EDGE EFFECTS IN INFESTATION PATTERNS OF INSECTS ON CROPS: A REVIEW AND A FIELD STUDY WITH SPECIAL REFERENCE TO THE TUBER FLEA BEETLE (*EPITRIX TUBERIS* GENT.)

by

Michel Cusson
B.Sc., Université de Sherbrooke, Québec, 1981

PROFESSIONAL PAPER SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF PEST MANAGEMENT
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY
May 1985

APPROVAL

NAME: Michel Cusson

DEGREE: Master of Pest Management

TITLE OF PROFESSIONAL PAPER: 'Edge effects' in infestation patterns of insects on crops: a review and a field study with special reference to the tuber flea beetle (Epitrix tuberis Gent.)

EXAMINING COMMITTEE:

Chairman:

Dr. B.D. Roitberg, Senior Supervisor

Dr. R.S. Vernon, Research Scientist, Agriculture Canada

Dr. J.H. Borden

Dr. B.D. Frazer, Research Scientist, Agriculture Canada,
Public Examiner

Date approved May 6, 1985

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

'Edge effects' in infestation patterns of insects on crops: a review and a field study with special reference to the tuber flea beetle (*Epitrix tuberis* Gent.)

Author: ______________________
(signature)

Michel Cusson
(name)

26 July 1985
(date)

ABSTRACT

Current sampling procedures for *Epitrix tuberis*, on potato, are highly time-consuming and vary in their reliability. Two features of the adults' infestation patterns have, to date, hampered the development of a more efficient sampling scheme: (1) *edge effects* of varying intensity, and (2) unpredictable 'pockets of infestations' in fields under continuous potato cropping.

A review of the phenomenon of *edge effect* indicates that margin-biased density gradients have either physical or behavioural causes. The former consist mainly of the various interactions between wind and windbreaks which draw windborn insects into sheltered zones. Among the latter, three hypothetical mechanisms are plausible: (1) as found for butterfly oviposition, a higher rate of encounter with edge plants would occur as a result of the females' tendency to return to a host patch soon after leaving it, (2) in the same context but possibly applicable to other insect taxa, species which must fly long distances to locate host plants would respond to first-encountered hosts regardless of the hosts' current conspecific loads and, thus, marginal plants would accumulate more visits, and (3) insects, e.g. *E. tuberis*, which hibernate in the immediate vicinity of their host fields would tend to colonize border plants first.

Results from a survey of commercial and experimental fields reinforced the possibility of a relationship between cropping history and 'pockets of infestation' of *E. tuberis*. However, observations made in May 1984 suggested that such patterns were unlikely caused by early-season oviposition on volunteer potatoes. Instead, it is speculated that the responsible factor is the overwintering of some beetles in the field.

Experiments involving the release of marked *E. tuberis* adults near the edges of test plots indicated that, when plants are small ($\bar{X}$=7.44 cm high), beetles travel further across rows and create weaker *edge effects* than in plots harbouring large plants ($\bar{X}$=33.2 cm high).

Also examined was the effect of plant density on the dispersion and density of *E. tuberis*. I observed 3 trends: at low plant density, beetle aggregation and per-plant beetle density were greater than at high plant density but per-10 m^2 beetle density was lower.

Two sampling systems, based on the results reported herein, are proposed.

To my wife, Ursula, for her encouragement and moral support.

ACKNOWLEDGMENTS

I am greatly indepted to my senior supervisor, Dr. B.D. Roitberg, for his continual support, expert guidance and encouragement during the course of this research, and for his invaluable help in editing this paper.

I also wish to thank: Dr. R.S. Vernon for sharing his ideas, for review of the manuscript, and for his expert advice and assistance; Dr. J.H. Borden for his pragmatic advice in clarifying the goals of this study and for his critical review; Mrs. D. Scott, Mr. R. Reusch, Mrs. D. Bartel, Mr. J. McKenzie, and Mr. K. Giles for their enthusiastic assistance in field work; Mr. R.G. Lalonde for taking some of the photographs presented at the defence; Mr. S. Villeneuve for helping with the format of Table 4; Mr. G.J.R. Judd, Mrs. M.Y. Steiner, and Dr. C. Vincent for providing some unpublished information; the B.C. Coast Vegetable Co-operative Association for allowing me to perform experiments in commercial potato fields, particularly Messers D. Law and P. Garvin who, as experienced growers, patiently answered my questions and encouraged me to go ahead with my investigations; and Agriculture Canada for providing equipment and facilities.

Financial assistance from the Science Council of British Columbia, the Vancouver Horticultural Society, *Fonds F.C.A.C. pour l'aide et le soutien à la recherche* (Québec), and A.R.D.S.A. is gratefully acknowledged.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

1.1 General

Accurate estimates of insect pest densities are essential to the success of modern pest management programs (Ruesink & Kogan 1975). Because such estimates may be strongly affected by the pests' inherent spatial patterns (Ruesink 1980), several workers (e.g. Anscombe 1949; Morisita 1959; Taylor 1961, 1984; Lloyd 1967; Iwao 1968) have developed methods to describe animal dispersion. However, their approach to pattern analysis -- not unlike the one adopted by plant ecologists for the study of plant dispersion (see Greig-Smith 1983) -- has been to treat animals as static entities. Although such methods have found wide application in the design of sampling systems for insects, some species require that the dynamics of their movement be studied before an effective sampling plan can be developed (e.g. *Sphenophorus callosus* (Olivier), Wright *et al*. 1983). Among these species is the tuber flea beetle (TFB), *Epitrix tuberis* Gentner, a common pest of potato (*Solanum tuberosum* L.) in British Columbia (Fulton *et al*. 1955).

Within its potato crop habitat, *E. tuberis* displays a colonization behaviour for which a lack of understanding has, to date, hampered the development of an efficient and reliable sampling scheme. In a study on the dynamics of this species, R.S. Vernon[1] reported two related problems: (1) *edge effects* of varying intensity (i.e. margin-biased density gradients which display varying rates of decline), and (2) unpredictable 'pockets of infestation' in fields under continuous potato cropping. From a technical standpoint, other empediments to the development of a sampling plan include: (1) the difficulty of calibrating TFB-related sampling techniques, and (2) the absence of a reliable economic threshold. The latter two aspects of the problem are currently under investigation at Agriculture Canada and the two former ecological aspects constitute the scope of the present paper.

1.2 Distribution and biology of the tuber flea beetle

The tuber flea beetle is believed to be a native of Northern Colorado (Gentner 1944) where it was first reported to cause serious injury to potato tubers in 1904 (Johnson 1904). It first appeared in British Columbia in 1940 (Fulton & Banham 1960) but remained mistakenly identified as *E. cucumeris*

---

[1] Vernon, R.S. 1981. Visual and sweep-net sampling efficiency in determining tuber flea beetle , *Epitrix tuberis* Gent., population levels, with observations on population dynamics, dispersal and damage. Report for the B.C. Ministry of Environment. Unpublished.
R.S. Vernon: Agriculture Canada, Vancouver Research Station, B.C., V6T 1X2.

(Harris) until 1944 when Gentner (1944) finally described the morphological and ecological differences between the eastern (*cucumeris*) and western (*tuberis*) species. Since then, *E. tuberis* has spread eastward to Alberta where it has been known to occur in Edmonton's home gardens for at least ten years (M.Y. Steiner[2], pers. comm.).

In British Columbia, *E. tuberis* is believed to have partially displaced a related native species, the western potato flea beetle, *E. subcrinita* (Lec.), which declined steadily in relative abundance concurrent with the spread of *E. tuberis* (Glenndenning 1945). Although very similar to *E. tuberis* in its appearance and habits, the western potato flea beetle is considered to be of little economic importance (Fulton *et al*. 1955; Jones 1944).[3]

Epitrix tuberis possesses a relatively simple life cycle. Upon emergence in the spring, overwintered adults feed on the foliage of early or volunteer potatoes[4] (Fulton *et al*. 1955) and begin mating within 24 h (Neilson & Finlayson 1953). Five to 6 days following mating, females commence laying eggs in the soil, at the base of the plants (Hill 1947), an activity in which they

---

[2] Alberta Environmental Center, Vegreville, Alberta, T0B 4L0.

[3] Because of the resemblance between the two species, a sample of 100 beetles from my 1984 study site was sent to the Biosystematic Research Institute, Ottawa. All specimens were confirmed to be *E. tuberis* by Dr. L. LeSage.

[4] The word 'early' refers to early varieties; the word 'volunteer' refers to plants produced by tubers which remained in the soil after harvest. Such plants emerge early in the spring and are considered weeds.

remain engaged for a period of ca. 1 month (Finlayson 1950). Larvae hatch from the eggs and quickly find their way to the developing tubers where they feed for two to three weeks (Fulton *et al*. 1955), causing roughened and pitted spots often referred to as 'worm tracks' or 'slivers' (Hoerner & Gillette 1928). This larval injury to the tuber often greatly reduces the quality of the crop (Hill & Tate 1942). The beetle pupates in the soil and the entire life cycle is completed in about 6 weeks (Fulton *et al*. 1955).

In British Columbia, *E. tuberis* is normally bivoltine (Neilson & Finlayson 1953) but, under field conditions, generations are often difficult to distinguish on account of the extended emergence periods and the relatively long adult life, which create overlapping of the broods (G.J.R. Judd[5], pers. comm.; Neilson & Finlayson 1953). On caged plants, first- and second-generation adults begin emerging in late July and early September, respectively. The latter hibernate in the soil and reemerge in late May (Finlayson 1950).

Although the potato plant is *E. tuberis*' preferred host, adults can feed and survive on several other plant species (Hill 1946, 1947). In addition, large numbers of adults can kill young potato plants by stripping their foliage but this occurs only rarely and is considered to be of no economic importance (Finlayson 1950).

---

[5] Simon Fraser University, Dept. of BioSciences, Burnaby, B.C., V5A 1S6.

1.3 Flight activity and overwintering sites of the tuber flea beetle

Hoerner and Gillette (1928) reported flight as being *E. tuberis*' most frequent means of across-field movement. They drew their conclusion from the fact that "potato fields half a mile from fields of the year before are sometimes heavily infested". Daniels (1941) observed that tuber flea beetles "fly low, from 2 to 4 feet from the ground, having a tendancy to follow prevailing winds as much as possible". Similarly, R.S. Vernon[1] noted a downwind trend in the dispersal of marked and released beetles, although he did not specify whether this movement was by flight or saltation. [illegible]

Jones (1944) employed a mechanized rotary trap to sample flea beetles in flight and reported that: (1) considerably more beetles fly in the afternoon than in the forenoon, (2) beetles do not fly when wind velocity exceeds 12 km/h, and (3) a much greater proportion of beetles fly at low (0.6 m)[6] than at high (2 m)[6] altitude. Clearly, knowledge regarding the dispersal flight of *E. tuberis* remains sparse.

Infestation patterns of tuber flea beetles may also be influenced by the location of overwintering sites in relation to potato fields. Unfortunately, the overwintering habits of

---

[6] Height of nets on the rotary trap.

E. tuberis have never been investigated thoroughly.

Tuber flea beetles are usually found concentrated along the edges of a field and it has generally been assumed that they infest potato fields from the outside in. Similar reasoning suggests that beetles normally spend the winter outside the field (R.S. Vernon[1], pers. comm.). Although this is likely to be generally true -- other species of flea beetles have been reported to behave in a similar way (Wolfenbarger 1940; Dominick 1971; Burgess 1981) -- there are reports indicating that this might not be a universal rule (nor is it one for the species described in the 3 aforementioned references). Fulton *et al.* (1955), for example, reported that overwintering TFB adults (in British Columbia) "usually choose rough, well-drained, weedy or scrub-covered places, or may remain in the field". Similarly, Hoerner and Gillette (1928), in Colorado, noted that tuber flea beetles often collect underneath piles of old potato vines where they enter the soil in large numbers. In another study, Hill (1942) observed several *E. tuberis* adults feeding on cull tubers left in a potato field following harvest. These observations suggest that some beetles might remain in the field during the winter. Such behaviour, if it actually occurs, would be of major importance in the context of crop rotation.

2. THE PHENOMENON OF "EDGE EFFECT" IN INSECT POPULATIONS: CAUSALITY AND IMPLICATIONS FOR SAMPLING.

An *edge effect*[7] occurs when outlying host plants -- individuals at the edge of a clump, a plot, or a field -- receive proportionately most attention from insect herbivores (Courtney & Courtney 1982). Such density gradients are relatively common in agricultural crops and often give rise to procedural problems with regard to sampling.

2.1 Causality

2.1.1 Physical causes

So important is the influence of wind on the dispersal of airborne insects (Rainey 1951) that it can be suspected to also play a role in the shaping of infestation patterns on crops. In fact, air currents, either alone or interacting with vertical obstructions (e.g. windbreaks), have often been reported to affect the distribution of insects flying above and alighting on crops.

---

[7] Also called *border effect* (Harcourt 1961).

Hartzell (1932), for example, observed decreasing numbers of pear midge-infested fruits from one edge of a pear orchard to its center. He attributed this difference to the protection provided by an adjacent woodland which apparently reduced wind velocity in the first few rows of the plantation. An alternative, but unexplored, hypothesis is that midges simply originated from the wooded area and diffused gradually into the orchard, giving most attention to the first encountered pear trees.

Along a slightly different line, Johnson (1950) showed that high concentrations of *Aphis fabae* Scop. on certain edges of a bean field were correlated with wind direction during primary migration. However, two subsequent investigations (Broadbent *et al*. 1951; Taylor & Johnson 1954) revealed that available shelter might also cause aphids and other insects to collect near obstacles to the wind.

The physical mechanisms controlling such accumulations were the subject of a series of publications by Lewis (1965a, 1965b, 1966a, 1966b, 1967, 1969a, 1969b, 1970), Lewis and Stephenson (1966), and Lewis and Dibley (1970). In these studies, physical and biological effects of windbreaks were distinguished by employing artificial[8] barriers such as wooden or wire-netting fences (see Lewis 1965a, 1965b). Above- and/or within-plant samples of windborne insects were taken along a line

---

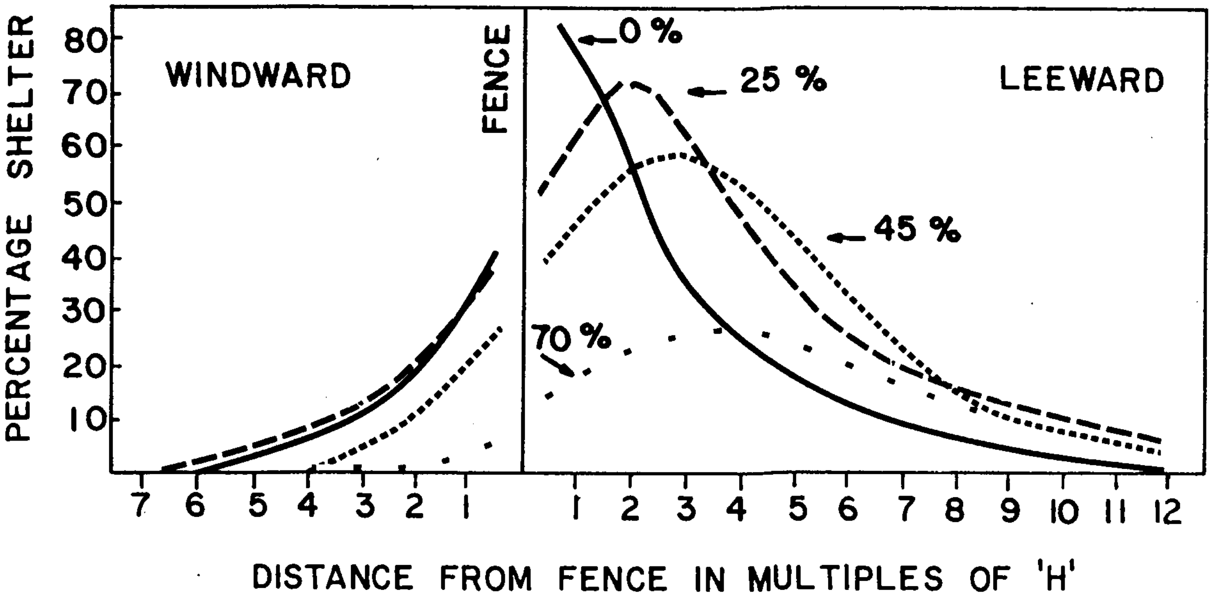
[8] Trees and hedges not only provide protection from wind but also offer suitable overwintering sites from which insects can spread to adjacent crops.

perpendicular to a fence. Density profiles (insect density *vs* distance to the fence) generated by these samples were then compared with wind velocity measurements made along the same perpendicular transect (on both windward and leeward sides). This analysis revealed that both intensity and pattern of insect accumulations often reflect spatial variations in the degree of wind protection offered by windbreaks (% shelter; see caption of Figure 1), i.e. many insects gather near obstacles, especially to leeward, where percentage shelter is maximum (Lewis 1965a, 1965b, 1966a, 1966b; Lewis & Stephenson 1966).

Among the various components of windbreaks which may affect the distribution of insect accumulations, permeability to airflow is probably the most important one. In general, the more open (permeable) a barrier, the less intense the shelter but the further it extends to leeward (Lewis & Stephenson 1966; Lewis 1969a) (Figure 1). On the other hand, windbreaks of same permeability but different heights produce profiles of relative density which do not differ in their shape and mode, if distance to the barrier is expressed in multiples of windbreak height (Lewis 1967).

Wind speed can also influence the position of maximum shelter and maximum aerial density of insects. Measurements made at various wind velocities indicated that the faster the wind, the farther behind the fence does the air become calm enough to allow insects to accumulate (Lewis & Stephenson 1966). For natural windbreaks of trees and hedges, this factor becomes even

Figure 1. Mean percentage shelter produced by fences of different permeability (%) to the wind. Percentage shelter: decrease in the run of wind expressed as a percentage of the run of wind at an unsheltered site. Run of wind: number of km of air moving past a point over four to six 10 min. periods. Fences were 1 m high (H) and incident winds blew on them at angles between 45° and 90°. Measurements were made 36 cm above the ground in wind speeds between 4.3 and 14.4 km/h. (Redrawn from Lewis and Stephenson (1966)).


PERCENTAGE SHELTER
80
70
60
50
40
30
20
10
WINDWARD
FENCE
LEEWARD
0 %
25 %
45 %
70 %
7 6 5 4 3 2 1
1 2 3 4 5 6 7 8 9 10 11 12
DISTANCE FROM FENCE IN MULTIPLES OF 'H'

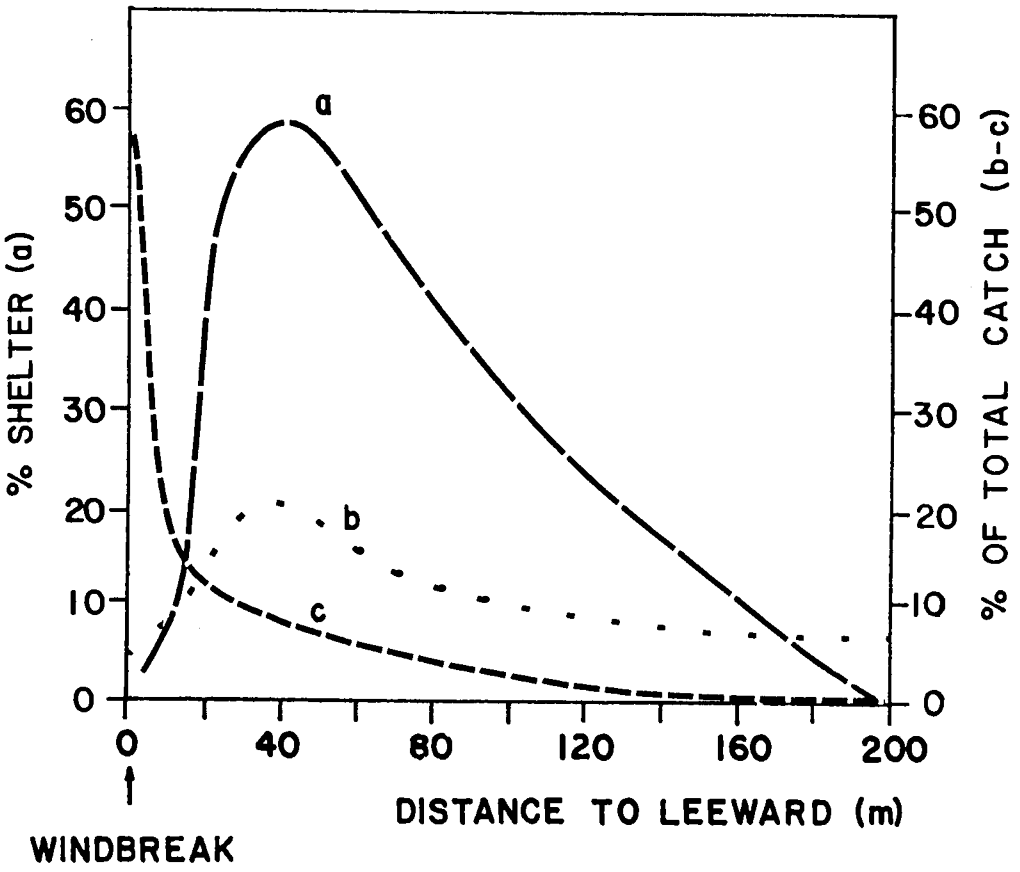
more important since it affects the degree of branch separation which, in turn, influences permeability.

The components of wind that most affect distribution of insects are its angle of incidence to the windbreak and the intensity of turbulence; the more direct and the less turbulent the wind, the greater the relative accumulation (Lewis 1966a; Lewis 1969a).

When compared to artificial barriers, natural windbreaks produce patterns of accumulation similar to those observed with wooden fences of equivalent permeability. However, trees and hedges often harbour overwintering insects (e.g. Cicadellidae) which disperse into adjacent crops and accumulate immediately to leeward of their source. In contrast, insects blown from distant locations (e.g. Aphididae) are drawn into zones of maximum shelter which, in the case of permeable barriers such as trees, normaly develop further to leeward (Lewis 1970; Figure 2). Therefore, if the distance separating a natural windbreak from a field were to be set so as to make maximum percentage shelter coincide with the first row of plants, the two patterns would theoretically become harder to distinguish.

Based on the above information, one might predict that wind-related *edge effects* will occur along the sheltered margin(s) of a field if: (1) the windbreak is impermeable and contiguous to the field or (2) the windbreak is open but separated from the field by a distance directly related to the windbreak's permeability.

Figure 2. Profiles of relative insect densities and percentage shelter near a windbreak of tall trees. (a) percentage shelter; (b) relative density of Aphididae (blown from distant locations); (c) relative density of Cicadellidae (originating on the trees). (Adapted from Lewis (1970)).


% SHELTER (a)
% OF TOTAL CATCH (b-c)
a
b
c
0
10
20
30
40
50
60
0
40
80
120
160
200
DISTANCE TO LEEWARD (m)
WINDBREAK

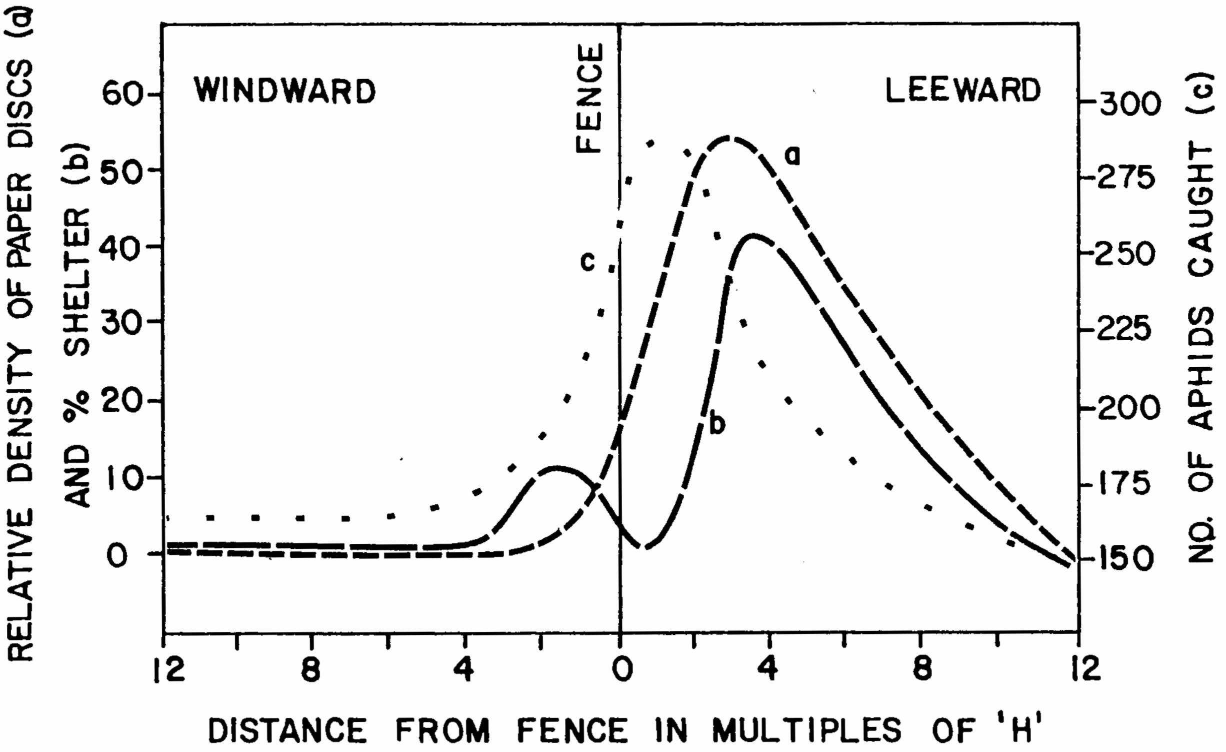
Although shelter certainly plays a major role in providing conditions that are conducive to the deposition of small and weak-flying insects, not always can the observed accumulations be attributed solely to wind protection. Lewis (1965a, 1966a), for instance, proposed that insect behaviour was responsible for differences between the modes of observed and predicted (shelter-based) density profiles. This was exemplified by the observation that a swarm of aphids amassed closer to a fence than inert particles (small paper discs) blown into the air (Lewis 1965a; Figure 3).

Some insects might have enough control over their flight trajectory to overcome weak air currents encountered just above the crop and alight more or less where they choose to (Lewis 1966a). Therefore, it would be incorrect to use the expression 'inert deposition' when refering to insect accumulations near windbreaks (Lewis & Dibley 1970).

No effort was made to explore the behavioural nature of the aforementioned shift towards the fence -- possibly because of its relative insignificance. Among the possible mechanisms which could have caused such deviation (e.g. attraction to the barrier's colour, favourable microclimatic conditions other than wind speed, higher quality of plants near the fence), only attraction to shade has been reported to, occasionally, favour the development of *edge effects* (Knowlton 1948).

The lack of comparison between sheltered and unsheltered edges by Lewis and others (above-cited papers), constitutes a

Figure 3. Relative density of paper discs (a) near a fence of height H=1 m compared with mean percentage shelter (b) and the relative density of aphids (c). (Adapted from Lewis (1965a)).


RELATIVE DENSITY OF PAPER DISCS (a)
AND % SHELTER (b)
0
10
20
30
40
50
60
WINDWARD
FENCE
LEEWARD
a
b
c
300
275
250
225
200
175
150
NO. OF APHIDS CAUGHT (c)
12
8
4
0
4
8
12
DISTANCE FROM FENCE IN MULTIPLES OF 'H'

major apparent weakness. However, the experiments did not examine the phenomenon of *edge effect per se* but, instead, studied the influence of shelter on infestation patterns. For this reason, most insect samples from wind-exposed sites were not taken on the field margins. This is unfortunate since insect counts from unsheltered borders might also have revealed *edge effects* that would have required alternative, possibly behavioural, explanations.

In conclusion, the physical conditions which prevail near windbreaks appear to promote the near-passive alightment of windborne insects on sheltered plants. However, some observations suggest that the active, self-induced movement of certain species probably alters the final pattern of accumulation. Although little is known about the degree to which behaviour affects such patterns, some studies have documented how behaviour can lead to *edge effects* where wind velocity is obviously not a factor of concern.

2.1.2 Behavioural causes

When searching for behavioural causes of *edge effects*, large and strong-flying insects make ideal candidates for field studies. The cabbage butterfly, *Pieris rapae* (L.), for example, has often been reported to lay more eggs on the edges of a plot than in the center (Harcourt 1961; Cromartie 1975; Jones 1977). Harcourt (1963) attributed this phenomenon to the females' propensity to leave the plot for short feeding bouts, i.e. they fly to the blooms of wild plants in order to find food and then return to the cultivated plot to resume oviposition. This type of movement results in marginal plants being encountered more often and receiving a greater number of eggs.

Jones (1977) meticulously examined the movement patterns of *P. rapae* through an analysis of the 'rules of movement'. The females' departures from and returns to the plot were shown to bear no relation with the alternate feeding and egg-laying sessions described by Harcourt (1963). Instead, the two following mechanisms were proposed: (1) after leaving a plot, females tend to return to it if they do not encounter host plants within a short period of time; and (2) females, because of their high directionality (i.e. they do not turn much), are likely to soon leave the plot again. The extent to which the former behaviour is displayed depends on a female's current fecundity and on the degree to which she is attracted to host plants in the plot. Changing values of these two parameters and variations in directionality have been shown to explain differences in *edge effect* intensity, especially with reference to Australian and Canadian butterflies (Jones 1977).

In an attempt to find a general explanation for *edge effects*, Courtney and Courtney (1982) examined six hypotheses related to the margin-biased oviposition in butterflies. Their field observations indicated that females of the pierid species *Anthocharis cardamines* (L.) do not turn at clump edges as does

P. rapae (Jones 1977), nor do they select border plants on the basis of their greater potential for maximizing larval survival or their different 'apparency'. Instead, the seeming preference of *A. cardamines* for outlying hosts appears to be the result of a searching behaviour that has evolved to increase reproductive success when host plants are at low density. Such reasoning is based on the observation that females reduce their discrimination against egg-laden plants when hosts are scarce. Thus, when the probality of locating an alternative host is low, the aforementioned behaviour becomes adaptive despite a high larval mortality resulting from competition.

The above adaptation was the basis for 2 complementary hypotheses, both corroborated by field data: (1) females are more responsive to host plants after flying long distances and tend to oviposit on the first encountered host, usually edge plants, regardless of the host's current eggload[9]; and (2) females sample host patches in such a way as to encounter low-density plants most often. Since plant density in the border rows of a plot is lower than in the center, marginal hosts will be visited more often.

Courtney and Courtney (1982) suggested that these and possibly other aspects of female searching behaviour accounted for the observed *edge effect* in butterfly oviposition. The same authors further implied that similar mechanisms could have been

---

[9] Similarly, Kennedy and Booth (1963) observed that aphids became increasingly responsive to host odours as the length of flight increased.

responsible for the edge-biased density gradients reported by Free and Williams (1979) for non-lepidopterous insect pests of cruciferous crops. Although not improbable, the latter proposition has never been tested but there are indications that simpler, colonization-related processes (see Price & Waldbauer 1975; Price 1976) might also be involved in the development of *edge effects* in agricultural situations.

Three examples illustrate how some traits common to many insect pests are likely to promote *edge effects* in crops. These traits include: (1) a marked tendency to overwinter immediately outside cultivated fields (necessitating annual recolonization of fields)[10], (2) limited flight capabilities, and (3) low food and habitat requirements relative to host abundance[11].

The carrot weevil, *Listronotus oregonensis* (LeConte), spends the winter in the headlands of carrot fields (Hudon & Martel 1973). From there, newly-emerged adults disperse to cultivated host plants by means of walking, since flight is apparently very seldom employed (Whitcomb 1968). Once adults have reached the edge of a field, the very close spacing of carrot plants provide them with high local abundance of foliage

---

[10] As will be stressed below, insects which hibernate within crop residues will be forced to recolonize new fields if the host plant they attack is under a strict rotation scheme.

[11] With reference to soybeans, Price (1976) provided a good description of this phenomenon: "Once a herbivore settles on a young plant, all resources are usually available. Food is plentiful and protection is obtained in folded leaves at the growing point, leaf axils and fluted stems. The herbivore is not forced to move from plant to plant."

and roots which are used as food and oviposition sites, respectively. With an average fecundity of 156 eggs (Martel *et al.* 1976) and a tendency to lay more than one egg per plant (Cusson, unpublished data), females probably need not move very far into the field to satisfy their food and oviposition requirements. Thus, *L. oregonensis* attacks almost exclusively within the first 15 rows of carrot fields (Martel & Hudon 1974; Cusson, unpublished data).

Unlike the carrot weevil, the wheat stem sawfly, *Cephus cinctus* Norten, does not leave its host plants in the fall. Instead, larvae hibernate in wheat stubble that remains in the field following harvest. However, the common practice of interspersing strips of wheat with strips of summer fallow containing the previous year's stubble forces the flies to infest new strips every spring (Holmes 1982). With regard to movement, adults are weak fliers and do not fly for any appreciable distance beyond the first encountered suitable hosts (Holmes 1978). Furthermore, females lay an average of only 33 eggs (Holmes 1978,1982) and are not deterred from ovipositing in stems which contain conspecific eggs (Criddle 1923; Holmes 1978). Together, these factors very likely account for the highly pronounced *edge effects* known to occur in *C. cinctus* infestations (Holmes 1982).

Among chrysomelids, the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze), is a species whose overwintering preferences for hedges and fencerows have been well documented (Burgess

1977, 1981). Also carefully studied is the adults' dispersal movement which is believed to be due mostly to saltation (Vincent & Stewart 1983). Such low-altitude displacement should, in theory, promote a high rate of encounter with border plants. Although little is known about *P. cruciferae*'s food and habitat requirements, Kareiva (1982) reported that populations of 50 beetles per collard plant were well within the natural range of flea beetle density. This indicates that one plant can probably satisfy the feeding requirements of several individuals. Therefore, it is not surprising that *edge effects* are common in *P. cruciferae* infestations (C. Vincent[12], pers. comm.).

The above examples suggest that variations in mobility and habitat requirements might affect *edge effect* intensity, especially for those insects which originate in the vicinity of their cultivated host fields. By contrast, the hypothetical mechanisms described by Courtney and Courtney (1982) more likely influence *edge effects* produced by insects which must travel long distances before finding their host plants.

Several factors, in addition to those already discussed, might influence the intensity of behaviour-related *edge effects*. Plant size, for instance, was observed to directly affect the relative proportion of pollen beetles, *Meligethes aeneus* F., found in border rows, i.e. the larger the plants, the more edge-biased the distribution (Free and Williams 1979).

---

[12] Agriculture Canada, Saint-Jean-sur-le-Richelieu Research Station, Québec, J3B 6Z8.

Similarly, low plant density was considered to be one of the factors responsible for the greater uniformity of wheat stem sawfly infestations observed in some wheat strips (Holmes 1982). For species which hibernate among their cultivated host plants, crop rotation can also have a dramatic effect on density gradients. For example, when wheat is planted in infested stubble, instead of next to it, field infestations of *C. cinctus* are evenly distributed (Holmes 1982).

Finally, when the number of colonizers increases to the point where border plants can no longer support additional immigrants, a large number of individuals are driven toward the center of the plot, decreasing the relative proportion of insects on the edge. Species for which this phenomenon occurs include: the red turnip beetle, *Entomoscelis americana* Brown (Gerber 1982); the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Harcourt 1964); the southern corn billbug (Wright *et al*. 1983); the seed weevil, *Ceutorhynchus assimilis* Payk (Free and Williams 1979); and the wheat stem sawfly (Holmes 1982).

2.1.3 Anti-edge effects

'Anti-*edge effects*', i.e. center-biased density gradients, have also been shown to occur in certain situations. However, they can rarely be linked to colonization processes. For example, van Emden (1965) attributed a post-invasion anti-*edge effect* in the cabbage aphid, *Brevicoryne brassicae* (L.), to the high number of predators diffusing into the field from the edges and to the slower reproductive rate of those aphids shaded by overhanging trees. Similarly, shade apparently caused lower densities of potato flea beetles along field margins bordered by large trees (Wolfenbarger 1940). In two other cases involving a mirid, *Orthotylus virescens* (Douglas & Scott) (Lewis & Waloff 1964) and the gypsy moth, *Lymantria dispar* L. (Barbosa 1978), the 'anti-*edge effect*' was attributed to a high rate of emigration from the edges and to the 'trapping effect' of the center.

2.2 Sampling

The solution to sampling problems created by *edge effects* depends largely on the purpose of the sampling program, i.e. whether the objective is to obtain information on the biology of the pest (mostly for research purposes) or to obtain density estimates (required for management).

In research, the strategy adopted usually depends on the goal of the study and on the type of information sought. For instance, the analysis of an insect's spatial distribution need not require the same sampling treatment as the description of temporal variations in *edge effect* intensity.

With regard to management, the function of sampling is more or less limited to determining whether pest densities are high enough to warrant a control action. This operation becomes complicated when the uneven distribution of insects (e.g. edge-biased infestations) indicates that pesticides need not be applied over the entire field. Further, the time required for the execution of a given sampling procedure is generally of greater concern to the pest manager than to the basic researcher since the former often has to survey several fields within a short period of time and make control decisions quickly.

2.2.1 The 'edge effect' problem in sampling for research

In a study on the spatial distribution of *P. rapae*, Harcourt (1961) avoided the problem of *edge effects* by excluding border rows from the sampling program. This approach appears justifiable since the high marginal densities of eggs and larvae would probably have obscured *P. rapae*'s highly specific spatial patterns. However, for this method to be applicable, *edge effects* must extend only a small distance into a plot since a gradual decline in density would have an impact over the whole sample area.

When *edge effects* and infestation patterns are the phenomena of interest, other procedures have been proposed. To describe the gradual infiltration of insects into a crop, for instance, a field can be divided into a grid of several squares from which random samples may be periodically taken (van Emden 1965; Wright *et al.* 1983). If the object of a study is to compare different populations of insects in their tendency to develop *edge effects*, schemes similar to those employed by Free and Williams (1979) might be more appropriate. Here follows a description of two such procedures: (1) 4 samples of 10 sweeps each are taken at a site near the crop center and one sample of 10 sweeps is taken along each of the 4 edges; (2) samples of 10 sweeps each are taken at 20 m intervals along two transect lines drawn from the center of both pairs of opposite edges (cross shape). Similarly, Holmes (1982) took samples of wheat stem sawfly along transect lines running perpendicular to the long edge of an experimental wheat strip.

2.2.2 The 'edge effect' problem in sampling for pest management

Virtually nothing has been published on the problem of *edge effect* in management-related sampling. Free and Williams (1979) suggested that the methods they developed (see above) be used to determine the number of rows for which an insecticide application is justified. Such methods, however might be of little value where infestation patterns tend to be highly irregular since an extremely large proportion of the field is left unsurveyed by the procedures. Instead, C. Vincent[12] (pers. comm.) proposed a sequential sampling plan whereby a field would be divided into long narrow strips in which samples would be taken at random. Independent control decisions could therefore be made for each strip.

Where fields are so narrow as to make the irregular distributon problem irrelevant (i.e. when the field is so narrow that little money could be saved by not spraying its entire area), allocation of sampling effort can usually be limited to marginal plants. Carrot fields in south-western Quebec and in the lower Fraser Valley of British Columbia, along with their associated pests, the carrot weevil and the carrot rust fly, *Psila rosae* (F.), are good examples of this phenomenon (Cusson, unpublished; G.J.R. Judd[5], pers. comm.).

In summary, *edge effects* are common in infestations of insect pests on crops. Their occurence has, in some cases, been linked to the presence of wind-sheltered zones near windbreaks. In other cases, they have been attributed to behavioural characteristics of insects. With regard to sampling, they usually demand special treatments depending on the purpose of the sampling program.

3. INFESTATION PATTERNS OF THE TUBER FLEA BEETLE: A FIELD STUDY

3.1 Introduction

At the outset of the first chapter, I referred to '*edge effects*' and 'unpredictable pockets of infestation' as being the factors responsible for the ineffectiveness of current TFB sampling procedures. The study reported herein addresses some aspects of these two problems.

My objectives were: (1) to compare infestation patterns of the TFB in fields with different cropping histories (i.e. continuous potato cropping *vs* yearly crop rotation); (2) to test the hypothesis that volunteer potatoes influence the occurence of patchy infestations within a potato field; (3) to test the hypothesis that plant size influences TFB movement and *edge effect* intensity; and (4) to examine the effect of plant spacing on the dispersion and density of the TFB.

3.2 Field survey: the relation between cropping history and infestation patterns

The objective of this survey was to verify the accuracy of earlier observations made by R.S. Vernon[1] and G.J.R. Judd[5] (pers. comm.) which suggested a connection between cropping history and the occurence of 'pockets of infestation' in some potato fields. Such patchy infestations disrupt the otherwise gradual decline of beetle density from field margin to center.

3.2.1 Methods

In June and early July 1984, three commercial potato fields in Cloverdale, British Columbia, were surveyed for *E. tuberis* adults. Two of the fields (G168E and G168W) were planted with the mid-season cultivar 'Norgold Russet' and one (G177W) was planted with the late-season cultivar 'Russet Burbank'. Field G168E was adjacent to field G168W but was smaller (46x135 m *vs* 86x175 m) and was seeded one week later. In addition, these two fields had different cropping histories: in 1983, G168E harboured potatoes[13] whereas G168W harboured onions[14]. Both fields were bounded by a farm road on their north edge and by a ditch on their south edge. West of G168W was a strip of uncultivated land and east of G168E was a a paved road separated

---

[13] Refered to here as second-year field.

[14] Refered to here as first-year field.

from the field by a ditch. The closest potato field was diagonally opposite the north-west corner of G168W. Field G176W was only a portion (45x150 m) of a larger 17-ha field which had a history of continuous potato cropping. Adjacent to the west edge of the sample area was a narrow strip of wild grasses and then a ditch. All other edges were bounded by potatoes.

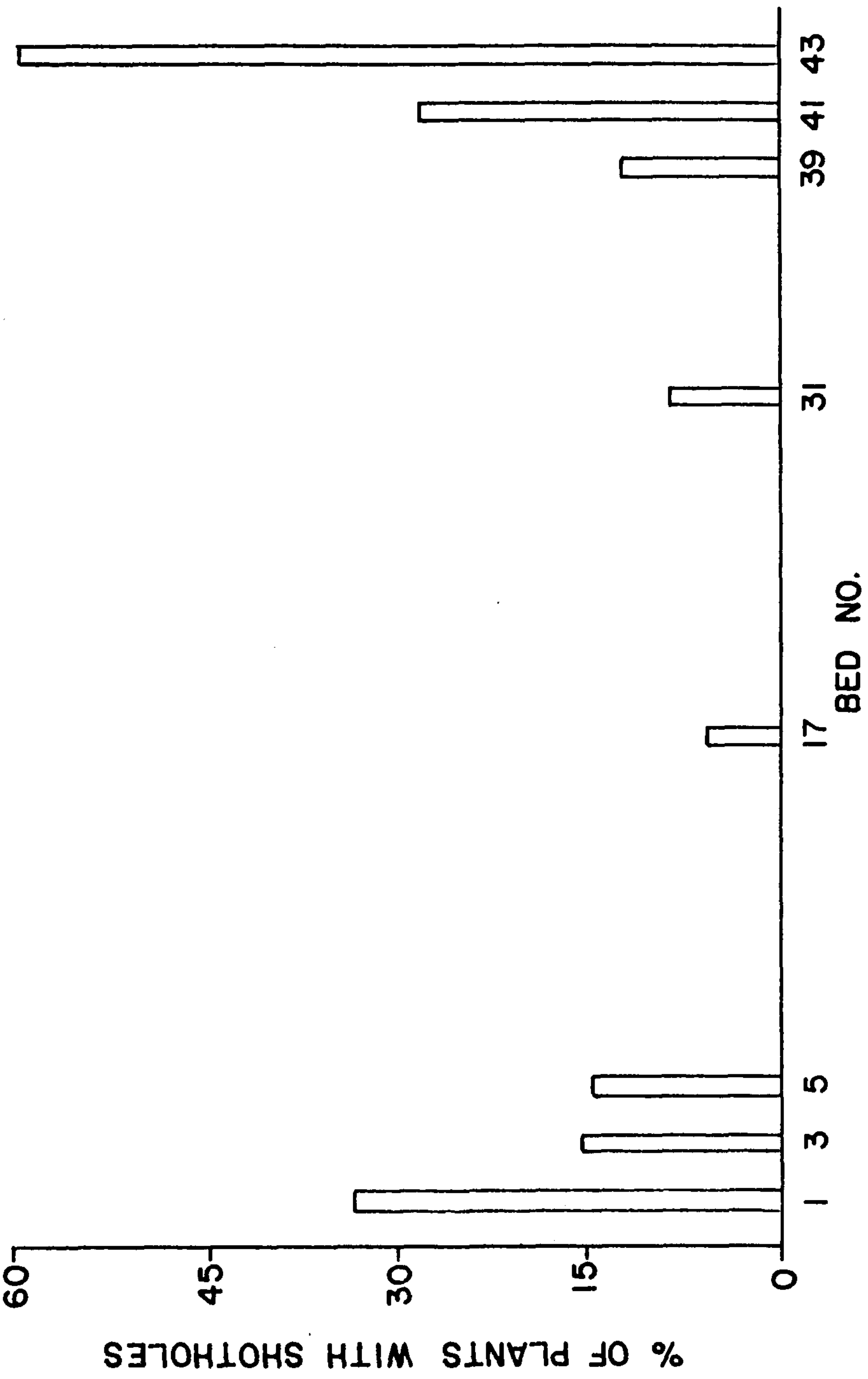
Beetle abundance was assessed indirectly by counting the number of plants with more than 5 feeding holes ('shotholes') in a row (G176W) or in a 2-row bed (G168E and G168W). Sample rows were chosen systematically and divided into adjacent 5 m sections from which single counts (no. of plants with 'shotholes' and total no. of plants) were obtained, transformed into percentages, and averaged over the entire row.

Vernon[1] showed that 'shothole' counts are a good indirect measure of beetle abundance. In order to compare this method with a direct one, a beetle sensus was taken in field G176W. Along the same rows that were selected for 'shothole' counts, groups of 10 plants, each separated by a distance of 10 m, were inspected for flea beetles. The counts were then averaged over the entire row.

3.2.2 Results and discussion

Based on indirect assessments of beetle abundance, the 'profile' of first-year field G168W (Figure 4) displayed two relatively steep edge-to-center gradients characterized by the

Figure 4. Density profile of *E. tuberis* in first-year field G168W on 13 June 1984. The left and right ends of the *x* axis represent the east and west edges of the field, respectively.


% OF PLANTS WITH SHOTHOLES
0
15
30
45
60
1
3
5
17
BED NO.
31
39
41
43

continuity of their decline. By contrast, 'profiles' of second-year fields G168E and G176W (Figures 5 and 6) exhibited irregular fluctuations which tended to reduce the intensity of *edge effects*. In field G176W (Figure 6), there was a significant positive correlation (parametric correlation test, $r=0.69$, $P< 0.05$) between direct and indirect measures of beetle abundance.

The above-described infestation patterns appear to support the hypothesis that 'pockets of infestation' are linked with continuous potato cropping. However, factors unrelated to cropping history might have contributed to the occurence of the patchier infestations in second-year fields. Of particular concern is plant size. Early in the season, near the peak of TFB emergence, plants were just beginning to break through the soil surface in the second-year fields whereas similar plants were larger and well established in the first-year field. Possibly TFBs spread further into potato fields when plants are small than when plants are large. A test of this hypothesis is discussed in section 3.4.

Figure 5. Density profile of *E. tuberis* in second-year field G168E on 15 June 1984. Bed no. 1 represents the east edge and bed no. 27 represents the west edge which is adjacent to the east edge of field G168W. The unseeded strip was ca. 10 m wide.

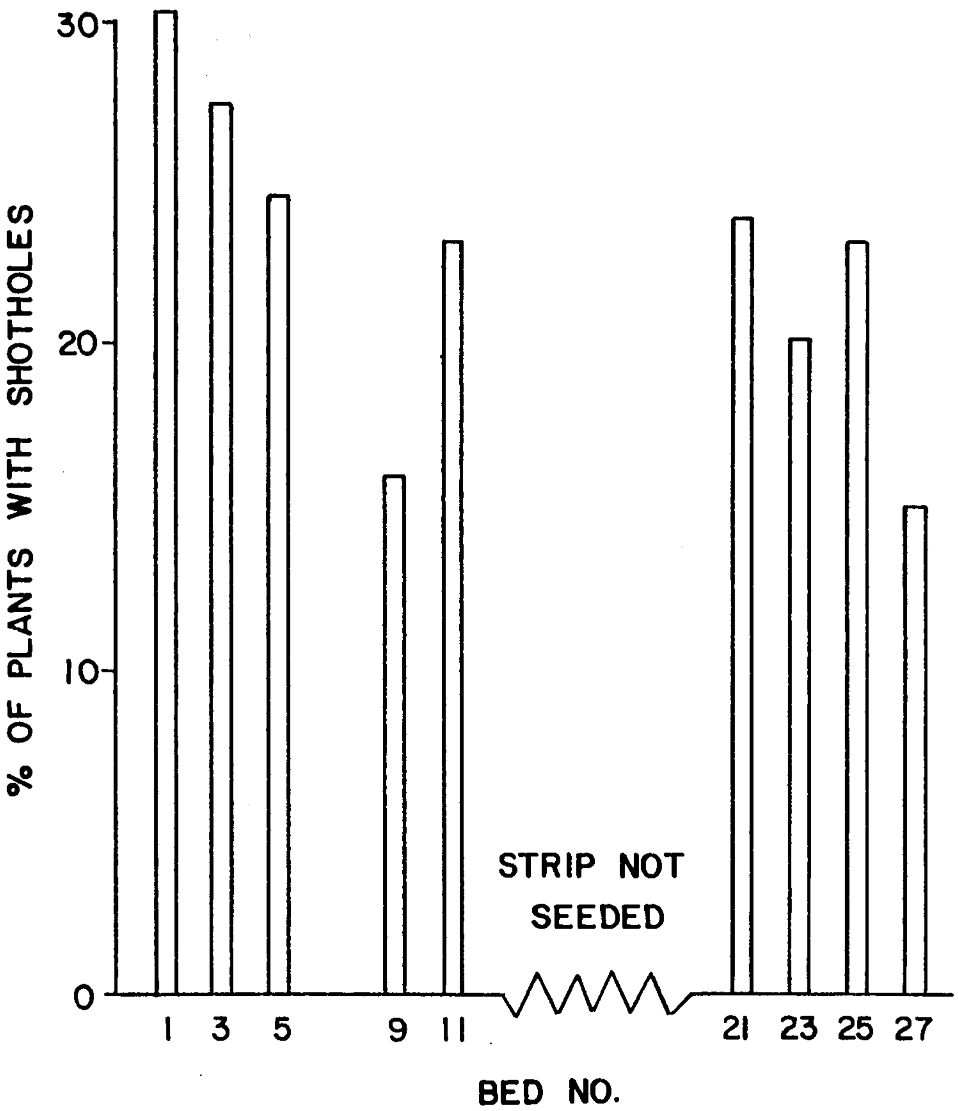
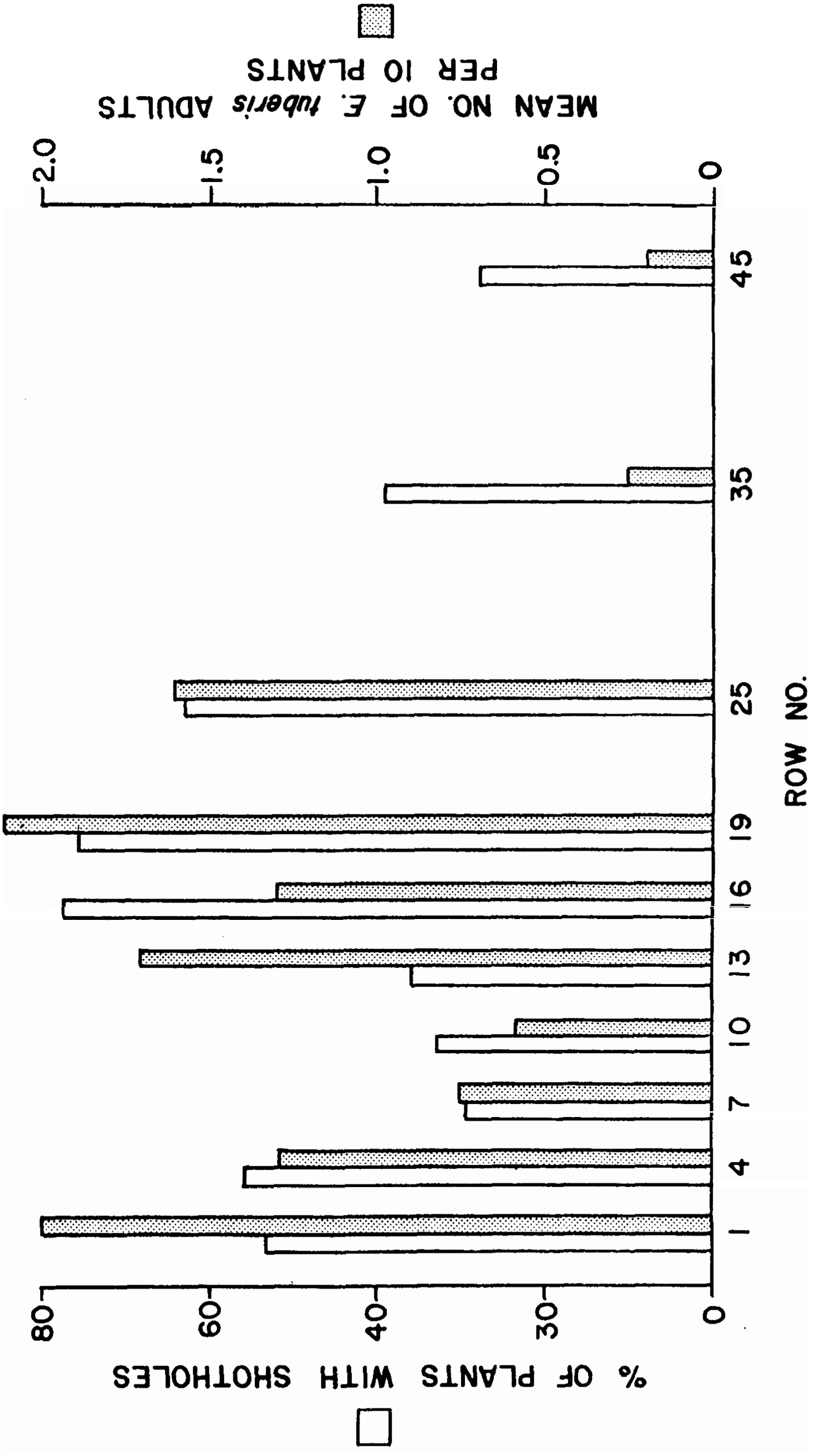

% OF PLANTS WITH SHOTHOLES
30
20
10
0
STRIP NOT SEEDED
1
3
5
9
11
21
23
25
27
BED NO.

Figure 6. Density profile of *E. tuberis* in second-year field G176W on 6 July 1984. The *x* axis does not represent the entire width of the field. Row no. 1 is the west edge.


% OF PLANTS WITH SHOTHOLES
80
60
40
30
0
MEAN NO. OF *E. tuberis* ADULTS PER 10 PLANTS
2.0
1.5
1.0
0.5
0
ROW NO.
1
4
7
10
13
16
19
25
35
45

3.3 The effect of volunteer potatoes on infestation patterns of the tuber flea beetle

The occurence of volunteer potatoes in fields subjected to two or more successive years of potato cropping led R.S. Vernon[1] (pers. comm.) to hypothesize that:

> Sparsely-distributed volunteer potatoes attract early-emerging beetles from their overwintering sites (outside the field). Eggs laid on those volunteers would give rise to pockets of infestation in the *following*, summer generation. By contrast, fields which do not harbour volunteers do not attract flea beetles until the crop emerges. At that time, the tight spacing of plants within rows and the high concentration of food thus provided would slow TFB movement towards the center of the field and cause the strong *edge effects* which persist in the summer generation.

Observations made during the first half of the field season (these observations did not involve a formal test of the hypothesis[15]) immediately called into question the explanatory power of the above hypothesis.

First, had the commercial potatoes been seeded near May 15, the normal seeding date for late-season cultivars, volunteers

---

[15] I had originally planned to perform a formal test of the aforementioned hypothesis by way of simulating volunteer potatoes with potted plants. However, the floods in the spring of 1984 prevented me from conducting the experiments as planned.

would have been destroyed by cultivation long before the first beetles emerged on May 28. Instead, most growers were forced to delay seeding until the end of May or the beginning of June on account of the prolonged flooding of their fields. Even then, beetles probably were not provided sufficient time to lay eggs on volunteers because of a requisite 5-day preoviposition period (Hill 1947). Moreover, in previous observations, *E. subcrinita* might have been mistaken for *E. tuberis* because it normally begins emerging ca. two weeks earlier than the TFB (Glenndenning 1945) and would therefore have sufficient time to oviposit on volunteers.

Secondly, if eggs are laid on volunteers, they would be exposed to cultivation (discing) and seeding since females oviposit in the soil near the base of the plants (Hill 1947). It is not known what percentage of eggs would survive this treatment, although such information could be easily obtained.

Finally, 'pockets of infestation' in fields which harbour volunteers do not seem to occur exclusively during the TFB's summer generation, as predicted by the hypothesis. For example, in 2 fields (Figures 5 and 6), populations of the *overwintering* generation (i.e. the generation which precedes the summer generation) were patchy. If 'pockets of infestation' were strictly the result of beetle oviposition on volunteers, no such 'pockets' would have occured while the overwintering generation was infesting the fields.

Briefly, the above observations provide little support for the 'volunteer hypothesis'. An alternative explanation will be discussed in the final chapter.

3.4 The effect of plant size on infestation patterns of the tuber flea beetle

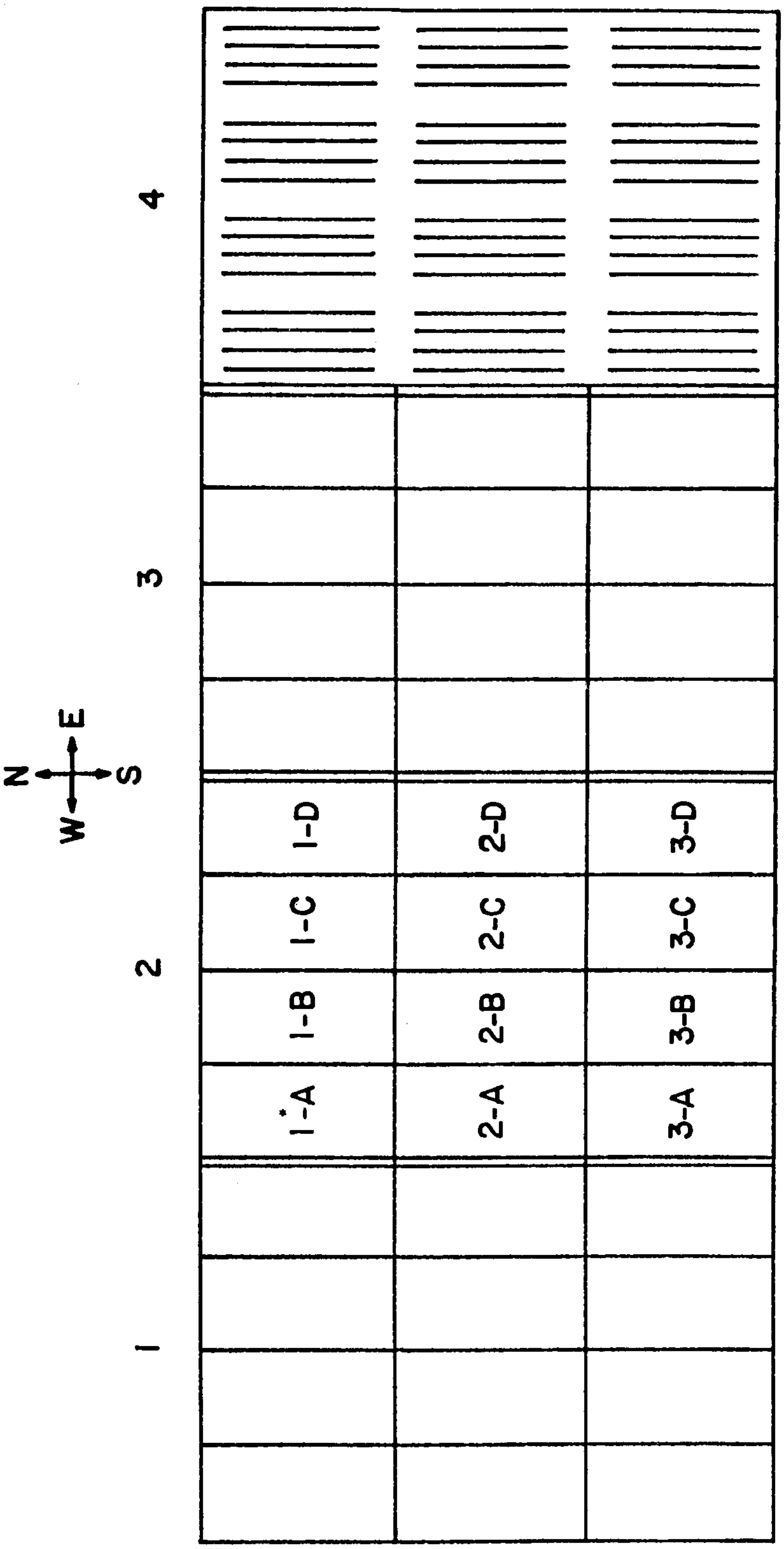
Based upon observations discussed in section 3.2, experiments were conducted to test the hypothesis that beetles travel further across rows in plots harbouring small plants than in plots harbouring large plants.

3.4.1 Materials and methods

Sequentially seeded plots (Figure 7) were employed on two occasions to conduct mark-recapture experiments. Statistics on plant height, for the different releases, are provided in Table 1.

On July 24, shortly after the summer-generation beetles first emerged, ca. 1000 TFBs were collected with an insect net, transfered into a cage with potato leaves, and held overnight at room temperature. On the following day, 400 beetles were mildly anesthetized with CO_2, individually marked with a small dot of paint on their pronotum with either of two acrylic (Liquitex®) colours (orange: 200, white: 200), and transferred to a holding

Figure 7. Map of the potato plots at the University of British Columbia, South Campus, 1984. 'Block' 2 is an example of the plot coding used in Tables 1 and 2 (e.g. 2.1.A is the *-marked plot). 'Block' 4 is an example of the disposition of rows: rows and groups of 4 rows are 1 m and 2 m apart, respectively. The four 'blocks' were seeded sequentially: 'block' 1 was seeded first and 'block' 4 was seeded last.



1
2
3
4
N
S
E
W
1-A
1-B
1-C
1-D
2-A
2-B
2-C
2-D
3-A
3-B
3-C
3-D

Table 1. Statistics on height[1] of potato plants for the mark-recapture experiment. A minimum of 20 plants per plot were measured.

	SMALL PLANTS			LARGE PLANTS		
DATE	PLOT #	MEAN HEIGHT (cm)	STD DEV	PLOT #	MEAN HEIGHT (cm)	STD DEV
26/7	3.2.B	6.65	2.92	2.2.B	29.7	4.19
11/8	4.2.C	6.79	3.73	3.1.B	33.8	4.03
11/8	4.2.D	7.80	3.53	3.1.C	29.2	5.39
11/8	4.1.B	6.68	3.47	3.3.B	37.3	7.03
11/8	4.1.C	8.90	4.50	3.3.C	34.4	6.26
GRAND MEAN:		7.44	3.77		33.2	6.31

---

[1] Differences in mean height of small and large plants were significant, pairwise *t*-test, $p<0.001$. Pairs are the same as those compared in the mark-recapture experiment (Table 2).

cage until the time of release.

Although tedious, the above method was preferred to the use of fluorescent dust which, in the case of the TFB, seemed to clog antennae and might have impaired the beetle's host searching ability. Also, care was taken not to paint the elytra which might have become glued together, thus preventing flight.

On the day of marking, at 9:00 pm, 200 white-marked beetles were released between two groups of four rows in the 'small-plant' plot and 200 orange-marked TFBs were released between two groups of four rows in the 'large-plant' plot. The top opening of each holding cage was at ground level.

A second release of marked beetles was carried out as described above on August 10, with the exception that beetles were chilled instead of anesthetized with CO_2. The two methods of anesthesia were equally effective but as chilling required fewer manipulations, it was preferred over the former method. In addition, the number of marked beetles was doubled so that two sets of 200 TFBs were released in each 'block' (Figure 7).

Mortality in the holding cages was very low for both experiments and recapture rates were reasonably high (mean=38%).

Fifteen to 32 hours following each release, all plants in the different groups of 4 rows adjacent to the release points were individually examined for marked beetles and the number of TFBs/plant was recorded. Approximately 10 and 15 sec/plant were spent looking for marked beetles on small and large plants, respectively.

In order to compare the two treatments statistically, counts were first transformed into proportions (see footnote of Table 2) which in turn were transformed into θ = arcsine $\sqrt{p}$, where p is the proportion (Sokal and Rohlf 1981). Replicates (groups of 4 rows) were treated in pairs (small and large plants). One pair was excluded from the analysis on account of an unusually low recapture rate in the small-plant replicate.

3.4.2 Results and discussion

Results are presented in Table 2 and examples of observed spatial patterns are shown in Figures 8 and 9. Assuming that TFBs have a much greater tendancy to move up and down a row than across rows (cf. *Phyllotreta crucifera* and *P. striolata* -- Kareiva 1982), then results in Table 2 strongly suggest that movement across rows was much greater in plots harbouring small plants than in plots harbouring large plants. This variation in movement patterns resulted in weaker *edge effects* when plants were small than when plants were large since proportionately fewer beetles tended to remain in border rows. Possibly for similar reasons, *edge effects* of pollen beetles on cruciferous crops were more pronounced in fields where plants were large than in those where plants were small (Free & Williams 1979).

As small plants have little food resource to offer, insects might be expected to spend less time on them than on large plants. In addition, if TFBs fly at very low altitude or simply

Table 2. Proportion of marked *E. tuberis* recaptured in the *n*th row from release point in small- and large-plant plots.

ROW #	SMALL PLANTS				LARGE PLANTS			
	DATE	PLOT #[a]	PROPORT.[b]	ARCSINE TRANS.	PLOT #	PROPORT.	ARCSINE TRANS.	*t* TEST[c] *P* LEVEL
1	26/7	3.2.B	0.558	48.3	2,2.B	0.969	79.9	0.0044
	11/8	4.2.C	0.769	61.3	3.1.B	0.905	72.0	
	11/8	4.2.D	0.588	50.1	3.1.C	0.976	81.0	
	11/8	4.1.B	0.587	50.0	3.3.B	1.000	90.0	
	11/8	4.1.C	0.486	44.2	3.3.C	0.986	83.1	
2	26/7	3.2.B	0.233	28.8	2.2.B	0.030	10.0	0.0140
	11/8	4.2.C	0.154	23.1	3.1.B	0.095	17.9	
	11/8	4.2.D	0.235	29.0	3.1.C	0.024	8.99	
	11/8	4.1.B	0.348	36.1	3.3.B	0.000	0.00	
	11/8	4.1.C	0.257	30.5	3.3.C	0.014	6.87	
3	26/7	3.2.B	0.116	19.9	2.2.B	0.000	0.00	0.0004
	11/8	4.2.C	0.051	13.1	3.1.B	0.000	0.00	
	11/8	4.2.D	0.118	20.1	3.1.C	0.000	0.00	
	11/8	4.1.B	0.065	14.8	3.3.B	0.000	0.00	
	11/8	4.1.C	0.114	19.8	3.3.C	0.000	0.00	
4	26.7	3.2.B	0.093	17.8	2.2.B	0.000	0.00	0.0296
	11/8	4.2.C	0.026	9.21	3.1.B	0.000	0.00	
	11/8	4.2.D	0.059	14.0	3.1.C	0.000	0.00	
	11/8	4.1.B	0.000	0.00	3.3.B	0.000	0.00	
	11/8	4.1.C	0.143	22.2	3.3.C	0.000	0.00	

[a] See Figure 7 for details.

[b] X_n= no. of TFBs in *n*th row; proportion = $X_n / \sum_{n=1}^{4} X_n$.

[c] Pairwise *t*-test (two-tailed).

Figure 8. Spatial patterns of *E. tuberis* after diffusion from release point in two small-plant plots. (Plot 4.1.B (left) and plot 4.1.C (right)). Each dot represents one beetle and each rectangle represents one plant. Note that some plants had not yet emerged from the soil.

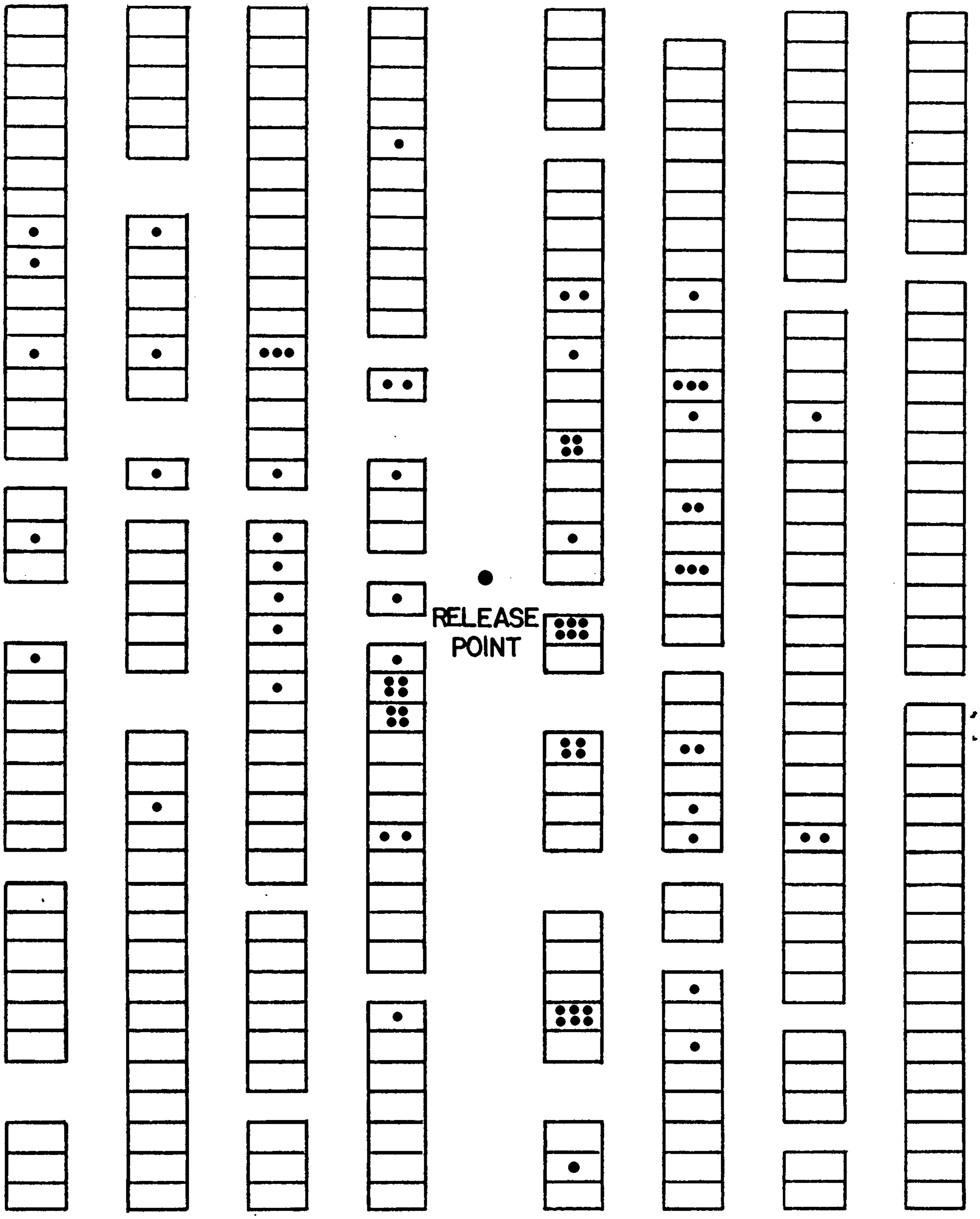
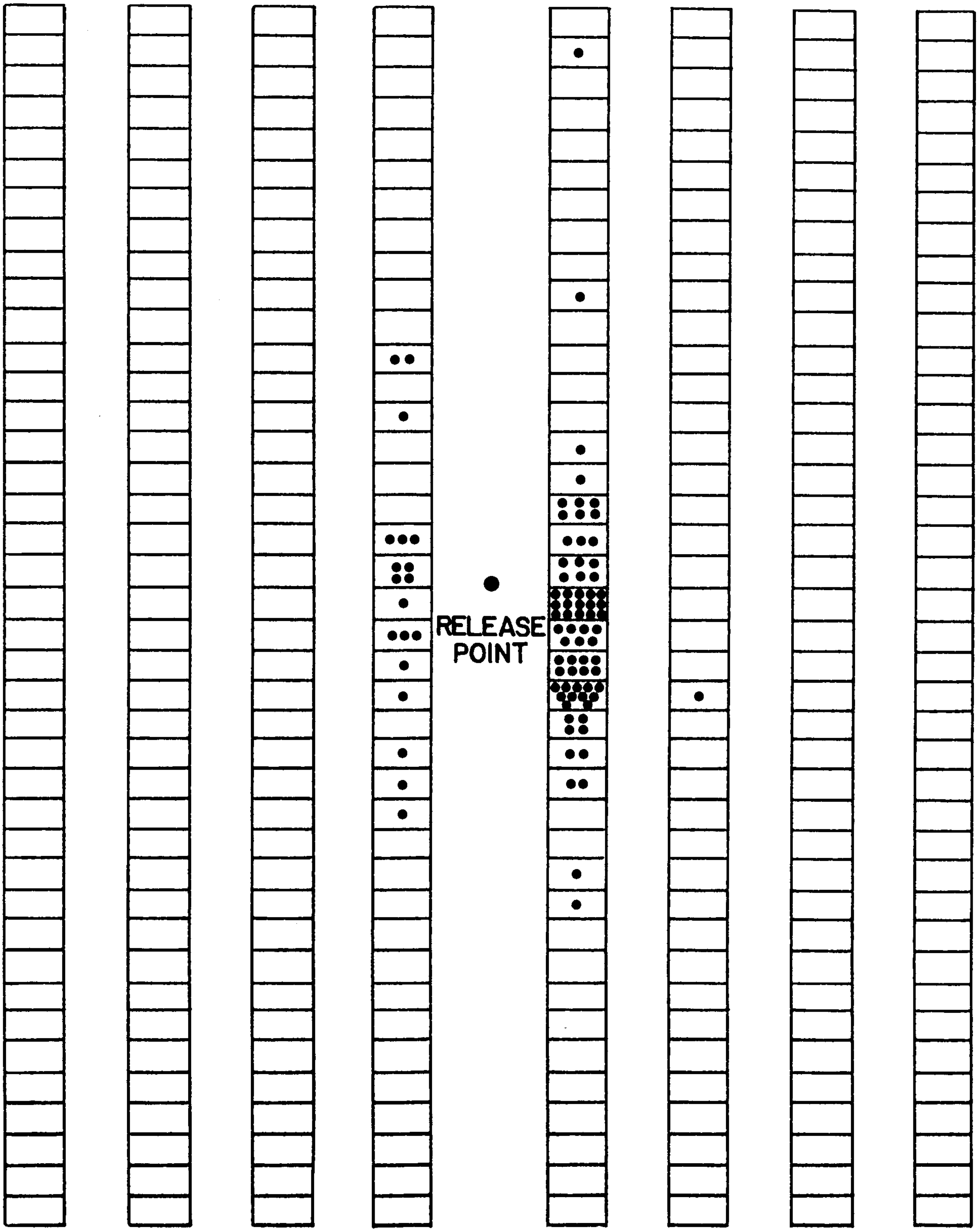

RELEASE POINT

Figure 9. Spatial patterns of *E. tuberis* after diffusion from release point in two large-plant plots. (Plot 3.3.B (left) and plot 3.3.C (right)). Each dot represents one beetle and each rectangle represents one plant.


RELEASE POINT

jump when dispersing from their overwintering sites, they are less likely to alight on plants in the first row if such plants have recently emerged than if they are high enough to intercept them. Each potato plant might be considered as a beetle trap that increases in efficiency (i.e. trapping surface) as it increases in size. This phenomenon most likely affects infestation patterns in large commercial fields as well. However, I do not know how important it might have been in affecting the results discussed in section 3.2.

3.5 The effect of plant spacing on the density and dispersion of the tuber flea beetle

Potted plants were employed to test the hypotheses that aggregation of the TFB increases with an increase in plant density and that per-plant densities of the TFB decrease when plant density increases.

3.5.1 Materials and Methods

A. THE PLOTS. On April 26, 2800 potato seeds (tubers) were sown in 26x52x6 cm plastic trays containing 18 square compartments each. One Russet Burbank certified seed was planted in each compartment and covered with muck soil. The trays were held outdoors in a wind-sheltered area at the Agriculture Canada Research Station, Vancouver, B.C., and watered periodically until the potted plants were transplanted into the field.

On May 30, 851 and 224 plants (ca. 15 cm high) were transplanted into plots 26x107.26 m in size at interplant spacing of 2 and 4 m, respectively. The two plots (plots 1 and 2 in field G; Figure 10) were 35 m apart. The plants were uniformly distributed and located on the hills (i.e. rows) of commercial potatoes seeded on May 25. Seeding of the commercial crop in that field was not completed until June 6.

On June 11 and 12, 683 and 600 plants were transplanted in field L at 2 m interplant spacing in plots 1 and 3 respectively (Figure 11) and 2x186 plants were transplanted in the same field at 4 m interplant spacing in plots 2 and 4. Plots 1, 2, and 4 were 104x20.76 m in size and plot 3 was 99x19.03 m (I reduced the size of this plot because of the loss of some of the plants). The plant pattern within each plot was uniform and the plots were 50 m apart. With the exception of plot 3, the plots ran across the entire width of the field.

Both fields have a history of continuous potato cropping (no rotation) but field L harboured no volunteers in 1984 because it remained under water until the end of May. Field G harboured some volunteers in areas well removed from the plots.

After transplantation, natural populations of TFBs were allowed to infest the plots for 4 to 6 days, after which I initiated beetle censuses. On 2, 3, or 4 occasions over a period of ca. 1 week, every plant in each of the 6 plots was thoroughly inspected for TFBs. The small size of the plants made accurate

Figure 10. Overview of field G. Plot 1: 2 m plant spacing; plot 2: 4 m plant spacing.

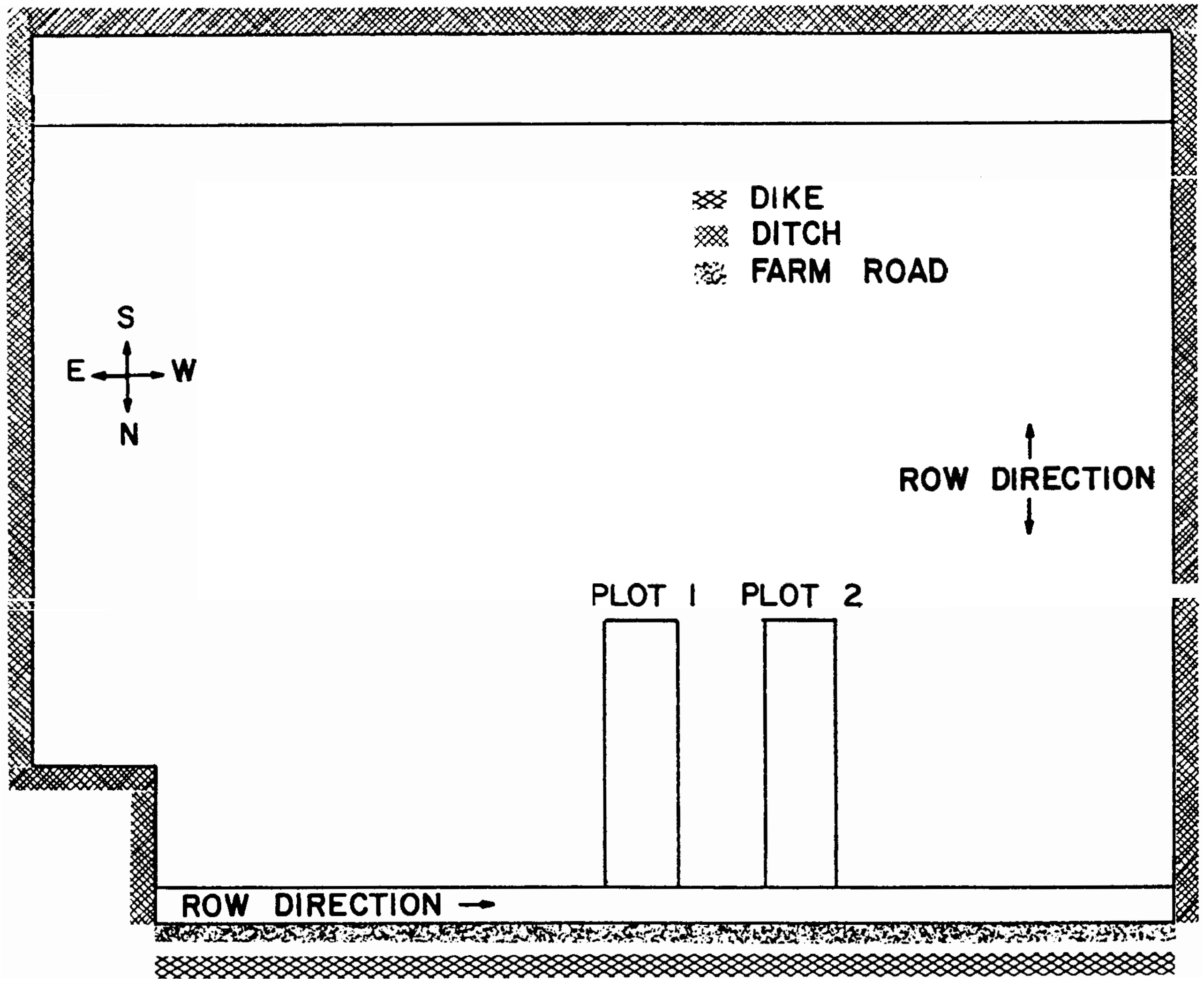
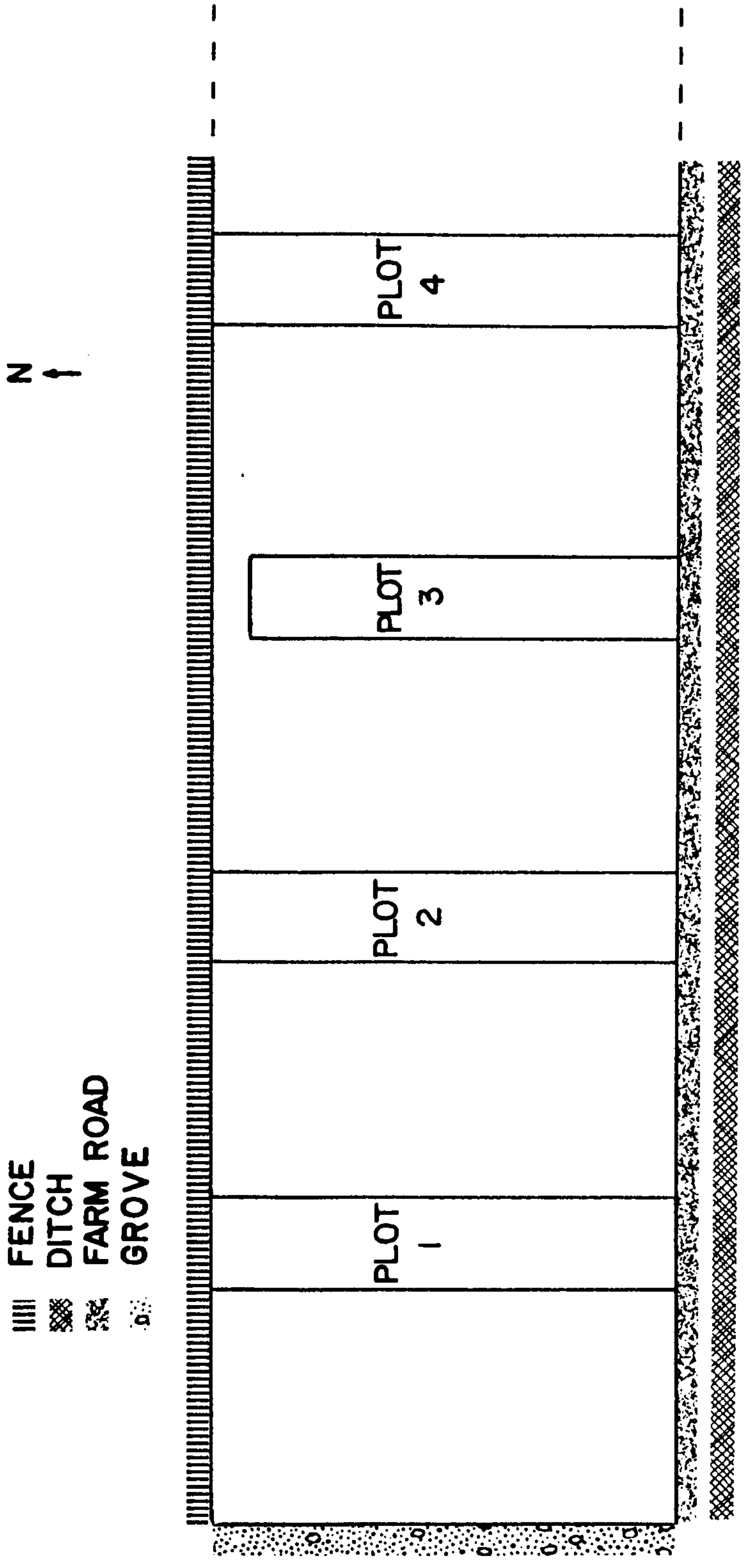

DIKE
DITCH
FARM ROAD
S
E
W
N
ROW DIRECTION
PLOT I
PLOT 2
ROW DIRECTION →

Figure 11. Overview of field L. Plots 1 and 3: 2 m plant spacing; plots 2 and 4: 4 m plant spacing.


FENCE
DITCH
FARM ROAD
GROVE
N
PLOT 1
PLOT 2
PLOT 3
PLOT 4

estimates of population size, within each plot, relatively easy to obtain. Beetle counts were mapped as shown in Figure 12. Pre-emergence herbicides applied to both fields caused the termination of the counts because the quality of the plants was deteriorating and the new crop was emerging.

B. CALCULATION OF DISPERSION INDICES. Dispersion maps of infestation revealed that some plots had obvious concentrations of beetles along one or two margins (Figure 12). Prior to calculating dispersion indices, it was important to eliminate (or reduce as much as possible) the heterogeneity brought about by such *edge effects* (see Harcourt 1961). In an attempt to quantify the *edge effects*, numbers of TFBs per 2 rows or per row were ranked and compared to the theoretical ranking of a perfect *edge effect* (Table 3, footnote) by means of Kendall's rank correlation test (Kendall 1955).

Decisions for eliminating rows in calculating dispersion indices were based upon: (1) the values of the rank correlation coefficients for *edge effects*, (2) qualitative evaluation of *edge effects* in mapped beetle counts, and (3) the necessity of having a number of rows that allows calculation of indices for different cell sizes. For an example, see the framed portion in Figure 12.

Three dispersion indices were calculated for each set of data: (1) the variance:mean ratio σ^2/m, (2) Green's (1966) coefficient of dispersion $(\sigma^2/m)/(\Sigma X - 1)$, where X is the number

Figure 12. Example of spatial pattern of *E. tuberis* in a potato test plot (L2-J20). Only the framed portion was employed for the calculation of the dispersion indices. Each rectangle represents one plant. (Not drawn to scale).

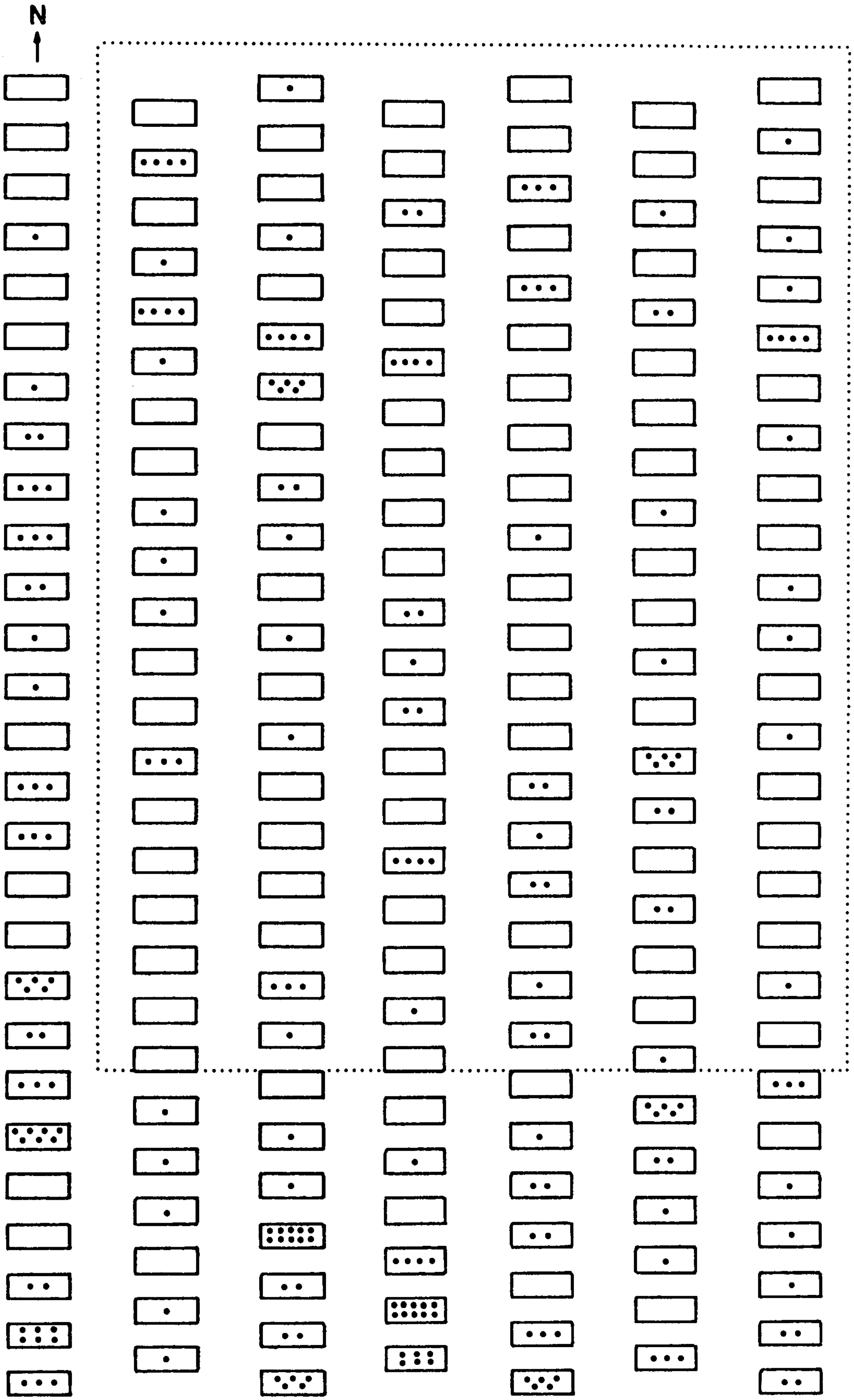

N

Table 3. Kendall's rank correlation coefficients for *E. tuberis* 'edge effects' in potato test plots.

	τ_b[1]			
PLOT-DATE[2]	NORTH EDGE	SOUTH EDGE	EAST EDGE	WEST EDGE
G1-J6	.313 (16)[3]	-.107 (16)	.293 (7)	.206 (7)
G1-J7	.348 (16)	.264 (16)	.586 (7)	.195 (7)
G1-J8	.446 (16)	.166 (16)	.488 (7)	.293 (7)
G1-J14	.291 (16)	.146 (16)	.867 (6)	1.000 (4)
G2-J6	.567 (8)	-.327 (8)	.548 (4)	.667 (4)
G2-J7	.400 (8)	-.473 (8)	.183 (4)	.333 (4)
G2-J8	.741 (8)	-.371 (8)	-.183 (4)	1.000 (4)
G2-J14	.000 (8)	-.113 (8)	-1.000 (4)	.548 (4)
L1-J15	.055 (27)	.440 (27)	.067 (6)	.828 (6)
L1-J19	.097 (27)	.509 (27)	.200 (6)	.828 (6)
L1-J20	.170 (27)	.422 (27)	.200 (6)	.600 (6)
L2-J15	-.023 (14)	.497 (14)	.000 (4)	.000 (4)
L2-J19	-.058 (14)	.520 (14)	.000 (4)	.000 (4)
L2-J20	-.058 (14)	.596 (14)	-1.000 (4)	.333 (4)
L3-J19	.382 (25)	.501 (25)	.333 (6)	.200 (6)
L3-J21	.175 (25)	.619 (25)	-.067 (6)	.333 (6)
L4-J19	.347 (14)	.506 (14)	-.333 (4)	.667 (4)
L4-J21	.422 (14)	.589 (14)	-.236 (4)	.913 (4)

[1] Rank correlation coefficient for the ranking of observed no. of TFBs per 2 rows (or per row: L1, L2, L3, and L4, east & west) and the theoretical ranking:1,2,3,...,n, where n is the rank assigned to the first row on the edge of the plot and 1 is the rank assigned to the row that devides the plot in two equal sections.

[2] G: name of field, 1: plot, J: June, 6: date.

[3] No. of ranks.

of individuals per cell, and (3) Lloyd's (1967) patchiness index $\overset{*}{m}/m$, where $\overset{*}{m} = m + (\sigma^2/m - 1)$. These indices were also calculated for the following cell sizes: 1, 3, 6, 12, and 24 plants. The variance:mean ratio and Green's coefficient were very little affected by variations in cell size but the patchiness index declined steadily with increasing cell size. The latter phenomenon is not surprising since the patchiness index is equivalent to Morisita's index of dispersion (Taylor 1984) and Morisita's index always declines with increasing cell size (Vandermeer 1981). For these reasons, only the indices based upon single-plant counts are presented here.

3.5.2 Results and discussion

DISPERSION

Although no statistical tests can be used to compare the different dispersion indices (Table 4), because not all of them satisfy the assumption of independence (Hubert 1984), values of the variance:mean ratio and Green's coefficient indicate a definite trend towards a greater aggregation of beetles in the 4 m than in the 2 m spacing plots. This trend appears to be contradicted by the calculated values of the patchiness index. However, Myers (1978) pointed out that, when density increases, a decrease in patchiness is to be expected as a result of a statistical artifact. Results reported in Table 4 indicate that beetle densities in the 4 m spacing plots were generally higher

Table 4. Indices of dispersion of *E. tuberis* for two different (potato) plant densities.

PLANT SPACING: 2m (3.1 plants/10m²)							PLANT SPACING: 4m (0.8 plant/10m²)						
PLOT-DATE	N	m (TFB/plant)	σ^2	σ^2/m	C_x	$\overset{*}{m}/m$	PLOT-DATE	N	m (TFB/plant)	σ^2	σ^2/m	C_x	$\overset{*}{m}/m$
G1-J7[1]	672	.0982	.1424	1.45[2]	.0069[3]	5.58[4]	G2-J8	192	.3385	.5183	1.53	.0083	2.57
G1-J8	672	.1027	.1578	1.54	.0079	6.23	L2-J15	120	.4083	.8991	2.20	.0250	3.94
G1-J6	672	.1116	.1887	1.69	.0093	7.19	L4-J19	120	.4417	1.324	3.00	.0384	5.52
L1-J15	480	.1917	.3264	1.70	.0077	4.67	G2-J7	192	.4531	1.223	2.70	.0197	4.75
L3-J19	480	.2333	.4131	1.77	.0069	4.30	G2-J6	192	.5000	1.162	2.32	.0139	3.65
L1-J19	480	.2417	.4759	1.97	.0084	5.01	L4-J21	120	.6167	1.247	2.02	.0140	2.66
L1-J20	480	.3083	.5561	1.80	.0055	3.61	L2-J19	120	.6667	2.022	3.03	.0257	4.05
L3-J21	480	.3125	.6328	2.03	.0069	4.28	L2-J20	120	.7917	1.477	1.87	.0092	2.09
G1-J14	504	.4048	.7308	1.80	.0040	2.99	G2-J14	192	1.422	2.894	2.04	.0038	1.73
			MEAN:	1.75	.0071	4.87				MEAN:	2.40	.0176	3.44
			(S.D.)	(0.18)	(.0016)	(1.30)				(S.D.)	(0.54)	(.0108)	(1.27)

[1] G=name of field, 1=plot no., J=June, 7=date.

[2] All variance:mean ratios tested for randomness (χ^2) (Southwood 1968). H_0 (variance=mean) rejected in each case.

[3] C_x is Green's coefficient of dispersion (Green 1966).

[4] An index greater than 1 indicates aggregation (Lloyd 1967).

than those in the 2 m spacing plots (in fact, the two ranges of densities were almost disjunct) making Lloyd's patchiness index a poor comparative measure. Green's coefficient and the variance:mean ratio are recommended for use when density changes because they are not and little (respectively) influenced by density (Myers 1978).

These results, which appear to refute the hypothesis stated above, are interesting in light of Kareiva's (1982) findings regarding the diffusion and aggregation of crucifer-feeding flea beetles on collards. Using the variance:mean ratio as a clumping index, he observed an increase in aggregation as distance between patches of collards declined. The same index, when applied to the TFB data, shows the opposite trend.

At least four factors may have contributed to this phenomenon. First, Kareiva (1982) ascribed the contradiction between his findings and the results predicted by the passive diffusion theory to a greater rate of beetle movement among closely-spaced than widely-spaced plants. This higher rate of movement would allow insects to choose patches on the basis of their quality and, therefore, to aggregate on the best patches or best individual plants. Some plants in Kareiva's (1982) test arrays were of better quality than others. By contrast, plant quality in my potato plots was very homogeneous; the fact that potatoes are grown as a clone (Ewing 1981) probably contributed to this homogeneity. I suggest that the discrimination power of *E. tuberis* might be too low to have allowed effective selection of the marginally better hosts. *Epitrix tuberis* would therefore satisfy the passive-diffusion-based argument according to which plant-to-plant variability in flea beetle density should be proportional to the distance between plants (Kareiva 1982).

A second factor which may have contributed to the difference between Kareiva's (1982) results and mine is the fact that his experiments were conducted in linear arrays instead of two-dimensional plots which allow multi-directional movement. However, it is difficult to predict how foraging behaviour would differ in these two types of plots.

Thirdly, the differences in TFB (per-plant) densities on the two plant spacings may have led to erroneous conclusions regarding aggregation. Ideally, dispersion indices should be compared when the ranges of per-plant densities are approximately the same (in my test plots, they were almost disjunct).

Finally, Morris (1960) noted that, at low density, contagious distributions often approach the Poisson distribution. Here, a similar phenomenon might be involved since beetle densities were relatively low in the 2 m spacing plots.

DENSITY

Employing the data collected for the analysis of beetle dispersion, it is possible to consider the effect of plant density on beetle abundance. Table 5 shows the calculated per-plant and per-10 m^2 TFB densities for the 2 plant spacings[16].

As the data are not all independent, no statistical tests can validly be applied to these results but it is nevertheless interesting to compare figures of beetle density for the two spacings (Table 5). As predicted by the hypothesis stated above, in each plot and at all sampling dates, per-plant densities of beetles were lower when plant density was greater (i.e. in 2 m spacing plots). Kareiva (1983) has argued that this phenomenon, also reported for several other species, contradicts the 'resource concentration hypothesis' (Root 1973) which states that herbivore abundance (per plant) should increase when plant density increases. However, it appears counter-intuitive to make such predictions since plant quality and plant size tend to be lowered by increases in plant density (Kareiva 1983). It follows that each individual plant has less to offer colonizers when plant density is high.

On the other hand, the more intuitive prediction that herbivore abundance per unit area should increase with plant density seems to be verified by the TFB data (Table 5). Except for the first three sampling dates in field G, per-10 m^2 beetle densities were greater in plots with the higher plant density. A similar phenomenon was reported by Jones (1977) for *P. rapae*.

---

[16] Note that the per-plant densities shown in Table 5 are higher than those presented in Table 4. This is the result of using all counts in calculating densities for Table 5 whereas some rows were not employed in the analysis of Table 4.

Table 5. *Epitrix tuberis* densities in 2m- and 4m-plant-spacing potato plots.

		PLANT SPACING: 2m[1]				PLANT SPACING: 4m			
DATE (June)	FIELD	PLOT	SURFACE AREA (m^2)	# TFBs /PLANT	# TFBs /$10m^2$	PLOT	SURFACE AREA (m^2)	# TFBs /PLANT	#TFBs /$10m^2$
6	G	1	2788	.138	.420	2	2788	.545	.438
7	G	1	2788	.115	.352	2	2788	.438	.352
8	G	1	2788	.109	.334	2	2788	.438	.352
14	G	1	2038[2]	.483	1.57	2	2788	1.69	1.31
15	L	1	2159	.253	.801	2	2159	.670	.574
19	L	1	2159	.409	1.28	2	2159	1.05	.880
20	L	1	2159	.442	1.38	2	2159	1.24	1.06
19	L	3	1884[3]	.319	1.01	4	2159	.742	.639
21	L	3	1884	.409	1.30	4	2159	1.02	.875

[1] 2m spacing = 3.1 plants/$10m^2$, 4m spacing = 0.8 plant/$10m^2$

[2] A portion of the plot was not sampled on June 14.

[3] Plot L3 had 1 fewer row than plot L1.

The above results were very likely affected by the number of available colonizers as well as the origin of such colonizers in relation to the spatial arrangement of the plots. The latter factor might, in fact, be responsible for the nearly equal per-10 m^2 beetle densities observed for the two plant spacings in field G on the first three sampling dates. Plot G-2 (4 m spacing) might have intercepted the first incoming beetles originating from the west side of the field[17], thus making such insects unavailable for colonization of plot G-1 (see relative position of the two plots in Figure 10).

With regard to the emigration of beetles from the plots, little is suspected to have occured since: (1) beetle densities never became so high as to create the kind of population pressure which would have forced the departure of individuals, (2) apart from the plants in the plots, the abundance of alternative hosts (to which beetles might have moved) in the immediate environment of the fields was low, and (3) beetle densities tended to increase from one sampling date to the next (the apparent density decreases observed in plots G-1 and G-2, over the first three sampling dates, were most likely brought about by the very low temperatures recorded on June 7 and 8 which may have caused some beetles to hide in parts of the plants (e.g. buds) where they could not be readily seen).

---

[17] This is suggested by the high rank correlation coefficients for the 'west edge' in plots G2-J8 and G1-J14 (see Table 3). These indicate that most beetles were entering the plots by the west edge.

In summary, the above results show some interesting trends which would be worth reexamining in future research but the low number of replicates employed in 1984 precludes any definitive conclusion.

4. CONCLUSION

In the second chapter of this paper, I reviewed several publications which dealt, either directly or indirectly, with the phenomenon of *edge effect* in infestation patterns of insects on crops. In an attempt to explain the occurence of such effect, various mechanisms have been proposed, all of which seem plausible, although in a particular situation, probably only one is operating.

With reference to *E. tuberis*, three of the suggested mechanisms might, at different times or in different environments, promote the occurence of *edge effects*. First, it appears that at least some individuals in any given TFB population have the ability to fly (Hoerner & Gillette 1928; Daniels 1941; Jones 1944). I have witnessed the flight of some beetles released on a host plant or on the ground. Further, it seems likely that a certain portion of any TFB population would undergo the 'oögenesis-flight syndrome' (*sensu* Johnson 1969)[18] so that the species can 'maximize its resources' (*sensu* Taylor & Taylor 1977). Such beetles might, at the end of a long flight, respond to border plants in a way similar to that described by Courtney and Courtney (1982). The second possible mechanism that

---

[18] There is evidence that the adaptive process of migration by female insects is based on the relation of the development of ovaries to that of the flight apparatus (Johnson 1969).

could promote *edge effects* is the physical influence of levees erected along the margins of some potato fields. At least some of these levees probably create wind-sheltered zones into which flying beetles might be drawn.

Above all, three behaviours which act upon the process of crop colonization seem most likely to give rise to *edge effects*, in TFB populations. These behaviours are: (1) an apparent propensity to overwinter near host fields, (2) a tendency to invade border plants first, and (3) a low rate of movement following the location of a host plant. Behaviours (1) and (2) are likely because released beetles showed a tendency to colonize and then remain[19] on first encountered hosts, especially when these were large. Although there is no direct evidence for overwintering near host fields, the occurence of this habit is suggested by the abundant supply of protective vegetation which often surrounds potato fields (and which is the TFB's preferred overwintering vegetation (Fulton *et al*. 1955)) and the very short period of time which normally separates host emergence and beetle attack.[20] Together, these three behaviours illustrate well the important role that distance from source plays in colonization of crops by herbivores (Price & Waldbauer 1975).

---

[19] One of the plots (see section 3.4) was reexamined 24 h after the first sensus and little movement seemed to have occured during the elapsed period.

[20] Almost immediately after potted plants were transplanted into the field (see section 3.5), some beetles were observed on them.

The observations discussed in the first part of the third chapter reinforce the hypothesis that the occurence of patchy infestations is linked to continuous potato cropping. However, generalizations are, at this stage, dangerous since only a limited number of fields were surveyed and at least one environmental factor (i.e. plant size) might have affected the observed patterns.

In an effort to elucidate the process by which cropping history appears to affect infestation patterns, a 'volunteer'-based hypothesis was proposed. However, observations reported in section 3.3 have indicated that volunteer potatoes are generally destroyed too early by cultivation to give females sufficient time to lay eggs on them. Therefore, only an unusually early beetle emergence or a reemergence of some volunteers shortly after cultivation (the latter phenomenon was not observed in any of the fields examined in 1984, i.e. when the volunteers emerged, they always did so synchronously with the crop, but the possibility is worth considering in future research), would allow such oviposition to occur. Moreover, eggs, if laid prior to cultivation, would need to survive discing and seeding. A more likely scenario is that some beetles spend the winter in the field instead of moving to uncultivated ground in the fall. Although not well documented, this alternative overwintering strategy has in fact been reported by early investigators (Hoerner & Gillette 1928; Fulton *et al.* 1955). Its obvious consequence would be to give resident beetles a headstart on those that must invade the crop from the outside and thus promote the occurence of 'pockets of infestation'. If this hypothesis proves to be correct, crop rotation would then limit *E. tuberis* infestations to border rows. In future research, the TFB's overwintering habits should be examined more closely so that pest managers can make better-informed recommendations regarding cultural practices and, ultimately, predict sources of infestation.

The data indicating that TFBs travel further across rows when plants are small than when plants are large (Table 2) suggest that timing of beetle emergence and plant emergence might be crucial in determining how far into the field beetles will spread. Hence the prediction that the earlier the planting, the larger the plants will be at the time of beetle emergence and the greater the proportion of beetles that will remain on border plants.

The above phenomenon further suggests the possible use of trap crops to prevent *E. tuberis* from reaching potato fields. For example, a trap-strip of potatoes might be seeded at the periphery of a field approximately two weeks before the remainder of the field is planted. When beetles emerge, the larger peripheral trap-strip plants would theoretically absorb most of the infestation, especially if these plants are separated from the main crop by a strip of bare soil. Insecticide applications, if necessary, could thus be limited to the trap crop.

Although the experiments on the effect of plant spacing on beetle dispersion and density have little immediate application in pest management, they are of theoretical interest and may be worth reconsidering in future research. For example, the apparent trend towards a greater TFB aggregation among low-density plants could be reexamined on a larger number of plots and with released beetles so that the experimenter has better control over the per-plant beetle densities.

Finally, my first objective was to gather information which could be employed towards the development of an efficient and reliable sampling system for *E. tuberis*. The results reported in this paper suggest that a simple model relating beetle density in the *n*th row to density in the first row could be developed for first-year potato fields. Taylor (1978, 1980) discussed different models intended to describe the distance-related density declines typical of several insect species when they disperse from a release point. Similar models might describe the edge-to-center density gradients characteristic of *E. tuberis*' infestations. Because timing of plant emergence and beetle emergence could play a major role in the shaping of such gradients, the proposed TFB model should include the following two parameters: (1) plant size and (2) the number of days elapsed since the start of beetle emergence. The wind's mean angle of incidence to the edge might also need to be taken into consideration. The user would then need to sample for beetles in the first row, average the counts over that row (or over separate portions of it), obtain an approximate measure of plant size and determine the date of first beetle emergence. In this way, it would be possible to estimate beetle density in any given row between the center and the edge of a field without conducting extensive sampling over the entire crop. Then, based on an economic threshold (not yet developed), the pest manager could recommend the number of rows that need to be sprayed.

Alternatively, a stratified sequential sampling procedure, similar to that described in section 2.2, could be developed for fields where some beetles are suspected to be winter residents. Ideally, the width of the longitudinal stratum (parallel to row direction) should be the same as that of the spray swath so that the pest manager can make his/her recommendations in terms of the number of adjacent sprayer passes that are necessary.

In summary, this research has clarified some aspects of *E. tuberis*' infestation patterns on potatoes and the findings reported herein will likely aid the development of an effective sampling system for this pest. Additional studies, however, are required before such a system is implemented.

5. LITERATURE CITED

Anscombe, F.J. 1949. The statistical analysis of insect counts based on the negative binomial distribution. Biometrics, 5:165-173.

Barbosa, P. 1978. Distribution of an endemic larval gypsy moth population among various tree species. Environ. Entomol., 7:526-527.

Broadbent, L., T.W. Tinsley, W. Buddin & E.T. Roberts. 1951. The spread of lettuce mosaic in the field. Ann. Appl. Biol., 38:689-706.

Burgess, L. 1977. Flea beetles (Coleoptera: Chrysomelidae) attacking rape crops in the Canadian prairie provinces. Can. Entomol., 109:21-32.

Burgess, L. 1981. Winter sampling to determine overwintering sites and estimate density of adult flea beetle pests of rape (Coleoptera: Chrysomelidae). Can. Entomol., 113:441-447.

Courtney, S.P. & S. Courtney. 1982. The 'edge effect' in butterfly oviposition: causality in *Anthocharis cardamines* and related species. Ecol. Entomol., 7:131-137.

Criddle, N. 1923. The life habits of *Cephus cinctus* Nort. in Manitoba. Can. Entomol., 55:1-4.

Cromartie, W.Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Applied Ecol., 12:517-533.

Daniels, L.B. 1941. Colorado potato pests. Colorado State College, Colorado Exp. Stn. Bull. no. 465.

Dominick, C.B. 1971. Overwintering and spring emergence of the tobacco flea beetle. J. Econ. Entomol., 64:88-89.

Ewing, E.E. 1981. Overview of potato physiology related to integrated pest management. *In*: Advances in potato pest management (J.L. Lashomb & R. Casagrande, eds.), pp. 1-12. Hutchinson Ross Bublishing Co., Stroudsburg.

Finlayson, D.G. 1950. The effects of certain insecticides on the biotic potential of *Epitrix tuberis* Gentner (Coleoptera: Chrysomelidae). M.A. thesis, Dept. Zool. University of British Columbia.

Free, J.B. & I.H. Williams. 1979. The distribution of insect pests on crops of oil-seed rape (*Brassica napus* L.) and the damage they cause. J. Agric. Sci., Camb., 92:139-149.

Fulton, H.G., F.L. Banham & C.L. Neilson. 1955. The tuber flea beetle in British Columbia. Can. Dept. Ag. Entomol. Div. Publ. no. 938.

Fulton, H.G. & F.L. Banham. 1960. A brief history of the tuber flea beetle, *Epitrix tuberis* Gent., in British Columbia. Proc. Entomol. Soc. Brit. Columbia, 57:47-49.

Gentner, L.G. 1944. The black flea beetles of the genus *Epitrix* commonly identified as *cucumeris* (Harris) (Coleoptera: Chrysomelidae). Proc. Entomol. Soc. Wash., 46:137-149.

Gerber, G.H. 1982. A pest management system for the red turnip beetle on rapeseed and canola. Can. Agric., 27:8-11.

Glenndenning, R. 1945. Population counts of potato flea beetles at Agassiz and Chilliwack, B.C. (Coleoptera: Chrysomelidae). Proc. Entomol. Soc. Brit. Columbia, 42:2.

Green, R.H. 1966. Measurement of non-randomness in spatial distributions. Res. Popul. Ecol., 8:1-7.

Greig-Smith, P. 1983. Quantitative plant ecology. pp. 54-104. Blackwell Scientific Publications, Oxford.

Harcourt, D.G. 1961. Spatial pattern of the imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae), on cultivated cruciferae. Can. Entomol., 93:945-952.

Harcourt, D.G. 1963. Biology of cabbage caterpilars in Eastern Ontario. Proc. Entomol. Soc. Ont., 93:61-75.

Harcourt, D.G. 1964. Population dynamics of *Leptinotarsa decemlineata* (Say) in Eastern Ontario. II. Population and mortality estimation during six age intervals. Can. Entomol., 96:1190-1198.

Hartzell, F.Z. 1932. Relation of shelter to abundance of pear midge. J. Econ. Entomol., 25:351-355.

Hill, R.E. 1946. Influence of food plants on fecundity, larval development and abundance of the tuber flea beetle in Nebraska. University of Nebraska, College of Ag., Ag. Exp. Stn. Res. Bull. no. 143.

Hill, R.E. 1947. Biology and control of the Tuber Flea Beetle, *Epitrix tuberis* Gentner, in Nebraska. Iowa State College J. Sci., 22:39-41.

Hill, R.E. & H.D. Tate. 1942. Life history and habits of the potato flea beetle in Western Nebraska. J. Econ. Entomol. 35:879-884.

Hoerner, J.L. & C.P. Gillette. 1928. The potato flea beetle. Colorado Exp. Stn. Entomol. Section, Bull. no. 337.

Holmes, N.D. 1978. The wheat stem sawfly. Proc. Entomol. Soc. Alta., 26:2-13.

Holmes, N.D. 1982. Population dynamics of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), in wheat. Can. Entomol., 114:775-788.

Hubert, S.H. 1984. Pseudoreplication and design of ecological field experiments. Ecol. Monogr., 54:187-211.

Hudon, M. & P. Martel. 1973. Les insectes des cultures maraîchères dans le sud-ouest du Québec en 1972. Ann. Soc. Entomol. Qué., 18:3-4.

Iwao, S. 1968. A new regression method for analysing the aggregation pattern of animal populations. Res. Popul. Ecol., 10:1-20.

Johnson, C.G. 1950. Infestation of a bean field by *Aphis fabae* Scop. in relation to wind direction. Ann. Appl. Biol., 37:441-450.

Johnson, C.G. 1969. Migration and dispersal of insects by flight. Methuen & Co. Ltd., London.

Johnson, S.A. 1904. Fall handling of potatoes to lessen injury from insects and fungi. Colo. Press Bul. no. 23.

Jones, E.W. 1944. Biological studies of two potato flea beetles in eastern Washington. J. Econ. Entomol., 37:9-12.

Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol., 46:195-212.

Kareiva, P. 1982. Experimental and mathematical analysis of herbivore movement: quantifying the influence of plant spacing and quality of foraging discrimination. Ecol. Monogr., 52:261-282.

Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. *In*: Variable plants and herbivores in natural and managed systems (R.F. Denno & M.S. McClure, eds), pp. 259-289. Academic Press, New York.

Kendall, M.G. 1955. Rank correlation methods. Charles Griffin & Co., London.

Kennedy, J.S. & C.O. Booth. 1963. Co-ordination of successive activities in an aphid. The effect of flight on the settling responses. J. Exp. Biol., 40:351-369.

Knowlton, G.F. 1948. *Empoasca filamenta* damage. J. Econ. Entomol., 41:115.

Lewis, C.T. & N. Waloff. 1964. The use of radioactive tracers in the study of dispersion of *Orthotylus virescens* (Douglas & Scott) (Miridae, Heteroptera). Ent. Exp. Appl., 7:15-24.

Lewis, T. 1965a. The effect of an artificial windbreak on the aerial distribution of flying insects. Ann. Appl. Biol., 55:503-512.

Lewis, T. 1965b. The effect of an artificial windbreak on the distribution of aphids in a lettuce crop. Ann. Appl. Biol., 55:513-518.

Lewis, T. 1966a. An analysis of components of wind affecting the accumulation of flying insects near artificial winbreaks. Ann. Appl. Biol., 58:365-370.

Lewis, T. 1966b. Artificial windbreaks and the distribution of turnip mild yellows virus and *Scaptomyza apicalis* (Diptera) in a turnip crop. Ann. Appl. Biol., 58:371-376.

Lewis, T. 1967. The horizontal and vertical distribution of flying insects near artificial windbreaks. Ann. Appl. Biol., 60:23-31.

Lewis, T. 1969a. Factors affecting primary patterns of infestation. Ann. Appl. Biol., 63:315-344.

Lewis, T. 1969b. The distribution of flying insects near a low hedgerow. J. Appl. Ecol., 6:443-452.

Lewis, T. 1970. Patterns of distribution of insects near a windbreak of tall trees. Ann. Appl. Biol., 65:213-220.

Lewis, T. & G.C. Dibley. 1970. Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. Ann. Appl. Biol., 66:477-484.

Lewis, T. & J.W. Stephenson. 1966. The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Ann. Appl. Biol., 58:355-363.

Lloyd, M. 1967. 'Mean crowding'. J. Anim. Ecol., 36:1-30.

Martel, P. & M. Hudon. 1974. Les insects des cultures maraîchères dans le sud-ouest du Québec en 1973. Ann. Soc. Entomol. Qué., 19:110-112.

Martel, P., H.J. Svec & C.R. Harris. 1976. The life history of the carrot weevil, *Listronotus oregonensis* (Coleoptera: Curculionidae) under controlled conditions. Can. Entomol., 108:931-934.

Morisita, M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.), 2:215-235.

Morris, R.F. 1960. Sampling insect populations. Ann. Rev. Entomol., 5:243-264.

Myers, J.H. 1978. Selecting a measure of dispersion. Environ. Entomol., 7:619-621.

Neilson, C.L. & D.G. Finlayson. 1953. Notes on the biology of the tuber flea beetle, *Epitrix tuberis* Gentner (Coleoptera: Chrysomelidae), in the interior of British Columbia. Can. Entomol., 85:31-32.

Price, P.W. 1976. Colonization of crops by arthropods: non-equilibrium communities in soybean fields. Environ. Entomol., 5:605-611.

Price, P.W. & G.P. Waldbauer. 1975. Ecological aspects of pest management. *In*: Introduction to insect pest management (R.L. Metcalf & W.H. Luckmann, eds.), pp. 37-73. John Wiley & Sons, New york.

Rainey, R.C. 1951. Weather and the movement of locust swarms: a new hypothesis. Nature, 168:1057-1060.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleacera*). Ecol. Monogr., 43:95-124.

Ruesink, W.G. 1980. Introduction to sampling theory. *In*: Sampling methods in soybean entomology (M. Kogan & D.C. Herzog, eds.), pp. 61-78. Springer-Verlag, New York.

Ruesink, W.G. & M. Kogan. 1975. The qualitative basis of pest management: sampling and measuring. *In*: Introduction to insect pest management (R.L. Metcalf & W.H. Luckmann, eds.), pp. 309-351. John Wiley & Sons, New York.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., San Francisco.

Southwood, T.R.E. 1966. Ecological methods with special reference to the study of insect populations. Chapman and Hall, London.

Taylor, C.E. & C.G. Johnson. 1954. Wind direction and the infestation of bean fields by *Aphis fabae* Scop.. Ann. Appl. Biol., 41:107-116.

Taylor, L.R. 1961. Aggregation, variance and the mean. Nature, 189:732-735.

Taylor, L.R. 1984. Assessing and interpreting the spatial distributions of insect populations. Ann. Rev. Entomol., 29:321-357.

Taylor, L.R. & R.A.J. Taylor. 1977. Aggregation, migration and population mechanics. Nature, 265:415-421.

Taylor, R.A.J. 1978. The relationship between density and distance of dispersing insects. Ecol. Entomol., 3:63-70.

Taylor, R.A.J. 1980. A family of regression equations describing the density distribution of dispersing organisms. Nature, 286:53-55.

Vandermeer, J. 1981. Elementary mathematical ecology. John Wiley and Sons, New YorK.

van Emden, H.F. 1965. The effect of uncultivated land on the distribution of cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. J. Appl. Ecol., 2:171-196.

Vincent, C. & R.K. Stewart. 1983. Crucifer-feeding flea beetle dispersal and statistics of directional data. Environ. Entomol., 12:1380-1383.

Whitcomb, W.D. 1968. The carrot weevil in Massachusetts: biology and control. Mass. Agric. Exp. Stn. Bull. no. 550.

Wolfenbarger, D.O. 1940. Relative prevalence of potato flea beetle injuries in fields adjoining uncultivated areas. Ann. Entomol. Soc. Am., 33:391-394.

Wright, R.J., J.W. van Duyn & J.R. Bradley Jr. 1983. Dispersal, flight, and diurnal activity patterns of adult southern corn billbugs (Coleoptera: Curculionidae). Ann. Ent. Soc. Am., 76:572-581.