants. The beetles which fall to the ground then would walk into the field infesting the edge plants. De Wilde 1976, repeatedly observed beetles falling from a height of several metres into a potato field or into the surrounding vegetation. In contrast, beetles drifting with the wind above the boundary layer could be deposited more uniformly within fields.

The correlation of the significance of the regressions in Table 3 with the number of larvae found in zone E suggests that when numbers of larvae are large near the edge of the field, a relationship with distance from the field margin will usually exist. If this is generally true, then sampling the edge of the field might provide information that could be used in pest control decisions. If a small number of larvae are present at the edge of the field, then it is fairly

certain that the densities elsewhere on that half-transect will also be low. If the numbers at the edge of the field are large then growers could sample the length of the entire half-transect, or could base decisions upon edge sampling alone.

The failure of the models using transformed larval density (Table 5) to provide good discrimination between areas exceeding, and not exceeding, the selected economic threshold is attributable to the transformation. Because the means of transformed variates are not equal to the means of their untransformed equivalents (Fisher and Yates 1963), the application of this model introduces a bias which results in underestimation of the true mean density of larvae.

When the untransformed larval densities are used, model fits are poorer, but the predictions are free of bias (Table 5) and so more useful in the context of decision making. Whether or not the distance from the field edge was subjected to a logarithmic transformation made little difference to the predictive performance, but the models using transformed distance were selected because of their slightly higher r^2 values.

In selecting a method of sampling for pest control decision making, it is necessary to balance the need for error-free predictions against the costs of sampling, and view this balance in the context of the costs of crop loss and crop protection. Therefore, even though the individual half-transect model provides the best predictions and results in the least percentage of samples misclassified (Table 5), it is too time-consuming to be of practical use. Typically, four half-transects require 3-4 person hours, and this would be the minimum amount of time necessary to make a decision for a single field using this method. Some saving of time over

the individual half-transect method can be achieved by deciding that when the total number of larvae in the nine samples in zone E is less than 10, the half-transect will be considered below the economic threshold, and no further sampling is done. Even so, this method still requires that many plants be sampled; in 1984 for example, 69% of all half-transects would have required complete sampling.

The analysis of covariance model is based upon the regression of distance from the field edge and on the number of larvae on samples in zone E, but tests to see if the regression coefficients changed during the two years of the study. There were significant changes between the two years, and the full ANCOVA model (Table 5) takes these into account in its predictions. The result is a decision method which is almost as good as individual half-transect methods, but which requires only a knowledge of the regression coefficients for each year and of the number of larvae in zone E. Unfortunately, the amount of data collected does not allow prediction of the specific coefficients for each year; so this method is not practical for decision making, as the only way to determine the regression coefficients is by sampling large numbers of transects.

The pooled model ignores the previously-detected significant differences in the regression coefficients between years, and uses the pooled data to estimate coefficients which are assumed to be constant from year to year. The predictive value of this method is only slightly inferior to the ANCOVA model, but it has the advantage that, once the coefficients are determined, the only input data required for each half transect is the total number of larvae in the nine samples of zone E. If this method were applied to the fields sampled (Table 6), the average

reduction in area sprayed in 1984 would have been 27%, and in 1985 would have been 66%; values for the individual fields are shown in Table 6.

It would be a better test of the pooled regression method of decision making to apply the method to an independent set of data, which was not used in its derivation; however, I was unable to do this because of time constraints.

The value of the method in potato production will depend upon how it performs under a variety of different spring weather conditions. It has been noted that edge effects are less pronounced during abnormally warm springs (B. Geisel, personal communication). If these climatically induced differences make the pooled method unworkable, then perhaps climatic indicators can be used to predict the specific regression coefficients for each year.

It is clear that without knowledge of the edge effects, sampling potato fields to make decisions about Colorado potato beetle control can lead to misleading results. Methods which depend only on sampling near the edge are more likely to be used than much more extensive sampling schemes, even if they are less precise. The alternative to using such schemes is likely to be the continuation of routine spraying without regard to insect numbers. This study demonstrates that in some years this leads to a 200% increase in insecticide use over what is economically justified. Furthermore, the continuation of routine spraying is likely to result in the onset of insecticide resistance in Manitoba, as it has in many other areas of North America (Forgash 1985, Cassagrande 1987, Harris and Svec 1981). Also in some potato producing areas, continuous use of persistent insecticides has resulted in contamination of ground water.

Crop rotation is widely used in Manitoba, and needs to be considered in commercial potato production in other areas. Rotation of a non-host grain crop reduces the population of Colorado potato beetle in the following year's potato crop and delays colonization (Wright 1984). Edge effects are associated with crop rotation, and the resulting uneven distribution of Colorado potato beetles must be understood if appropriate control decisions are to be made.

TABLE 1. Characteristics of fields sampled.

Year	Field Number	Area (ha)	Cultivar	Size (m)		Side	Windbreak			Distance to previous potato crop (m)	
				E-W	N-S ^a		Type	Distance (m)	Height (m)		WBTAN ^b
1984	202	19.0	Norland	280	680	East	Road	3	3	1.000	>1000
						West	None	-	-	0.000	3
						North	None	-	-	0.000	>1000
						South	Fraxinus	8	5	0.625	800
	205	26.9	Norland	640	420	East	Road	3	3	1.000	>1000
						West	None	-	-	0.000	>1000
						North	Fraxinus	1	5	5.000	10
						South	Populus	10	15	1.500	400
	210	2.7	Russet Burbank	56	480	East	None	-	-	0.000	3
						West	Salix	4	3	0.750	400
						North	Populus	8	15	1.875	500
						South	None	-	-	0.000	>1000
	216	17.6	Russet Burbank	980	180	East	Populus	15	18	1.200	>1000
						West	Road	9	3	0.333	>1000
						North	Road	10	3	0.300	>1000
						South	None	-	-	0.000	3
1985	3	14.3	Norland	420	340	East	Prunus	350	3	0.007	>1000
						West	Road	1500	2	0.001	10
						North	Populus	400	8	0.019	20
						South	Populus	5	4	0.700	>1000
	217	20.8	Norland	800	260	East	Quercus	20	18	0.900	100
						West	None	-	-	0.000	>1000
						North	Quercus	12	18	1.500	400
						South	None	-	-	0.000	>1000
	229	14.1	Russet Burbank	160	880	East	None	-	-	0.000	12
						West	Quercus	30	15	0.500	>1000
						North	None	-	-	0.000	>1000
						South	None	-	-	0.000	>1000
	910	37.8	Russet Burbank	700	540	East	None	-	-	0.000	>1000
						West	None	-	-	0.000	>1000
						North	Quercus	18	20	1.111	>1000
						South	Populus	5	10	2.000	5

^a E-W = East to West; N-S = North to South.

^b Tangent of angle at the edge of the field which is subtended by windbreak.

TABLE 2. Mean (\pm SEM) numbers per plant and variance/mean ratio (s^2/m) of different stages of Colorado potato beetles before insecticide applications in commercial fields.

Year	Sample week ^a	N	Adults		Egg masses		Larvae	
			Mean(\pm SEM)	s^2/m	Mean(\pm SEM)	s^2/m	Mean(\pm SEM)	s^2/m
1984	1	690	0.086 \pm 0.007	0.39 *	0.117 \pm 0.014	1.16 *	0	-
	2	690	0.079 \pm 0.013	1.48 *	0.109 \pm 0.013	1.07	0.314 \pm 0.077	13.03 *
	3	690	0.033 \pm 0.007	1.02	0.028 \pm 0.007	1.21 *	3.048 \pm 0.291	19.17 *
1985	1	750	0.013 \pm 0.005	1.44 *	0.025 \pm 0.007	1.47 *	0	-
	2	750	0.020 \pm 0.006	1.35 *	0.065 \pm 0.014	2.26 *	0	-
	3	750	0.020 \pm 0.005	0.94	0.045 \pm 0.011	2.01 *	1.137 \pm 0.221	32.22 *

* Indicates a variance/mean ratio significantly different from that expected if the insects' distribution is random.

TABLE 3. Density of larvae per plant in third week of sampling and relationship with distance to field edge.

Year	Field	Side	N	Mean (\pm SEM) larvae per plant	Regression ^a			Larvae at edge ^b
					Intercept	Slope	r ²	
1984	202	East	34	0.23 \pm 0.13	+0.288	-0.048	0.04	2
		West	34	1.09 \pm 0.78	+0.574	-0.115	0.06	11
		North	54	0.50 \pm 0.26	+0.362	-0.053	0.03	8
		South	54	0.28 \pm 0.14	+0.345	-0.053	0.04	3
	205	East	52	0.37 \pm 0.22	+0.352	-0.062	0.05	1
		West	52	2.92 \pm 0.87	+1.868	-0.339	0.37 *	105
		North	41	3.88 \pm 1.32	+2.174	-0.444	0.46 *	88
		South	41	2.83 \pm 1.06	+1.336	-0.255	0.18 *	48
	210	East	18	4.00 \pm 1.76	-0.110	+0.325	0.08	48
		West	18	18.11 \pm 4.29	+1.981	-0.073	0.01	138
		North	41	0.67 \pm 0.45	+0.595	-0.128	0.12 *	18
		South	41	0	-	-	-	0
216	East	69	5.74 \pm 1.09	+1.660	-0.199	0.10 *	141	
	West	69	5.87 \pm 1.23	+2.297	-0.322	0.29 *	114	
	North	29	7.03 \pm 1.99	+3.081	-0.749	0.61 *	157	
	South	29	4.03 \pm 1.38	+1.255	-0.147	0.03	50	
1985	3	East	42	0	-	-	-	0
		West	42	0.02 \pm 0.02	-0.021	+0.013	0.01	0
		North	38	0.03 \pm 0.03	+0.071	-0.013	0.01	0
		South	38	0	-	-	-	0
	217	East	62	1.77 \pm 1.03	+0.951	-0.178	0.20 *	40
		West	63	0	-	-	-	0
		North	35	0	-	-	-	0
		South	34	0.24 \pm 0.24	+0.189	-0.044	0.03	8
	229	East	29	1.57 \pm 0.95	+0.131	+0.038	0.00	15
		West	29	1.21 \pm 0.79	+1.363	-0.401	0.45 *	34
		North	65	0.44 \pm 0.19	+0.617	-0.112	0.16 *	19
		South	65	0	-	-	-	0
910	East	56	0	-	-	-	0	
	West	56	0.75 \pm 0.38	+0.135	+0.00778	0.00	0	
	North	48	0.60 \pm 0.52	+0.104	-0.007	0.00	0	
	South	48	11.87 \pm 2.65	+2.593	-0.426	0.28 *	98	

^a Regressions are of $X^{0.25}$ transformed numbers of larvae per plant on the \log_e of distance from the edge of the field.

^b Total number of larvae in the nine samples in zone E (Fig. 1).

* Indicates that the slope of the regression is significantly different from 0 ($P < 0.05$).

TABLE 4. Analyses of covariance for $Z = X^{0.25}$ transformed densities of larvae in third week of sampling.

Source of variance	Code	d.f.	Mean square	F ratio	Coefficient
<u>A: 1984 Differences among 16 half-transects from 4 fields. ($r^2 = 0.42$)</u>					
Distance from field edge ^a	A	1	16.758	44.9 *	-0.166
Among half-transects	B	15	3.831	10.3	-
Interaction	AxB	15	2.056	5.5 *	-
<u>B: 1984 Effects of cultivar, windbreak and distance to previous crop. ($r^2 = 0.19$)</u>					
Residual	-	641	0.373	-	-
Distance from field edge ^a	A	1	2.099	4.21 *	-0.160
Cultivar	B	1	9.530	19.14 *	-0.350
Windbreak ^b	C	1	7.489	15.04 *	0.279
Distance to previous crop ^c	D	1	0.008	0.02	0.004
Interaction	AxB	1	1.294	2.60	0.032
Interaction	AxC	1	3.426	6.88 *	-0.051
Interaction	AxD	1	0.049	0.10	0.003
Residual	-	665	0.498	-	-
<u>C: 1985 Differences among 16 half-transects from 4 fields. ($r^2 = 0.39$)</u>					
Distance from field edge ^a	A	1	4.799	31.8 *	-0.070
Among half-transects	B	15	2.578	17.1 *	-
Interaction	AxB	15	1.345	8.9 *	-
Residual	-	702	0.151	-	-
<u>D: 1985 Effects of cultivar, windbreak and distance to previous crop. ($r^2 = 0.29$)</u>					
Distance from field edge ^a	A	1	0.275	1.6	-0.058
Cultivar	B	1	1.519	9.0 *	-0.138
Windbreak ^b	C	1	13.462	79.4 *	0.792
Distance to previous crop ^c	D	1	1.582	9.3 *	-0.068
Interaction	AxB	1	0.365	2.2	0.017
Interaction	AxC	1	6.564	38.7 *	-0.144
Interaction	AxD	1	0.253	1.5	0.008
Residual	-	726	0.170	-	-

^a Log distance (m) from edge of field along half-transect.

^b Tangent of angle at the edge of the field which is subtended by windbreak.

^c Log of distance (m) from edge of field to nearest site of potatoes in the previous year. Distances exceeding 1000 m were set at 3000 m.

TABLE 5. Comparison of methods of assessing which areas of fields have larval densities above or below a threshold density of 1 larva per plant (in the third week of sampling). Regression models were used to predict zones above and below the threshold; the table compares these predictions with the actual larval populations in the zones, as indicated by 1408 individual plant samples.

Transformation of larval density	Transformation of distance	Regression model	r ²	Samples in zones above threshold		Samples in zones below threshold	
				Mean (\pm SEM) larval density	% of samples < threshold	Mean (\pm SEM) larval density	% of samples > threshold
None	None	Individual ^a	-	5.56 \pm 0.49	63.4	0.19 \pm 0.05	2.6
		Edge ^b	-	5.57 \pm 0.49	63.3	0.19 \pm 0.05	2.6
		Pooled ^c	0.21	4.74 \pm 0.43	68.6	0.30 \pm 0.07	3.3
		ANCOVA ^d	0.25	4.87 \pm 0.44	67.8	0.28 \pm 0.07	3.2
None	Log _e	Individual	-	5.56 \pm 0.49	63.4	0.19 \pm 0.05	2.6
		Edge	-	5.57 \pm 0.49	63.4	0.19 \pm 0.05	2.6
		Pooled	0.25	4.92 \pm 0.44	67.5	0.30 \pm 0.07	3.3
		ANCOVA	0.28	4.89 \pm 0.44	67.6	0.29 \pm 0.07	3.1
x ^{0.25}	Log _e	Individual	-	7.13 \pm 0.78	59.4	0.90 \pm 0.11	8.4
		Edge	-	10.92 \pm 1.12	39.4	0.87 \pm 0.11	8.2
		Pooled	0.37	7.42 \pm 1.07	48.3	1.60 \pm 0.17	11.2
		ANCOVA	0.38	13.15 \pm 1.39	27.5	1.05 \pm 0.12	9.2

^a Regressions on distance calculated separately for each half-transect where there are larvae.

^b The same as the "Individual" model except that when the total number of larvae in samples in zone E was less than 10, the half-transect was considered to be below the threshold.

^c Dependent variables are distance from field edge, number of larvae in samples from zone E, and their interaction. The regression was pooled over both years.

^d Dependent variables are distance from field edge, number of larvae in samples from zone E, and their interaction. Years and the interactions of years with each of the dependent variables were used as a covariate.

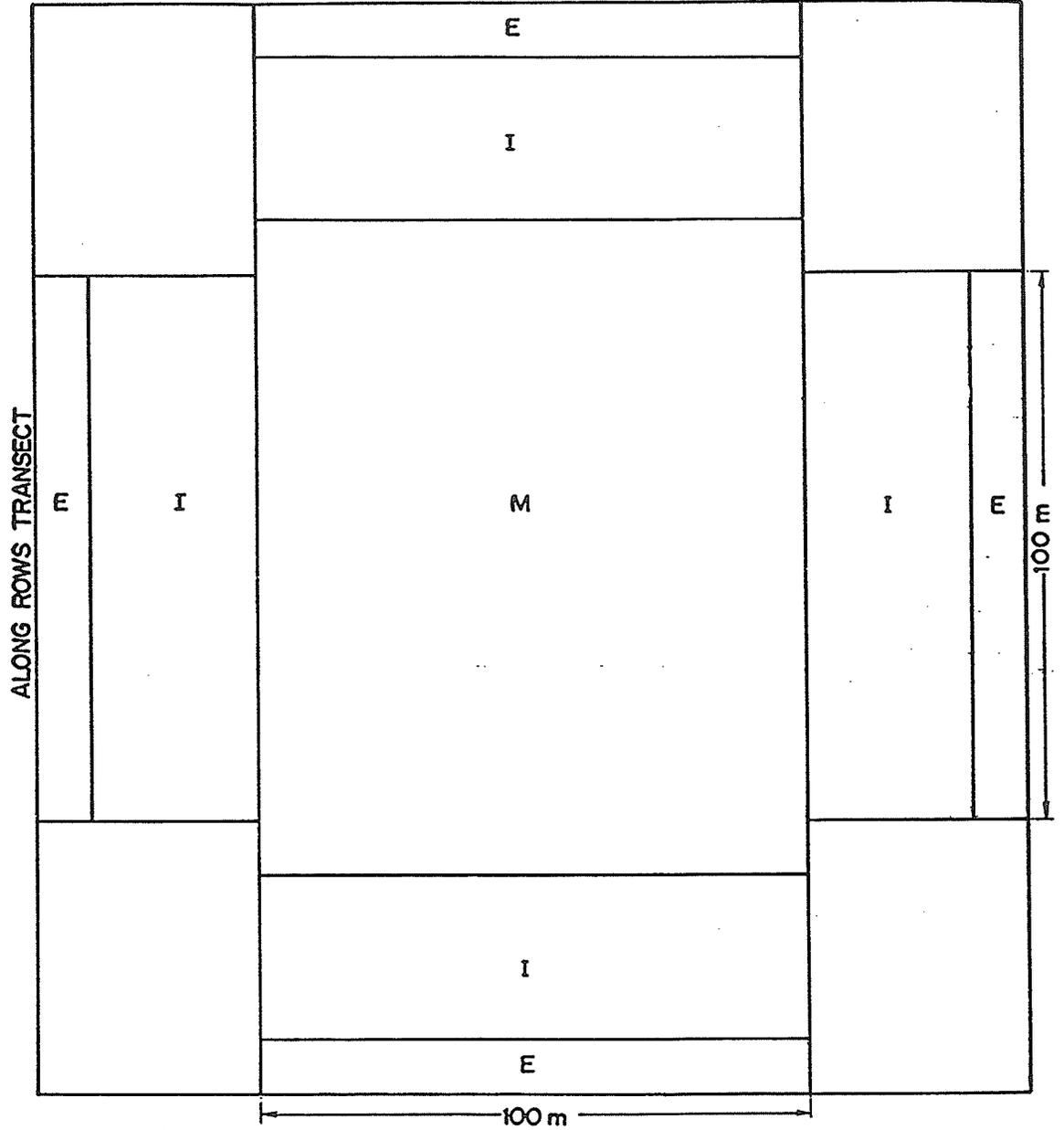
TABLE 6. Potential reduction in sprayed area of applying the pooled regression model of untransformed larval density on \log_e distance from the edge of the field. The economic threshold is assumed to be 1 larva per plant in the third week of sampling.

Year	Field	Area	Transect			Area exceeding threshold (ha)	% of area requiring spraying
			Side	Length (m)	Length (m) above threshold		
1984	202	19.0	East	140	0	1.1	6
			West	140	16		
			North	340	6		
			South	340	0		
	205	26.9	East	320	0	26.6	99
			West	320	320		
			North	210	210		
			South	210	200		
	210	2.7	East	28	28	2.7	100
			West	28	28		
			North	240	50		
			South	240	0		
	216	17.6	East	490	350	17.6	100
			West	490	330		
			North	90	90		
			South	90	90		
1985	3	14.3	East	210	0	0.0	0
			West	210	0		
			North	170	0		
			South	170	0		
	217	20.8	East	400	0	0.5	2
			West	400	0		
			North	130	0		
			South	130	6		
	229	14.1	East	80	36	10.5	74
			West	80	80		
			North	440	60		
			South	440	0		
	910	37.8	East	350	0	18.9	50
			West	350	0		
			North	270	0		
			South	270	270		

Fig. 1. Diagram of potato field showing region from which transects were randomly selected, and zones of different sample intervals along transects. Samples were taken 1 m apart in zone E, 2 m apart in zone I, and 10 m apart in zone M.



ACROSS ROWS TRANSECT



ALONG ROWS TRANSECT

100 m

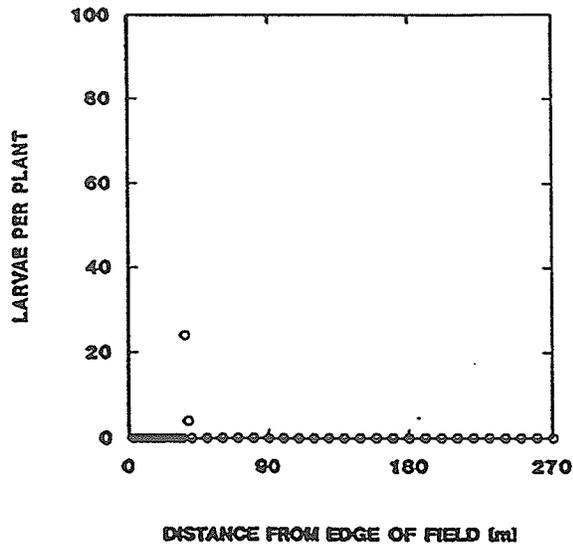
100 m

E=EDGE (10 m)
I=INTERMEDIATE (30 m)
M=MIDDLE

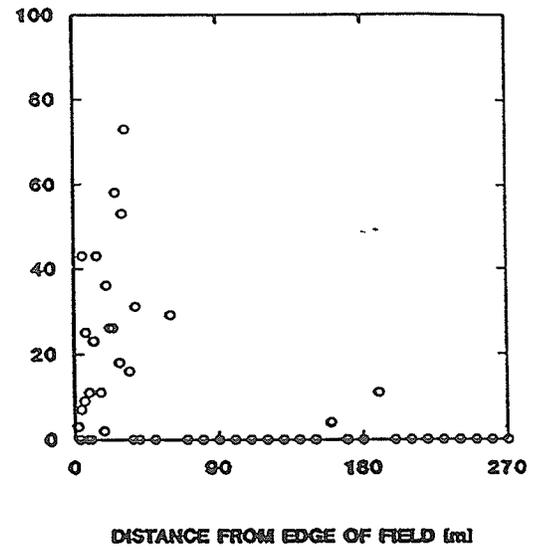
10 m

Fig. 2. Examples of half-transects in third week of sampling. A. Field 910 North side, B. Field 910 South side, C. Field 210 East side, D. Field 210 West side. Note differing horizontal and vertical scales.

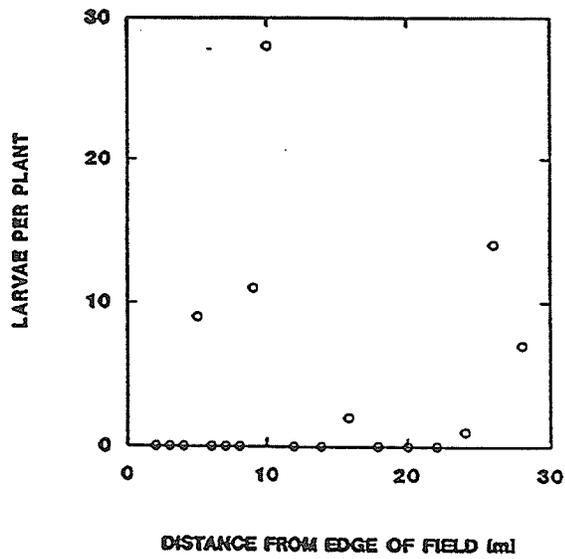
A: FIELD 910, NORTH SIDE



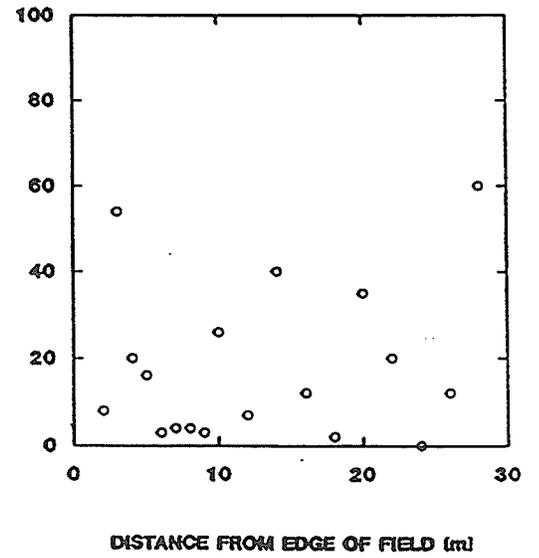
B: FIELD 910, SOUTH SIDE



C: FIELD 210, EAST SIDE



D: FIELD 210, WEST SIDE



CHAPTER 3 PART 2

DISPERSAL OF COLORADO POTATO BEETLES,
Leptinotarsa decemlineata (Say) (COLEOPTERA: CHRYSOMELIDAE),
IN POTATO PLOTS

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Abstract

In 1984 and 1985 field-collected Colorado potato beetle adults were individually marked with numbered disks and released in field plots of potato plants. Plants in plots were examined for three days following release of beetles, and the incidence and direction of movement of beetles was determined.

Overwintered beetles were significantly more mobile than were those which had recently emerged from pupation. Beetles released on plants bearing a total of 20 beetles dispersed within one hour of release, whereas beetles released singly on plants did not leave the release site so rapidly. Beetles showed a preference for movement in a north easterly direction, with south west the second most frequent direction. Beetles showed inconsistent responses to wind direction. It is hypothesized that the preference for movement in the north east - south west axis may be related to the orientation of the potato rows in the plot.

Introduction

The biology of the Colorado potato beetle (*Leptinotarsa decemlineata* [Say]) in Canada has been described by Gibson et al. (1925), and information more specific to the life cycle in Manitoba is given in Cole (1951), Senanayake (1987), and Holliday and Parry (1988). The following account is taken from these sources. In Manitoba, the Colorado potato beetle has one complete generation per year; in some years there is a second, incomplete generation. Overwintered adults emerge from the soil in June and enter potato fields; mating and oviposition occurs soon after, and larvae appear in July. The mature larvae pupate in the soil and new adults emerge in late July or August. After feeding for a while, the new adults hibernate in the soil.

Larvae seldom move far from the plant on which they hatch, unless food is short (Gibson et al. 1925). Therefore most dispersal occurs during the adult stage. The adults are weak fliers (Hurst 1975), and require relatively high temperatures (20-30°C) and insolation (Grison and Le Berre 1953, Le Berre 1962) before taking flight.

Dispersal of Colorado potato beetle has an effect on the distribution of insects and damage in the potato crop (Skuhavy et al. 1968, Morris this thesis, Chapter 3 part 1), yet only a few studies (e.g. Ng and Lashomb 1983, Boiteau 1986) have used mark-release techniques to study movement of beetles. The current study was designed to obtain information on factors affecting the initiation, distance, and direction of dispersal.

Materials and Methods

Mark-release experiments of adult Colorado potato beetle were conducted in experimental plots of cv. Norland potatoes at the Point Field Laboratory situated on the north east portion of the campus of the University of Manitoba, Winnipeg. In 1984, releases were made in a square plot (5 x 5 m) (Fig. 3a) and a rectangular plot (2 x 8 m) (Fig. 3b); in 1985, all experiments were done in a 17 x 12 m plot (Fig. 3c). In each plot, the plants were 0.3 m apart in rows, 1.0 m apart. Records of wind direction and velocity, and of temperature were obtained from the Winnipeg International Airport for the duration of the mark-release experiments. Rainfall data were obtained from the Point weather station, which did not record information about wind; temperatures recorded at the Point do not differ significantly from those at the airport (J. Watson personal communication).

Beetles for release were collected from growers' fields at Morden and Portage la Prairie and marked in the laboratory on the same day. Each beetle was individually marked by attaching a 3 mm diameter plastic numbered disk (Chr. Graze Institute, Federal Republic of Germany) to the pronotum with the liquid glue supplied with the disks. After gluing, a coating of colourless nail polish was painted over the disc to ensure longer adhesion. Marked beetles were held overnight in an incubator at 25°C and 18 h L: 6 h D. The next day beetles were cooled at 5°C for 20 minutes to prevent immediate movement on release. All releases were conducted at about 9 AM Central Daylight Time. Two release methods were used: central and scattered. In the central release method, all individually marked beetles were released on a single potato plant in the

middle of the experimental plot. In the scattered method, only one marked beetle was released on each plant, and plants on which releases were made were approximately uniformly distributed throughout the plot.

Following release, the location of individual beetles was determined by examining all potato plants in the experimental plot. These examinations were made on five occasions 1 h apart on the day of release, beginning 1 h after release. On each of the next 2 days, observations were made on five occasions, each occasion was 24 or 48 h after the corresponding observation period on the day of release.

In 1984 in the square plot, and in 1985, the central release technique was used in experiments to compare the dispersal behaviour of overwintered beetles with those that had newly emerged. Because these two types of beetle were not available simultaneously, trials of overwintered beetles were conducted earlier in the season than were those on newly emerged beetles.

In 1984, an experiment was conducted to determine the effect of high and low beetle densities at the release site on dispersal behaviour. The dispersal behaviour of the 1984 overwintered adults which were centrally released (those in the experiment above) was compared with that of overwintered adults released simultaneously using the scattered method. Both release methods were carried out in the square plot.

To examine the effect of plot shape and size, the dispersal behaviour of the newly emerged adults in the 1984 experiment in the square plot (those in the first experiment) was compared with behaviour of a group of newly emerged beetles in the rectangular plot. In both cases the central release method was used.

Data were analyzed to examine influences on the frequency with which beetles remained at their release site, moved within the plot, or left the plot; these data were analyzed using log-linear models applied to multi-dimensional contingency tables (Bishop et al. 1975, Wilkinson 1988).

The data were also analyzed to examine influences on the direction of movement of beetles. Analysis depended upon observation of an individual at two consecutive observation times. A circle of 2.5 m radius around the location of a beetle at the first time was divided into eight 45° sectors (octants) centred on a compass direction: N, NE, E, SE, S, SW, W, and NW. The octant in which the beetle was found at the second observation was recorded. Because plots were small and the plant spacing did not result in equal numbers of plants in each octant, the expected number of beetles in each octant was calculated from the proportion of the total number of plants within the 2.5 m circle which were in each octant. This was based on the assumption that beetles oriented to potato plants. The cumulative observed and expected frequencies for all beetles observed on successive occasions during each experiment were compared using the likelihood ratio chi-square (G statistic) (Sokal and Rohlf 1981). The influence of wind was assessed by a similar method but the octants in the circle were centred on eight angular deviations from upwind (0°), in a clockwise direction: 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°. This analysis was restricted to the movement which occurred during a time period when there was no change in wind direction.

Results

Incidence of Beetle Movement

There were differences between the dispersal behaviour of overwintered and that of newly emerged beetles in 1984 (Appendix Table 1) and 1985 (Appendix Table 2). Preliminary analysis indicated that there was no significant effect of hour of observation or of the interaction of hour of observation with factors related to the age of beetles in either year ($P > 0.05$); therefore the contingency tables were collapsed about hours (Bishop et al. 1975) to simplify and increase the reliability of the analysis. Table 7 shows the percentage of beetles in each "movement category": those that did not move, those that moved but remained within the plot of release, and those not found in the plot. In each year, the age of beetles affected the overall movement category (1984: $G = 204$, d.f. = 2, $P < 0.001$; 1985: $G = 170$, d.f. = 2, $P < 0.001$), and the day on which movement occurred (1984: $G = 164$, d.f. = 4; $P < 0.001$; 1985: $G = 61$, d.f. = 4, $P < 0.001$). In both years the percentage of newly emerged beetles which remained at the release site was initially much higher than that of overwintered beetles (Table 7). Temperatures were not identical during all four parts of the experiment; the pattern of temperatures was similar in the overwintered 1984 and newly emerged 1985 experiments (Table 7), it was somewhat warmer for the other two parts of the experiment. Rainfall occurred only in the overwintered portions of the experiment.

In the experiment to compare the effects of release densities on incidence of beetle movement, almost all changes in location took place on the day of release (Appendix Table 3) and so only data for the day of release were analyzed. When the results of the five observation occasions

on the day of release (Table 8) were analyzed, the density of release significantly affected the location of released beetles ($G = 10$, d.f. = 2, $P < 0.01$). However this resulted mainly from a significant effect at the first observation ($G = 13.25$, d.f. = 2, $P < 0.01$) : all the centrally-released beetles left the release site in the hour after release, but 40% of the singly released beetles were still at the release site at the first observation (Table 8). After the first observation, there were no significant differences ($P > 0.05$) in beetle location attributable to release method.

Preliminary analysis of the effect of plot size and shape on beetle location (Appendix Table 4) revealed that interactions of hour of observation with beetle location were not significant and so the contingency table was collapsed about the dimension of hours (Bishop et al. 1975). The simplified contingency table (Table 9) revealed that there was a significant effect of plot type on the way in which beetle location changed over the three days of the experiment ($G = 106$, d.f. = 4, $P < 0.001$). There was a significant effect of plot type on the rate of leaving the release site ($G = 56$, d.f. = 2, $P < 0.001$); on the day of release, more beetles remained at the release site in the square plot than in the rectangular plot. For those beetles that left the release site, the type of plot also affected the proportion that were found in the plot on each day ($G = 50$, d.f. = 2, $P < 0.001$); in the square plot for the first two days, about 44 % of beetles which had left the release site did not leave the plot; however the percentage was not more than 30% in the rectangular plot.

Direction of Movement

Figs. 4 and 5 show the compass direction of movement of the released adults. The Figures show the frequency of each direction of the steps between sequential observations throughout the three day period. It is evident that the direction of movement of beetles was non-uniform in many cases. Analysis (Table 10) indicates significant non-uniformity in five of the six tests; when significant non-uniformity occurred, there was always a large number of beetles moving towards the north east, and in four of the five cases, beetles also moved in large numbers to the south west.

Figs. 6 and 7 summarize the frequency of movement relative to wind direction throughout the 3 day period. The G-tests show that wind often influenced the direction of movement, but that this was not consistent throughout the experiments. Wind influence was significant at velocities of 13-14 km/h ($P < 0.05$) but not at lower or higher velocities. It is noticeable that significant non-uniformity of compass direction (Table 10) is often associated with significant non-uniformity of direction relative to the wind (Table 11).

Discussion

Incidence of Movement

Although weather conditions were not uniform during all the experiments, there does not appear to be a simple relationship between weather conditions and the experimental results of the comparison of overwintered beetles with newly emerged beetles (Table 7). Therefore the finding that newly emerged beetles were significantly less mobile than

overwintered beetles is unlikely to be an artefact due to weather.

Overwintered adults that emerge in spring did not remain long on plants on which they are released, but tended to move around within the plot or leave the plot. Most newly emerged adults remained on the plants they were first released on throughout the first day; by the end of the experiment many of them had also left the plot (Table 7).

The difference in movement is probably due to the state of development of the flight muscles. Colorado potato beetles cannot fly until several days after emergence, because the flight muscles are immature and short of glycogen (Johnson 1976b). In my laboratory rearing, at 30°C and 18 h L: 6 h D, newly emerged adults had soft elytra which hardened only after 5 days. However, hardening of the elytra is not the only component of the process. The enzyme system develops flight worthiness after about two weeks (Johnson 1976b), and this time includes a period of feeding. Newly emerged adults have been found to require 10 days feeding before being able to fly (Le Berre 1950).

The activity of overwintering adults too, depends on flight muscle regeneration after hibernation (Johnson 1969, Johnson 1976a, b). The activity of overwintered adults in my experiments indicates that regeneration of flight muscles was probably completed before the experiments began.

My findings appear consistent with those of Bach (1982), who concluded that beetles stayed on the plants they originally colonized, for at least 5 days after release. Bach conducted her experiments in September, therefore the beetles she used had not overwintered and were probably new adults. My experiments conducted with newly emerged adults

show similar low mobility. My findings are also in agreement with the results of Boiteau (1986), who found that overwintered beetles move from plot to plot, apparently in search of young potato plants. In Europe, overwintered beetles are also considered more mobile than subsequent generations (Le Berre 1950, Gimingham 1950). Trouvelot (1935) drew attention to the importance of spring migration of Colorado potato beetles in North America. In contrast, a much cited paper by Tower (1906) indicated that long migration flights of the insect occur in late summer, before hibernation. At this time, the flight muscles of new adults would have to develop and the beetles fly from fields with senescing potato leaves to fields with younger plants. If the flight muscles do not have time to develop, then the new adults would enter the soil to hibernate when short day length and shortage of food prevails. I found that, when harvesting my plots in late August and early September, hibernating beetles were uncovered from the soil and some were gathered together under the tubers. If this phenomenon occurs in all potato fields in Manitoba, then Tower's statements may not be applicable to Colorado potato beetles in this province.

There was a strong influence on overwintered beetles of the density of beetles on the release plant (Table 8). Dispersal is almost immediate when there are 20 beetles per plant, even though initially beetles would be unable to fly because they had been cooled before release. This finding is important in the context of the high densities of overwintered beetles observed at the edges of fields (Skuhravy et al. 1968, Morris this thesis, Chapter 3 part 1); it appears that beetles will tend to move rather than remain at the field edge, if the densities are very high.

This will result in beetles spreading further into fields when densities at the edge are high, and this will influence the distribution of feeding larvae.

The differences between movement in the rectangular plot and the square plot (Table 9), are what might be expected from the shape and size of the plot. Beetles that moved from the release site were more likely to leave the rectangular plot than the square plot; this is probably the result of two of the edges of the rectangular plot being very close to the release site, whereas in the square plot all edges were 2.5 m from the release site. It is not clear why the number remaining at the release site on the first day was higher in the square plot than in the rectangular plot.

Direction of Movement

In five trials out of six (Table 10) there was significant non-uniformity in the compass direction of movement of adult beetles and a strong trend of movement towards the north east, and less so to the south west. Rows in all plots were oriented north east - south west (Fig. 3) therefore it is very likely that beetles are influenced by row direction. However, because there were no experiments in which rows were oriented differently, this hypothesis cannot be tested with the present data.

Directional preference in walking beetles in New Jersey was recorded by Ng and Lashomb (1983), but in that case the preferred direction of movement was north west. Ng and Lashomb suggested that the pattern of movement might be adaptive in the mountainous regions from which Colorado potato beetles are thought to have originated: movement to the north west might benefit beetles on mountain slopes by placing them in places where

they can maximize their heat uptake from isolation. However if this was a relict phenomenon, then the direction of orientation should be the same in New Jersey and in Winnipeg. Therefore, unless beetles in Manitoba and New Jersey are the descendants of different original populations, the differences in preferred direction of movement suggests response to local conditions rather than a relict instinct. Cytological studies (Hsiao 1985), do not support the idea of a different origin for Manitoba and New Jersey populations of Colorado potato beetles. Ng and Lashomb created unfamiliar habitats which were totally different from mine. Beetles were all released on potato plants in my experiments. Therefore I conclude that beetles on plants behave differently to beetles in a non-host plot or habitat. When in plots of host plants, beetles appear to respond to plants in the plot. In a non-host habitat, beetles probably use other orientation cues such as sun or wind direction.

The apparent response to the plant rows in my plots could result if beetles placed on a plant within a plot moved preferentially to the nearest potato plant. They would thus travel along the row, to the north east or to the south west. My findings show a distinct trend towards the north east and less so the south west. The preference for movement towards the north east, rather than to the south west, may be due to sun orientation or to the direction of the wind blowing at the time of activity.

Wind influence was not consistent in my experiments. A closer examination of the analysis shows that wind influence was significant only in experiments where higher numbers of movement steps were analyzed (Table 11). However comparison of Table 11 with Table 10 shows that when wind

direction gave a significant effect, there was also a significant effect of compass direction. Since the latter was much more consistent, it may be that the response to wind direction is largely an artefact.

Beetles have been observed to fly against low velocity winds such as 2m/sec (ca. 7 km/h). (Wiluz 1958). Probably at a high wind velocities, beetles cannot fly against the wind but are carried downwind. These effects of velocity may make detection of directional effects more difficult. Detection of such effects may also have been complicated because the only hourly wind direction records available were from the Winnipeg Airport. The plots were 13 km away from the Airport.

The dispersal pattern of the Colorado potato beetle could be more accurately assessed if the beetles stayed longer in experimental plots. This could be achieved by using bigger plots. Also, because of limited manpower, data were recorded only up until 2 PM daily. The wind continues to blow throughout the night and the degree of movement of beetles during the night is not known. Increasing the plot size or the duration of observations would require additional resources and personnel. The importance of row direction to beetle movement could be explored by releasing beetles in plots with different directions of plant rows. If the directional trend changed the importance of orientation to nearest potato plant within the row would be verified. If the direction of rows is an important determinant of beetle movement, but movement is also influenced by other stimuli such as wind direction or direction of the sun, it may be possible to arrange the direction of plant rows in fields to minimize the spread of beetles.

TABLE 7. Comparison of location of centrally-released overwintered and newly emerged Colorado potato beetle adults.

Year	Adult type	Number released	Day	Daily weather			Percentage of beetle observations			
				Temperature		Rainfall (mm)	At point of release	Moved but in plot	Not found in plot	
				max °C	min °C					
1984	Over-wintered	20	1	20.8	4.6	0.0	0	34	66	
			2	21.5	9.6	16.7	0	1	99	
			3	25.7	13.0	0.0	2	0	98	
	Newly emerged	40	1	27.6	17.8	0.0	91	3	6	
			2	29.2	17.2	0.0	30	31	39	
			3	31.3	13.3	0.0	3	4	92	
1985	Over-wintered	50	1	27.4	17.9	0.0	51	18	30	
			2	25.2	18.2	0.0	12	19	69	
			3	22.5	17.8	69.8	2	6	91	
	Newly emerged	50	1	20.8	4.2	0.0	87	6	8	
			2	23.3	10.5	0.0	54	6	40	
			3	24.7	13.5	0.0	22	9	69	

^a Each plot was examined five times on each day; percentages indicate the number of observations of each type expressed as a percentage of the total number of observations per day.

TABLE 8. Effect of initial beetle density on location of overwintered beetles on the day of release.

Hour after release	Single release (N = 20)			Central release (N = 20)		
	Percentage of beetles			Percentage of beetles		
	At point of release	Moved but in plot	Not found in plot	At point of release	Moved but in plot	Not found in plot
1	40	25	35	0	35	65
2	10	40	50	0	55	45
3	5	20	75	0	35	65
4	0	20	80	0	30	70
5	5	30	65	0	15	85

TABLE 9. Location of centrally released newly emerged Colorado potato beetles in a rectangular plot (2 x 8m) and a square plot (5 x 5m).

Plot shape	Date	Daily weather			Percentage of beetles ^a		
		Temperature		Rainfall (mm)	At point of release	Moved but in plot	Not found in plot
		max °C	min °C				
Rectangle	24 Jul	26.3	10.2	0.0	64	8	28
	25 Jul	28.0	12.5	0.0	39	18	43
	26 Jul	26.7	10.9	0.0	9	24	67
Square	31 Jul	27.6	17.8	0.0	91	4	5
	1 Aug	29.2	17.2	0.0	30	31	39
	2 Aug	31.3	13.3	0.0	4	4	92

^a Each plot was examined five times on each day; percentages indicate the number of observations of each type expressed as a percentage of the total number of observations per day; 60 beetles were released in the rectangular plot and 40 beetles were released in the square plot.

TABLE 10. Compass direction of movement of Colorado potato beetles.

Experiment ^a	G	G test of departure from uniformity (7 d.f.) Significance	Octants with >20%	N ^b
Overwintered beetles 1984	4	n.s.	S,W	25
Overwintered beetles 1985	75	P<0.001	NE,SW	59
Newly emerged beetles 1984	16	P<0.05	NE,S,SW	24
Newly emerged beetles 1985	47	P<0.001	NE	16
Scattered release	18	P<0.05	NE,SW	33
Rectangular plot	39	P<0.001	NE,SW	48

^a The central release experiment was the same as the 1984 overwintered beetles; the square plot experiment was the same as the newly emerged 1984 experiment.

^b Total number of movement steps (lines between sequential observations) in analysis.

TABLE 11. Direction of movement of Colorado potato beetle in relation to wind direction.

Experiment ^a	G	G test of departure from uniformity (7 d.f.) Significance	Octants ^c with >20%	N ^b	Weather during experiment Mean temperature °C	Mean windspeed km/h
Overwintered beetles 1984	13	P<0.10	270°, 0°	20	16	13
Overwintered beetles 1985	33	P<0.001	45°, 90°	35	22	14
New beetles 1984	9	n.s.	0°, 180°, 315°	7	23	6
New beetles 1985	13	P<0.10	0°, 45°, 270°	8	16	15
Scattered Release	14	P<0.05	135°	22	16	13
Rectangular plot	12	n.s.	0°, 180°	6	19	5

^a The central release experiment was the same as the overwintered beetles 1984; the square plot experiment was the same as the newly emerged beetles 1984 experiment.

^b Number of movement steps with no change in wind direction.

^c 0° is upwind.

APPENDIX TABLE 1. Hourly weather conditions and location of centrally released overwintered and newly emerged Colorado potato beetle adults in 1984 experiment.

Adult type	Date	Hours since release	Temperature °C.	Wind in previous hour Direction	hour Speed (km/h)	At point of release	Numbers of Beetles Moved but in plot	Not found in plot
Over-wintered	6 Jul	0	15.2	NW	9	20	0	0
		1	16.4	W	6	0	7	13
		2	16.6	W	9	0	11	9
		3	17.6	ESE	6	0	7	13
		4	17.5	NNE	9	0	6	14
	7 Jul	5	18.8	NE	11	0	3	17
		25	19.0	S	33	0	1	19
		26	20.1	S	39	0	0	20
		27	20.0	S	35	0	0	20
		28	19.6	S	24	0	0	20
	8 Jul	29	17.0	S	20	0	0	20
		49	21.4	SSW	9	1	0	19
		50	22.9	SSW	2	1	0	19
		51	24.7	SSE	15	0	0	20
		52	24.4	S	22	0	0	20
		53	25.6	S	15	0	20	
Newly emerged	31 Jul	0	20.2	NNE	6	40	0	0
		1	21.4	NNE	6	40	0	0
		2	23.2	ENE	2	39	1	0
		3	25.1	NE	2	36	1	3
		4	25.8	NNW	2	32	3	5
	1 Aug	5	26.3	NE	6	35	2	3
		25	22.8	SE	9	14	13	13
		26	24.3	NE	2	12	11	17
		27	26.2	E	7	11	13	16
		28	27.0	SE	15	11	13	16
	2 Aug	29	28.0	S	9	11	13	16
		49	26.2	-	0	1	3	36
		50	27.6	SSE	6	0	3	37
		51	29.0	SSE	9	0	3	37
		52	30.0	SSE	13	3	0	37
		53	30.2	SE	13	3	37	

APPENDIX TABLE 2. Hourly weather conditions and location of centrally released overwintered and newly emerged Colorado potato beetle adults in 1985 experiment.

Adult type	Date	Hours since release	Temperature °C.	Wind in previous hour Direction	Speed (km/h)	At point of release	Numbers of Beetles Moved but in plot	Not found in plot	
Over-wintered	2 Aug	0	20.5	SSE	19	50	0	0	
		1	22.7	S	22	35	5	10	
		2	24.3	S	19	36	8	6	
		3	24.7	SSE	20	21	10	19	
		4	25.3	SSE	22	21	11	18	
	3 Aug	5	26.5	S	22	15	12	23	
		25	23.2	S	15	7	7	36	
		26	22.7	SSE	17	7	9	34	
		27	23.0	S	11	7	10	35	
		28	23.0	E	7	6	10	33	
		29	23.8	ESE	19	3	10	37	
		49	20.4	ESE	11	2	6	42	
		50	20.3	ESE	13	2	8	40	
	4 Aug	51	19.3	E	13	2	2	46	
		52	20.4	E	13	0	0	50	
		53	21.0	ENE	19	0	0	50	
		Newly emerged	29 Aug	0	14.5	NE	7	50	0
	1			16.8	E	9	50	0	0
	2			17.2	ENE	15	48	2	0
3	18.6			ENE	13	41	2	7	
4	19.0			E	9	41	4	5	
30 Aug	5		19.8	ENE	11	37	6	7	
	25		19.6	S	19	30	0	20	
	26		20.8	S	22	30	0	20	
	27		22.0	S	26	30	0	20	
	28		22.2	S	24	23	7	20	
31 Aug	29		23.0	S	28	23	7	20	
	49		21.3	SSW	17	20	5	25	
	50		23.9	W	15	10	4	36	
	51		22.4	WNW	15	7	6	37	
	52		22.2	W	13	13	0	37	
53	23.3	W	30	6	7	37			

APPENDIX TABLE 3. Location of overwintered adult Colorado potato beetles released either singly on plants, or from a single central plant. The experiment was performed in 1984.^a

Date	Hours since release	Temperature °C	Wind in previous hour Direction	hour Speed (km/h)	Number of singly released beetles			Number of centrally released beetles		
					At point of release	Moved but in plot	Not found in plot	At point of release	Moved but in plot	Not found in plot
6 Jul	0	15.2	NW	9	20	0	0	20	0	0
	1	16.4	W	6	8	5	7	0	7	13
	2	16.6	W	9	2	8	10	0	11	9
	3	17.6	ESE	6	1	4	15	0	7	13
	4	17.5	NNE	9	0	4	16	0	6	14
7 Jul	5	18.8	NE	11	1	6	13	0	3	17
	25	19.0	S	33	0	3	17	0	11	9
	26	20.1	S	39	0	3	17	0	0	20
	27	20.0	S	35	0	3	17	0	0	20
	28	19.6	S	24	0	3	17	0	0	20
	29	17.0	S	20	0	3	17	0	0	20
8 Jul	49	21.4	SSW	9	0	3	17	1	0	19
	50	22.9	SSW	2	2	1	17	1	0	19
	51	24.7	SSE	15	0	0	20	0	0	20
	52	24.4	S	22	0	0	20	0	0	20
	53	25.6	S	15	0	0	20	0	0	23

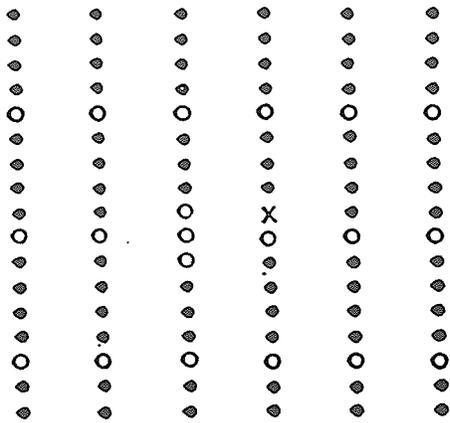
^a Weather data and data on centrally released beetles were previously presented in Appendix Table 1.

APPENDIX TABLE 4. Location of centrally released newly emerged Colorado potato beetle adults in square and rectangular plots in 1984.^a

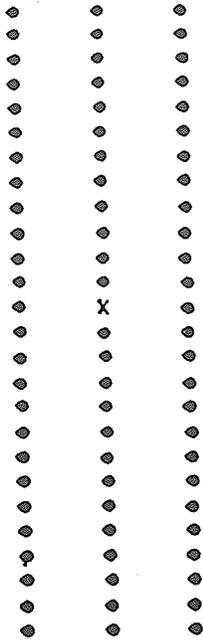
Plot shape	Date	Hours since release	Temperature °C	Wind in previous hour Direction	Speed (km/h)	Numbers of beetles		
						At point of release	Moved but in plot	Not found in plot
Rectangle	24 Jul	0	20.6	E	2	60	0	0
		1	22.0	W	2	44	4	12
		2	23.4	SW	2	33	4	23
		3	24.0	NW	6	39	4	17
		4	24.8	W	6	38	6	16
	25 Jul	5	24.8	WSW	6	39	6	15
		25	22.0	SSW	11	26	9	24
		26	23.0	SSW	13	22	13	25
		27	24.2	SW	7	21	17	22
		28	24.8	SSW	6	24	7	29
	26 Jul	29	26.7	WSW	6	24	7	29
		49	22.0	NNE	6	5	14	41
		50	23.1	NE	9	5	15	40
		51	23.7	N	6	5	15	40
		52	25.7	NNW	6	5	15	40
		53	25.6	-	0	6	14	40
	Square	31 Jul	0	20.2	NNE	6	40	0
1			21.4	NNE	6	40	0	0
2			23.2	ENE	2	39	1	0
3			25.1	NE	2	36	1	3
4			25.8	NNW	2	32	3	5
1 Aug		5	26.3	NE	6	35	2	3
		25	22.8	SE	9	14	13	13
		26	24.3	NE	2	12	11	17
		27	26.2	E	7	11	13	16
		28	27.0	S	15	11	13	16
2 Aug		29	28.0	SE	9	11	13	16
		49	26.2	-	0	1	3	36
		50	27.6	SSE	6	0	3	37
		51	29.0	SSE	9	0	3	37
		52	30.0	SSE	13	3	0	37
		53	30.2	SE	13	3	0	37

^a Weather data and data for square plot were previously presented in Appendix Table 1.

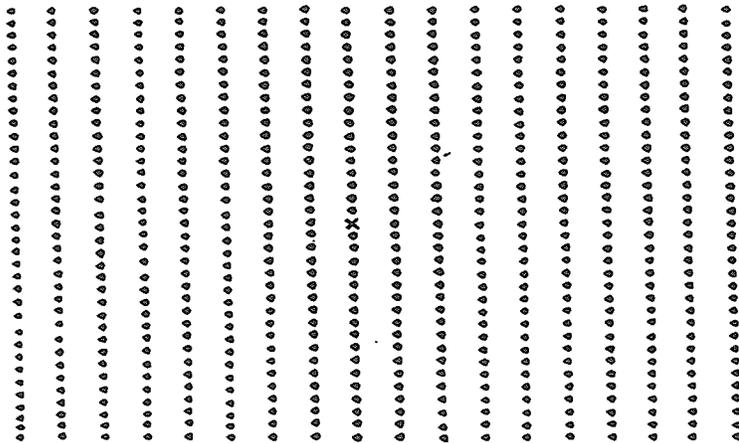
Fig. 3. Plans of plots used in mark release experiments. Dots represent individual potato plants. (a) 1984 Square plot; (b) 1984 Rectangular plot; (c) 1985 plot.



a



b



c

X = CENTRAL RELEASE POINT
O = SCATTER RELEASE POINT
● = POTATO PLANT



Fig. 4. Percentage of adult Colorado potato beetles moving in each compass direction in four mark release trials: overwintered beetles 1984, overwintered beetles 1985, newly emerged beetles 1984, and newly emerged beetles 1985. The height of bars represents the percentage of all movement steps within a trial which were in the indicated direction.

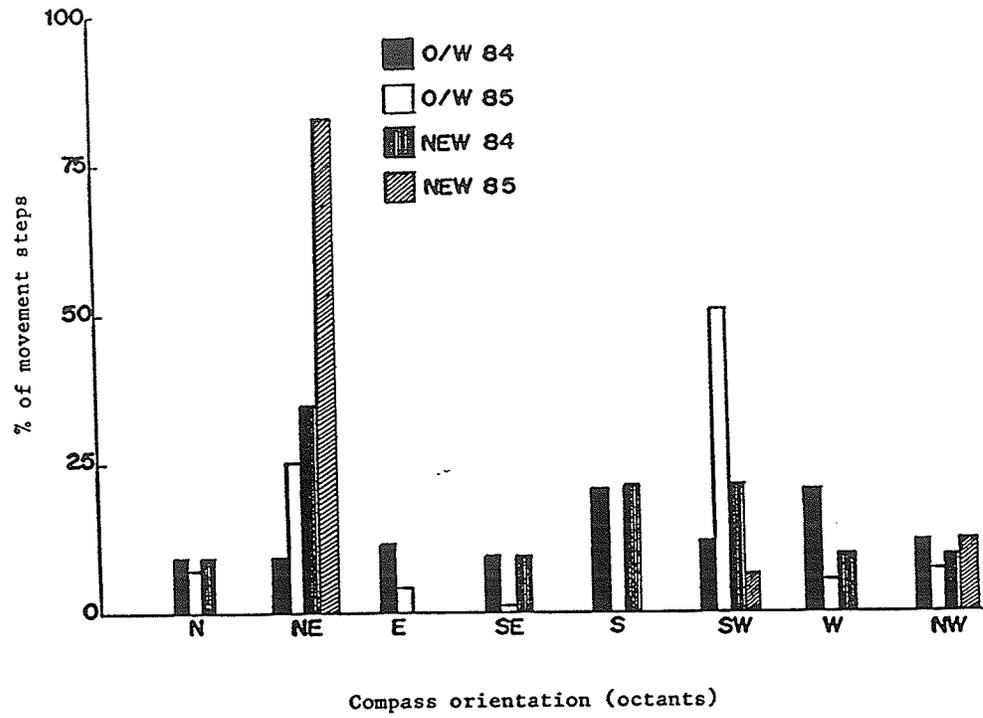


Fig. 5. Percentage of adult Colorado potato beetles moving in each compass direction in two mark release trials conducted in 1984: the scattered release method in the square plot, and the central release method in the rectangular plot. The height of bars represents the percentage of all movement steps within a trial which were in the indicated direction. Note that the legend "long" refers to the releases in the rectangular plot.

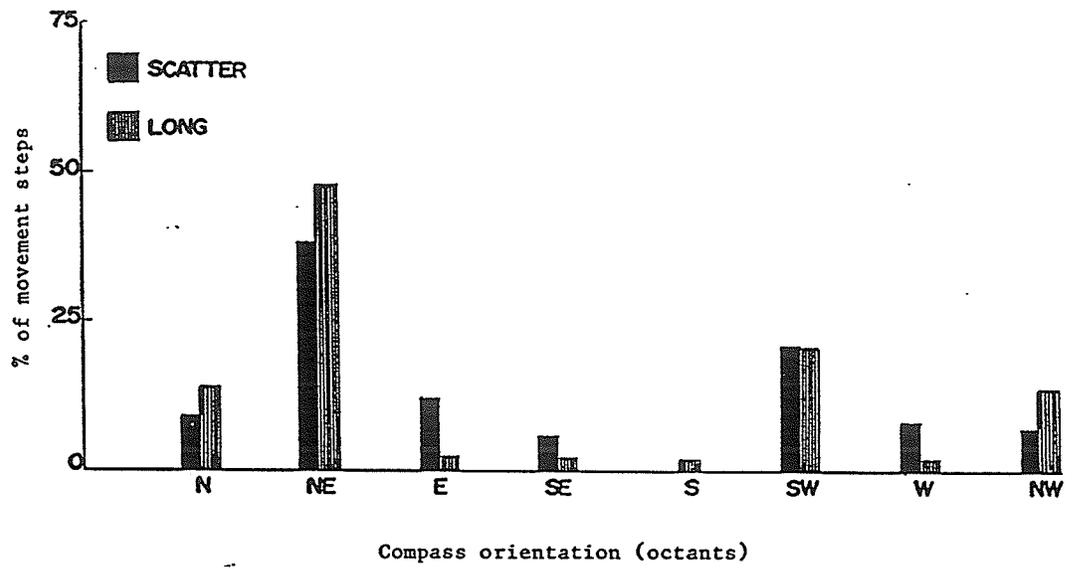


Fig. 6. Percentage of adult Colorado potato beetles moving in each quadrant relative to the wind direction in four mark release trials: overwintered beetles 1984, overwintered beetles 1985, newly emerged beetles 1984 and newly emerged beetles 1985. The height of bars represents the percentage of movement steps within a trial which were in the indicated direction relative to the wind. Only movement steps during periods when wind direction was constant are included.

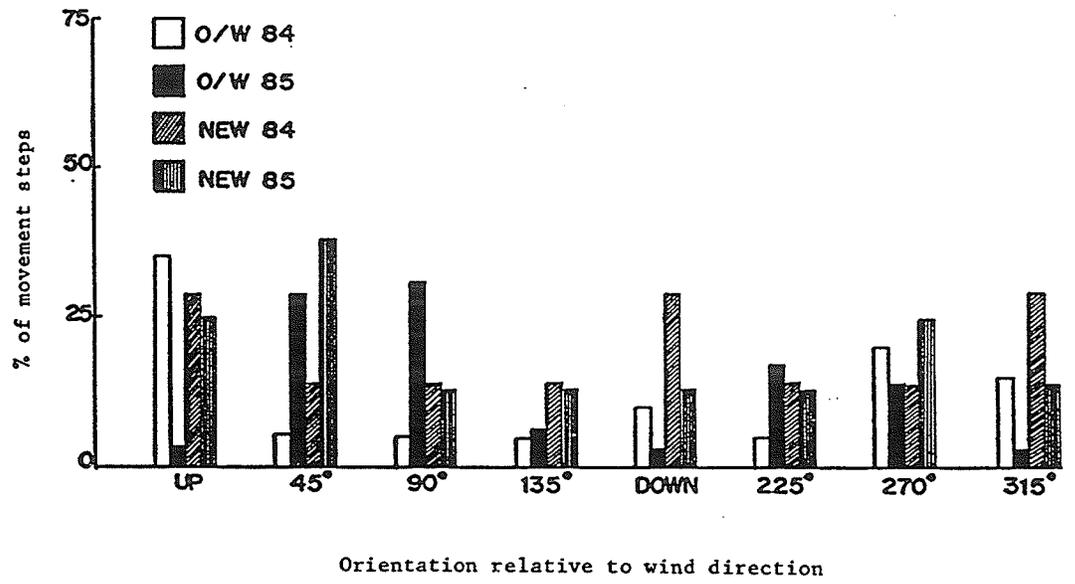
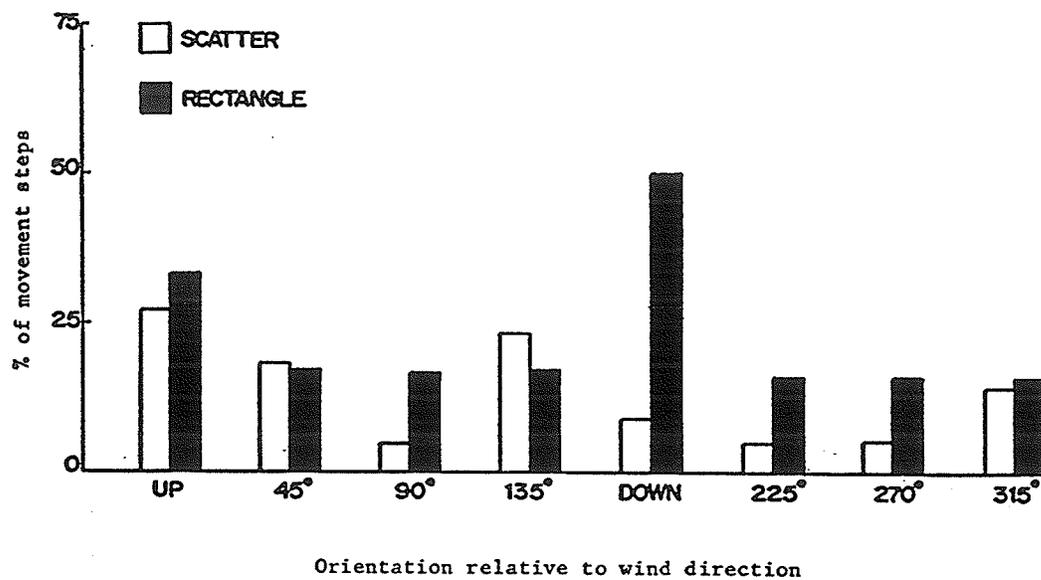


Fig. 7. Percentage of adult Colorado potato beetles moving in each quadrant relative to the wind direction in two mark release trials conducted in 1984: the scattered release method, and release in the rectangular plot. The height of bars represents the percentage of movement steps within a trial which were in the indicated direction relative to the wind. Only movement steps during periods when wind direction was constant are included.



CHAPTER 3 PART 3

DISPERSAL BEHAVIOUR OF COLORADO POTATO BEETLES,
Leptinotarsa decemlineata (Say) (COLEOPTERA: CHRYSOMELIDAE)
ON CAGED POTATO PLANTS

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Abstract

The dispersal of Colorado potato beetle larvae, newly-emerged adults and overwintered adults was recorded in a large cage designed to mimic three potato plants in a single row of a commercial field. Insects were released on the middle of the three plants. The effect of the initial density on, and of defoliation of, the middle plant was examined.

Most larvae did not leave plants unless they were defoliated. When the middle plant was defoliated at the beginning of the experiment, 46% of larvae which left the release site moved to another plant. However, only 7% of larvae which moved went to another plant when defoliation occurred later in the trial as the result of high densities of larvae on the middle plant.

Newly-emerged adult beetles released on defoliated plants were more likely to move than were overwintered adults released on undefoliated plants. Both types of adult, whether released on defoliated or undefoliated plants, were more likely to move at high densities than at low. Almost all newly-emerged beetles which moved went to the downwind plant, but most of the overwintered adults which moved went to the upwind plant. Larvae were less likely to move than adults under approximately similar conditions.

Introduction

In Manitoba, Colorado potato beetles undergo a single generation on the crop in each year (Holliday and Parry 1988). In spring, adults emerge from overwintering sites near the potato fields in which they fed the previous summer, and make their way to newly-emerged potato fields; there they feed and lay their eggs. In many cases, this process results in high densities of larvae at the periphery of fields (Chapter 3, Part 1), and lower densities in the middle of the fields. It is desirable to understand the behavioural bases for these patterns, and to determine whether, if insecticides were not applied, the larvae and adults would move from the areas of high density. In the case of adults, these questions have already been addressed in a field plot study (Chapter 3, Part 2). In this paper, the same questions are addressed both for larvae and adults in more controlled conditions in a laboratory cage.

Colorado potato beetles are highly selective in host plant choice (May and Ahmad 1983), and the behavioural and sensory bases of this selection have been studied both in adults and larvae. Much of the work on host-seeking behaviour of adult Colorado potato beetles has been done using wind tunnels in which insects, which are not on plants, are exposed to wind and windborne odours. In these circumstances, in the absence of host-plant odours, beetles exhibit positive anemotaxis and this response is enhanced by starvation (de Wilde et al. 1969, Visser 1976, de Wilde 1976, Visser and Avé 1978). Positive anemotaxis is also enhanced by the odour from several solanaceous species (Visser and Nielsen 1977). However, when presented with a choice of odours in a Y-tube olfactometer, adult beetles are attracted to potato leaf odour only after they have fed

on potato foliage; newly emerged unfed beetles do not show any preference for host plant odour (Jermy 1958).

Host plant selection of the Colorado potato beetle larva also has been studied. Gibson et al. (1925) stated that larvae move around aimlessly when plants are defoliated. But Cass (1957) and de Wilde (1958) showed that several environmental factors such as wind, light and host plant odour aid larvae in finding host plants. Optical and olfactory stimuli are also involved. Chin (1950) suggested that larvae select their host plant by a sequential process involving several physical and chemical properties of the plant.

The above studies do not indicate the circumstances in which larvae or adults leave a host plant, and what their behaviour is once they have done so. Insects in wind tunnels are not exposed to the range of stimuli that they might experience in a row of potatoes in the field. Therefore this study was initiated to examine the behaviour of larvae and adults in a more realistic, but still simple, system. The roles of insect density and of defoliation in inducing insects to leave a plant were examined. Additionally, for those insects which did leave the plant, orientation with respect to wind and plants was investigated.

Materials and Methods

Trials of the dispersal behaviour of three different stages of Colorado potato beetles were carried out on caged plants in the laboratory. The stages tested were "new" adults which had emerged from pupation within the previous 12-24 h, "old" adults which overwintered in

the field and were collected in the spring, and a mixture of larvae.

Overwintered adults were collected in June or early July from farmers' fields at Morden. Three pairs of these adults were reared in 15 cm petri dishes in an incubator at 25°C with a photoperiod of 18:6h L:D; fresh potato leaflets were supplied daily. Eggs were collected daily and placed in new petri dishes, and the larvae which hatched were maintained in petri dishes in the same incubator. Some of the hatched larvae were used in the experiments. Different instars were distinguished based on age and head capsule width; third and fourth instars were used in all but one of the trials. Larvae which were not used in the experiments, when ready to pupate, were placed in soil in plant pots in a growth room. Newly emerged adults were collected in cages placed over the pots. Cages were 60 x 60 cm and 75 cm high and were covered with fine netting. The newly emerged adults were used in the experiments. Old adults for the experiments were collected in spring at Morden, as described above. The adults were placed in a 25°C incubator overnight and used in the experiments the following day.

Potato plants, cv. Norland, were grown in a growth room to provide food for beetle cultures and to supply plants for trials of dispersal behaviour. Seed potato pieces of ca. 30-60g were planted in 30 cm diameter plastic pots. Plants were grown under fluorescent lights with a photoperiod of 16:8h L:D. From some plants, leaves were removed daily and fed to insects in the laboratory colony. Leaves were not removed from those plants used in the trials of dispersal behaviour.

The cage for dispersal trials was 3.5 m long, 1.5 m wide and 1.5 m high, and was covered with 3 mm wire mesh. Three potato plants were

introduced into the cage for each experiment; these plants were 6 weeks old and ranged from 25 -30 cm in height. For each experiment, plants were chosen to be as similar as possible in height and in number of leaves. The pots containing the plants were placed 65 cm apart on the centre line of the long axis of the cage. The pots stood on the floor of the cage, and on top of the pots were placed two sheets of aspenite. Semicircular cuts had been made in the aspenite sheets to fit around the plants. The sheets were covered with soil so that the experimental arena mimicked three plants growing in a row in soil.

The cage was illuminated by two 120 cm fluorescent tubes which provided a light intensity in the cage of 870 lx with a photoperiod of 16:8h L:D. An electric fan was used to blow air through the cage in a direction parallel to its long axis. Wind velocities were measured with a cup anemometer, and were 3 km/h, 1 km/h, and 0.3 km/h at the upwind, middle and downwind plant respectively. A cigarette smoke test was conducted to assess the wind turbulence in the cage. A lighted cigarette attached to the end of a long stick was placed at the upwind, middle and downwind plants. The plume of smoke showed that the flow of the air stream from the upwind to the downwind plant was moderately turbulent.

In the dispersal trials, a range of densities of larvae, old adults, or new adults were released in the cage on either undefoliated or defoliated plants. In all cases, the middle potato plant was the release site for all the insects. Non-defoliated plants were used first as middle plants. After insect defoliation these plants were used as defoliated release sites. The upwind and downwind plants were undefoliated at the beginning of all experiments.

The behaviour of insects while moving, and the location of insects, was recorded intermittently between 9 am and 5 pm daily for 3 days after release. To allow comparisons of different trials, only data taken at 31 h after release are reported here. The distribution of the insects at 31 h was assessed by the analysis of contingency tables (Sokal and Rolf 1981); for tables with more than two dimensions, log-linear modelling was used (Bishop et al. 1975).

Results

Larvae

The distribution of Colorado potato beetle larvae 31 h after release is shown in Table 12. All trials used third and fourth instar larvae, except the defoliated trial with 138 larvae; in this trial some younger larvae were also used. Preliminary analysis was done to determine whether initial density at the release site affected whether larvae moved from that plant (Table 13). When the site of release (the middle plant) was defoliated, density significantly affected the number of larvae moving ($G = 18.2$, d.f. = 1, $P < 0.001$); the percentage of larvae moving was greater at lower density (Table 13). When the site of release was undefoliated, density also affected whether larvae moved ($G = 41.4$, d.f. = 2, $P < 0.001$); in this case the pattern was complex (Table 13).

The initial densities did not match exactly in the trials for defoliated and undefoliated release sites (Table 12). However, it was considered that the initial densities of 32 and 138 for the defoliated release sites were sufficiently close to those of 35 and 126 for the

undefoliated release sites that a contingency table of "low" (32 - 35) and "high" (126 - 138) initial densities categorized against defoliation state could be analyzed (Table 14). Fitting of hierarchical log-linear models to the contingency tables (Bishop et al. 1975) revealed that movement was significantly affected by the interaction of defoliation and density ($G = 18.1$, d.f. = 1, $P < 0.001$). The rules of hierarchical modelling dictate that the interaction of density with movement ($G = 2.8$, d.f.=1, $P > 0.05$) and of defoliation state with movement ($G = 3.6$, d.f.=1, $P > 0.05$) be included in the fitted model, despite their non-significance. Examination of the percentages of larvae moving (Table 14), revealed that at high densities larval movement was unaffected by the defoliation status of the plant on which the release occurs; however, at low densities, the frequency of movement was higher when the release site was defoliated.

The influence of density and defoliation of the release site on whether larvae which left the release site went to other plants was examined by categorizing densities as "low" or "high", as described above. The only significant influence on whether the larvae went to other plants or abandoned plants altogether was the defoliation status of the release site ($G = 30.8$, d.f. = 1, $P < 0.001$). When the release site was defoliated, 46% of the larvae which left the release site were found on another plant; when the release site was undefoliated, only 7% of those larvae which had left the release site were found on another plant. All larvae represented by this 7% were from the high density undefoliated release site (Table 12). Some of the larvae which had left the undefoliated plants were seen entering the soil.

A similar analysis of whether larval movement to upwind or downwind

plants was affected by "low" or "high" densities, or by defoliation of the release site, was carried out. There were no significant influences of density, or defoliation status, or of their interaction, on whether larvae went to upwind or downwind plants. Of the 43 larvae in all trials which moved to other plants, 60% moved to the downwind plant and 40% moved to the upwind plant. This does not differ significantly from the expectation of equal numbers moving in each direction ($\chi^2 = 1.9$, d.f. = 1, $P > 0.1$).

Observation of the behaviour of larvae moving on the soil in the cage indicated that larvae were apparently unable to detect plants until close to them. Larvae did not appear to exhibit directed movements when leaving the release site; directed movements only occurred at a distance of about 2 mm from a potato plant.

Adults

Data on the location of adults 31 h after release are presented in Table 15. For the new adults released on defoliated plants, density significantly affected whether movement occurred ($G = 13.2$, d.f. = 2, $P < 0.01$); 50 % of beetles moved when the initial density was 10, but at higher densities more than 90% moved (Table 16). For old adults released on undefoliated plants, higher densities also resulted in significantly increased frequency of movement ($G = 18.2$, d.f. = 1, $P < 0.001$) (Table 16).

Two of the initial densities of the overwintered adults are the same as those used in the trials of newly emerged beetles, and so these two densities can be included in a contingency table to examine differences in the responses to density. However, interpretation of these analyses is complicated by the non-orthogonality of the types of adults and the defoliation status of the release site. Thus it is not possible to

distinguish whether any effect is the result of a change in adult type or a change in defoliation status of the release site. Analysis of the contingency table of the influences on whether adult beetles moved from the release site revealed significant effects of density at the release site ($G = 16.5$, d.f. = 1, $P < 0.001$) and of the defoliation status or beetle age ($G = 19.4$, d.f. = 1, $P < 0.001$). The interaction of these factors was not significant ($G = 2.1$, d.f. = 1, $P > 0.1$). New beetles released on defoliated plants were more likely to move than were old beetles released on undefoliated plants, also, for both types of beetles, movement was more likely to occur if the density at the release site was high (Table 16).

Analysis of the contingency table for the influence of density and of adult stage or defoliation status on whether adults that move go to other plants or not (Table 17) revealed an effect of density ($G = 7.6$, d.f. = 1, $P < 0.01$). At the higher density 62% of the adults which moved from the release site moved to other plants, but only 39% of beetles did so at the lower density. No other factors in the table were significant.

Adult beetles which moved to other plants, differed markedly in their preference for upwind or downwind plants ($G = 28.3$, d.f. = 1, $P < 0.001$). Of the new beetles which left the defoliated release site and went to other plants, 91% ($N=46$) went to the downwind plant and 9% went to the upwind plant. In contrast, of the old beetles which left undefoliated release sites, only 30% ($N=27$) went to the downwind plant and the remaining 70% went to the upwind plant.

Observations on adult beetles moving on the soil revealed that both old and new walking beetles often stopped. Head and thorax were elevated, the head turned from left to right and antennae waved alternately. When

walking resumed, the antennae were sometimes waved alternately but the head was not turned from side to side. Old adult beetles leaving the middle plant did not walk directly to the upwind plant. They walked around in all directions and slowly approached the plant. Directed movement occurred only when plants were about 5 mm away.

Differences between Larvae and Adults

Comparisons of frequency of movement of larvae and adults were made for initial densities at the release site in the range 30 - 35 (Table 18). The frequency of movement was affected both by whether larvae or adults were tested ($G = 4.2$, d.f. = 1, $P < 0.05$) and by whether the release site was defoliated ($G = 26.3$, d.f. = 1, $P < 0.001$). Although interpretation of this analysis is complicated by the non-orthogonality of defoliation and adult type, it is clear that, at this range of densities, larvae are less likely to move than adults.

Discussion

Larvae were less likely to move from undefoliated plants than were adults, when the density of insects was in the range 30-35 (Table 18). When larvae did leave the undefoliated plants, movement to other plants was rare, so it is likely that these larvae which were third and fourth instars at the beginning of the experiment, were seeking pupation sites rather than food. This result is consistent with Gibson et al.'s (1925) observation that larvae are normally sedentary creatures, and with the observation that on the third day of the experiments, larvae were seen entering the soil.

Interpretation of the responses of larvae to defoliation and density are complicated by the use of young instars in the high density defoliated

trial. It would have been better to redo this trial using the same instar composition as in other trials; however this could not be done. I expect that the younger instars in the high density defoliated trial would be less mobile; they would probably be more likely to seek food than to enter the soil, if they did leave the release site.

If the high density defoliated trial is excluded, the frequency of larval movement increased when the release site was defoliated or when initial densities were high (Table 14). It has previously been observed that, once plants are stripped of foliage, larvae begin to leave plants (Cass 1957). Thus it was expected that when the release site was already defoliated at the beginning of the experiment, larvae would leave the plant and seek other food; the relatively high proportion of larvae found on other plants is in agreement with this expectation.

High densities of larvae on initially undefoliated release sites eventually caused these plants to become defoliated too, and the proportion of larvae moving from these plants was, by 31 h, the same as that when the density was high and the plant was defoliated at the beginning (Table 14). However, the subsequent behaviour of these larvae differed: larvae from initially undefoliated plants seldom moved to other plants. It seems likely that when these larvae abandoned the release site, most of them had obtained sufficient food for them to attempt to pupate. Larvae on the initially defoliated plants often moved to other plants, but it is not clear whether this is solely due to the presence of earlier instars or whether part of the effect is the result of different responses by the third and fourth instar larvae.

Positive anemotaxis is a behavioural pattern which results in

organisms arriving at the source of a chemical born in an airstream, and is a response that might be expected when a food-seeking insect is placed in an airstream bearing the odour of its host plant. However, larvae moving to other plants did not exhibit any detectable anemotactic response. There are at least two explanations for this. Firstly, the speed of the airstream close to the soil surface may not have been great enough to induce anemotaxis. Secondly, anemotaxis may not be exhibited by larvae. The range at which larvae appeared able to detect, and move toward, a potato plant was small. In this study, as in others, directed movement of larvae occurs only within a few centimetres of the potato plant (de Wilde 1958, de Wilde and Pet 1957). The larvae which did find the upwind or downwind plants presumably did so by "randomly" wandering until they were within close range of these plants.

The results of trials with larvae suggest that, in the field, late instar larvae would stay on the plant in all but the most adverse conditions, and when forced to leave the plant, would pupate if possible. It may be that, because of the limited mobility of larvae, anemotaxis or other highly-developed host-seeking behaviour would not significantly increase fitness under field conditions.

Overwintered adults, after emerging from the soil, fly or walk to host plants to feed and reproduce (Gibson et al. 1925). In the cage study, old beetles left undefoliated release sites more frequently at higher densities than at low densities, and most of them moved upwind. Previous studies have shown that the windborne odour of potato plants induces positive anemotaxis in adult Colorado potato beetles (Visser 1976, de Wilde 1976). The flight muscles of diapausing beetles are not fully

developed during hibernation but regenerate soon after emergence from diapause (Johnson 1969, 1976a, 1976b.). Therefore overwintered adults are likely to exhibit host-seeking behaviour which is effective in the context of flight. Anemotaxis may be more useful during flight than during walking when the insect is close to the ground where wind speed is low; this may explain why overwintered adults responded to wind direction but larvae did not. Although no beetles were seen flying, there is indirect evidence that flight may have occurred: some overwintered adults were found on the top portion of the cage where they had probably landed after flight; new adults were never found at the top of the cage.

New adults released on defoliated plants were more likely to leave the release site as the density increased. Almost all newly-emerged adults moved to the downwind plant. This is in contrast to published results from wind tunnel experiments, in which starved adults respond to the odour of potato plants with positive anemotaxis (de Wilde *et al.* 1969, Visser 1976, Visser and Avé 1978). These differences between the orientation behaviour described in the literature and that observed in this study may result from the differences between the experimental cage and a wind tunnel. In the cage, wind velocities at ground level are likely to be less than those experienced by insects in a wind tunnel. Also, in wind tunnels, beetles are not presented with the choice of movement to a plant downwind of the release site.

New adults cannot fly until several days after emergence because the flight muscles and enzyme systems are immature and are also short of glycogen (Johnson 1976b). This difference in the physiological condition of new adults compared to the flightworthy old adults may be associated

with the observed differences in anemotactic response. However, it is not clear what advantage there is to a new beetle under field conditions responding by negative anemotaxis to a potato-odour laden airstream.

Defoliation appears to be a powerful stimulus for dispersal in larval and adult Colorado potato beetles. This is not surprising because an insect remaining on a defoliated plant faces starvation. Defoliation may be the only factor which induces larvae to leave a plant and seek another plant. High densities did not result in larvae immediately leaving the plant. They probably moved only when the plant became defoliated, and then they pupated rather than sought another plant. Therefore, it appears that the locations of larvae in fields may not change much during the larval development period, except when populations are so high that defoliation occurs early in larval development.

In this study, the potato plants in the cage were small enough that their foliage did not intermingle; however, when the plants in potato fields grow large, the vines of the plants within a row intertwine. Therefore, other plants in a row may be accessible to a larva without descending to the ground. This may mean that, after the foliage of adjacent plants intermingles, dispersal along rows is greater than the results of this study suggest.

Increased density resulted in increased dispersal of adults. It is not clear whether this dispersal was a direct response to density, or whether it was a response to defoliation. Over-compensating density dependent dispersal of Colorado potato beetle adults was reported by Harcourt (1971). In addition to causing defoliation and thus starvation, high densities may negatively affect Colorado potato beetles by

interfering with feeding behaviour, either by direct competition for food on one leaf, or by increasing searching time for favourable shoots and leaves by obstruction of movement along leaves and stalks. High densities may also attract predators and parasitoids (Varley et al. 1973). Therefore avoidance behaviour may occur at high densities. Taylor (1978) uses the terms attraction for aggregating organisms and repulsion for dispersers. There may be a certain limiting number of insects above which repulsion occurs and insects move away from each other.

TABLE 12. Location of larvae in the cage 31 h after release.

Initial density on middle plant	Initial state of middle plant	NUMBER OF LARVAE			
		Middle plant	Upwind plant	Downwind plant	Not on plants
32	Defoliated	6	3	8	15
138	Defoliated	82	13	14	29
35	Undefined	26	0	0	9
60	Undefined	59	1	0	0
126	Undefined	74	0	4	48

TABLE 13. Effect of initial density on the percentage of larvae moving from the middle plant. Note that N for percentages is the initial density on the middle plant.

Initial density on middle plant	Initial state of middle plant	PERCENTAGE OF LARVAE	
		Moved	Not moved
32	Defoliated	81	19
138	Defoliated	41	59
35	Undeveloped	26	74
60	Undeveloped	2	98
126	Undeveloped	41	59

TABLE 14. Effect of initial density on the percentage of larvae moving from the middle plant.

Initial density	Initial state of middle plant					
	Defoliated			Undefoliated		
	Larvae Moved (%)	Larvae not moved (%)	N	Larvae Moved (%)	Larvae Not moved (%)	N
Low	81	19	32	26	75	35
High	41	59	138	41	59	126

TABLE 15. Location of adult beetles in the cage 31 h after release.

Initial density on middle plant	Initial state of middle plant	Adult stage	NUMBER OF ADULTS			
			On middle plant	On upwind plant	On downwind plant	Not on plants
10	Defoliated	New	5	0	2	3
30	Defoliated	New	2	1	12	15
50	Defoliated	New	2	3	30	15
30	Undefined	Old	17	1	2	10
50	Undefined	Old	6	18	6	6

TABLE 16. Effect of initial density on the percentage of adults moving from the middle plant. Note N for percentages is the initial density on the middle plant.

Initial density on middle plant	Initial state of middle plant	Adult stage	Percentage of Adults	
			Moved	Not moved
10	Defoliated	New	50	50
30	Defoliated	New	93	7
50	Defoliated	New	96	4
30	Undefoliated	Old	43	57
50	Undefoliated	Old	88	12

TABLE 17. Effect of density at release site and adult stage and defoliation status of the release site on the percentage of adults which moved to another plant or moved but did not go to another plant.

Initial density on middle plant	Initial state of middle plant	Adult stage	PERCENTAGE OF MOVED ADULTS		N
			which went to another plant	which did not go to another plant	
30	Defoliated	New	46	54	28
50	Defoliated	New	69	31	48
30	Undefoliated	Old	23	77	13
50	Undefoliated	Old	55	45	44

TABLE 18. Comparison of movement of adults and larvae at initial densities of 30 - 35 insects on the middle plant. Note that adults from defoliated release sites were newly-emerged, whereas those from undefoliated sites had overwintered.

	Initial state of middle plant					
	Defoliated			Undefoliated		
	Moved (%)	Not moved (%)	N	Moved (%)	Not moved (%)	N
Larvae	81	19	32	26	75	35
Adults	93	7	30	43	57	30

CHAPTER 4

GENERAL DISCUSSION

The transect sampling of farmers' fields shows that some fields have evident edge effects while others do not. The causes of edge effects are very complex and a variety of factors need to be considered. Most of factors concern either the source of beetles which colonize the potato field, or the subsequent behaviour of overwintered adult beetles and their offspring. Much of my experimental work concerned the behaviour of adults and larvae which might influence their distribution within the crop; however, I will first consider factors influencing the source of the colonizing beetles.

Potato is by far the most abundant food plant for Colorado potato beetles in Manitoba, so the source of colonists is certain to be associated with the potato crops of the previous year. All potato fields within an area are potential sources for the following year's colonists, but how important a source a particular field will be is dependent upon the abundance of Colorado potato beetles in the field late in the growing season. The late season abundance will be dependent upon the effectiveness of Colorado potato beetle control measures during the year, and the stage of development of the crop relative to that of the beetle population. Foliage of early maturing potato cultivars such as Norland senesces in August, while that of late varieties such as Russet Burbank remains actively growing for several additional weeks. Senescent foliage will induce adult beetles either to disperse to other fields, or to diapause. Diapause induction will occur if the foliage senescence occurs simultaneously with low temperatures and the photoperiods characteristic

of the later part of the season (Norris 1964, de Wilde and Hsiao 1981). However, if photoperiod is longer, and temperatures are high enough for flight to occur, beetles fly from the senescing plants to other potato fields. My work has shown that newly-emerged beetles are not very mobile, but the literature indicates that such beetles can fly after about 10 days (Le Berre 1950). Thus, if beetles have emerged from pupation in early August, as many do in Manitoba (Senanayake and Holliday 1989), and plants senesce by about mid-August, one would expect many beetles to fly from those fields and land in fields of later-maturing potato fields. These fields of later maturing cultivars would be important sources of colonists for the following year because they would be the hibernation sites for beetles which had hatched there and for fugitives from early-senescing fields.

The effectiveness of Colorado potato beetle control, the cultivar, and the date of plant senescence in previous years' potato fields are all sources of variation which may account for my finding that distance to the nearest of last year's potato fields lacks value as a predictor of edge effects. However, information on these factors is difficult to obtain because it involves knowing where growers plan to plant potatoes in the following season.

In addition to the location of sources of colonists, the distribution of Colorado potato beetles within a field also depends upon the dispersal behaviour of the colonists and their offspring. Environmental conditions at the time of colonization are important. If temperatures are high in the spring beetles are more likely to fly to the fields, whereas in cool springs walking will predominate. The former is

likely to result in less pronounced edge effects than the latter (Skuhravy et al. 1968, Le Berre 1950).

My findings provide fundamental ideas for control methods. The field sampling shows that if edge effects occur then only the periphery of the field need be sprayed instead of the whole field. Furthermore, sampling schemes which accommodate edge effects need to be developed.

Additional measures could be taken to reduce spring colonization by beetles. Beetles respond less to the green leaf volatiles of potatoes when they are masked by the odour of other plant species (Visser and Avé 1978). Colorado potato beetle populations on potato plants are reduced 60-100% when interplanted with tansy, *Tanacetum vulgare* L., and 58-83% when interplanted with catnip, *Nepeta cataria* L. (Panasiuk 1984). However, mixed cropping can create problems with mechanical harvesters. If this is a problem, then aromatic plants and herbs could be grown around fields to prevent initial olfactory orientation.

The olfactory attractiveness of a patch of host plants changes with patch size and density (Stanton 1983). Therefore it may be possible to modify potato field size and layout in relation to direction of the prevailing wind and so reduce the odour and the number of colonizing beetles. The direction of plant rows could be rearranged to minimize the spread of beetles within fields. Changes should be made in the configuration of potato fields. Potatoes should be grown in large fields or contiguous blocks of small fields, and rotation of crops should always be carried out.

More research is needed to understand the insects' dispersal behaviour fully. Field sampling should be continued to find out the distribution pattern under different summer conditions. Migratory flights

in early spring and late summer need to be studied, as well as the conditions which cause beetles to enter diapause or to take flight. Additional experiments are also needed on upwind and downwind movement in the cages and how these relate to field conditions.

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