ECONOMIC INJURY LEVELS AND FEEDING STUDIES FOR THE POTATO FLEA BEETLE, *Epitrix cucumeris* (Harris), IN MANITOBA

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by

Stephen F. Pernal

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ECONOMIC INJURY LEVELS AND FEEDING STUDIES FOR THE POTATO FLEA BEETLE, *Epitrix cucumeris* (Harris), IN MANITOBA

BY

STEPHEN F. PERNAL

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

MASTER OF SCIENCE

Dedicated to my parents,

Nan Barton

and

Andrew Bolesław Pernal

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Major Professor: N. J. Holliday

ABSTRACT

In 1989 and 1990, cv. Russet Burbank potato plants were grown in cages in field plots, and densities of potato flea beetles, *Epitrix cucumeris* (Harris), and Colorado potato beetles, *Leptinotarsa decemlineata* (Say), were introduced in different multiples of naturally occurring field densities. Colorado potato beetles were introduced only in the early part of the growing season, but potato flea beetles were introduced for the duration of the season. Numbers of feeding punctures per leaflet were counted in the lower, middle, upper and upper non-terminal strata of plants. The yield of tubers was weighed, graded and examined for common scab, *Streptomyces scabies* (Thaxter).

Without early season injury by Colorado potato beetle, plants had no yield loss up to 290 flea beetles per plant; above this density, yield was inversely proportional to flea beetle density. The level of economic damage for these plants ranged between 0.43-1.87%, equivalent to a peak density of 300-335 flea beetles per plant. For plants which had sustained early season Colorado potato beetle injury, yield loss was linear and inversely proportional to flea beetle density over the entire response. For these plants, the level of economic damage ranged between 0.40-1.88%, equivalent to a peak density of only 4-19 potato flea beetles per plant.

Behavioral models were used to describe the spatial and temporal switching pattern of flea beetle feeding. Beetles changed their preferred site of feeding from lower parts of the plant to upper regions as the growing season progressed. High densities of flea beetles had an inhibitory effect on the amount of defoliation caused per individual, and this may alter the pattern of feeding preference by causing beetles to disperse more evenly throughout the plant. A population model was also derived which established a relationship between feeding punctures per leaflet and average potato flea beetle weeks. This relationship enables the estimation of flea beetle numbers per plant, but is very sensitive to the accuracy of feeding puncture counts.

Very few tubers exhibited signs of common scab disease, but there was a positive correlation between number of feeding punctures and numbers of immature potato flea beetles. The absence of scab disease suggests that its incidence is less affected by flea beetle densities, than by abiotic factors such as soil moisture, and varietal differences in susceptibility.

A preliminary examination of feeding by *Melanoplus bivittatus* (Say) and *Melanoplus sanguinipes* (Fabricius) on potato plants showed no significant yield response to occur at varying densities of these species.

CHAPTER I

INTRODUCTION

The potato plant, *Solanum tuberosum* L., is one of about 2,000 species in the family Solanaceae. There are 160 wild and 20 cultivated species of tuber-bearing Solanaceae, all of New World origin (Burton 1989). Such plants as tomato, tobacco, eggplant, pepper, bittersweet, horse nettle, ground cherry and petunia are also placed in this family. The closest wild relative of *S. tuberosum* is *Solanum andigenum* Juz. & Buk., which is indigenous to the Andes Mountains (Thornton and Sieczka 1980). There are over 170 different cultivars of *S. tuberosum* available in North America. The most widely grown, Russet Burbank, is a late maturing variety which requires a 140-150 day growing season. Average yield for Russet Burbank is 18-27 t/ha in Manitoba (B. Geisal, pers. comm.), but may exceed 65 t/ha in the Canadian Maritimes (Campbell et al. 1984). Plants of this cultivar have long leaflets, white blossoms and vigorous growth. The large cylindrical tubers are characterized by having shallow eyes, white flesh and russetted skin. The variety is resistant to common scab, but is susceptible to Fusarium wilt, Verticillium wilt, leafroll and virus Y (Campbell et al. 1984). Russet Burbank plants require uniform soil moisture and nitrogen, otherwise knobby tubers result.

The economic importance of potatoes to Canada is great. Agriculture Canada (1990) statistics indicate that gross revenue paid to potato producers was over 400 million dollars in 1990. Manitoba is a leading potato grower, having over 19,000 ha of land sown in 1990; this area of potatoes was exceeded only in New Brunswick and Prince Edward Island.

Manitoba stands fifth in total production, with 352,000 t of potatoes being grown in 1990, equivalent to 12% of all Canadian production.

The potato flea beetle, *Epitrix cucumeris* (Harris) is an important pest of potatoes. Unlike the tuber flea beetle, *Epitrix tuberis* Gentner (Gentner 1944), injury to tubers by the subterranean larvae of *E. cucumeris* is rare. Adult potato flea beetles injure plants by chewing small round holes in leaflets. The timing of such defoliation is important because, if it occurs during the tuber bulking phase of plant growth, yield may be considerably compromised (Cranshaw and Radcliffe 1980; Shields and Wyman 1984). In Prince Edward Island, significant yield losses due to this pest have been documented in several different potato cultivars (Thompson 1984, 1985, 1987). In Manitoba, insecticides are applied when high densities of the insect are present in late summer (Senanayake 1987), but little is known about what levels are actually economically injurious to the crop.

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) originated in Mexico, where it fed on native host plants such as buffalobur, *Solanum rostratum* Dunal (Neck 1983). *Solanum tuberosum* was included in its host range about 150 years ago, and late in the 19th century it was first reported to be a pest of potatoes (Edgerton 1861, cited by Casagrande 1987). The pest rapidly became the most destructive insect pest of potatoes in North America (Hare 1990). During World War I Colorado potato beetle was inadvertently introduced into western Europe, where it is now well established, except in the British Isles. It continues to extend its geographic range southward and eastward throughout

Europe and Asia (Hurst 1975).

Populations of larval and adult Colorado potato beetles, if uncontrolled, can easily completely defoliate field crops of potatoes in Manitoba (Senanayake 1987). If plants are attacked during specific stages in the growth cycle, yield may be totally lost (Hare 1980). Colorado potato beetle was one of the first targets of large-scale insecticide use in field crops (Hare 1990). The insect is still adapting to new geographic areas (Hsiao 1978), and resistance to a wide range of insecticides has developed in some populations (Forgash 1981). As a consequence of effective insecticidal control earlier this century, research on ecological relationships between this pest and environmental factors, host plants and natural enemies was reduced (Hare 1990). Recently, much emphasis has been placed on the need to implement integrated pest management strategies to control Colorado potato beetle, as the pesticide race appears to be a losing battle.

The causal organism of common scab disease of potatoes is *Streptomyces scabies* (Thaxter) Waksman & Henrici (syn. *Actinomyces scabies* (Thaxter) Gussow). This is a widespread soilborne disease that can infect fleshy roots and underground stems of several crops and weeds (Rich 1983). Common scab produces no above ground symptoms on potato crops, and has little or no effect on yield, but has a tremendous effect on the marketability of the crop. Common scab occurs in Africa, Asia, Australia, Europe and North and South America (Rich 1983).

Tubers infected with common scab have brown, roughened, irregularly shaped areas that may be raised or sunken and can cover the entire surface of the tuber. The type and severity of symptoms exhibited in this disease are influenced by the strain of the organism and the variety of potato affected (Hooker 1981). Most scab damage on potato tubers can be removed during processing, but market value of table stock is severely diminished.

Very little published information is available concerning *E. cucumeris*. Although this insect is a potential source of yield reduction in commercial potato production, very little work has been done to determine what levels of this insect are economically injurious, or how it interacts with other potato pests. The objectives of this study were:

1. To estimate an economic injury level for *E. cucumeris* on cv. Russet Burbank potatoes and examine how such an injury level is affected by early season defoliation by *L. decemlineata*.

2. To examine the spatial and temporal patterns of accumulation of feeding punctures by potato flea beetle on cv. Russet Burbank potatoes, and determine if feeding punctures can be used as an index of actual population numbers of this insect.

3. To determine whether the density of potato flea beetles per plant has an effect on the incidence or severity of common scab on cv. Russet Burbank tubers.

A fourth objective was addressed during the summer of 1990, which was not part of the main objectives of this thesis. During that time, a surplus of caged potato plants and the presence of large numbers of grasshoppers prompted a study to be undertaken with little preplanning. The objective of this study was to determine whether the grasshoppers *Melanoplus bivittatus* (Say) and *Melanoplus sanguinipes* (Fabricius) feed on potato plants, and if so, whether any relationship exists between pest density and yield.

This thesis is written in a paper style. Chapter II is a review of pertinent literature. The methods of research, results and discussion are presented in Chapter III as three papers and a scientific note, written in a form suitable for publication. Part 1 of Chapter III will be combined with data from Senanayake (1987) for preparation of a manuscript to be submitted to the Journal of Economic Entomology. Part 2 of Chapter III will be submitted to the same journal. Chapter IV contains an overall discussion of the research in this thesis.

CHAPTER II

LITERATURE REVIEW

The Potato Plant

Morphology

A thorough description of the morphology and vasculature of the potato plant is given by Artschwager (1918) and McCauley and Evert (1988). The morphology of the basal leaves of the main potato shoot is variable, ranging from simple to pinnate compound in arrangement. The upper leaves are generally more uniform; they are odd pinnate with three major pairs of lateral leaflets and a number of folioles. The primary vascular system of this dicotyledonous plant consists of three large and three small bundles. The three large bundles are highly interconnected through a repeated series of branchings and arch-producing mergers. Each of the small bundles in the stem is a median leaf trace which extends three internodes before diverging into a leaf. Potato leaflet margins are lined toward the abaxial side by short, simple tooth-like trichomes. In addition to marginal trichomes, two other types of trichomes are found on leaves: glandular hairs with knob-like secretary swellings at the tips of short, uniserate stalks; and simple uniserate, multicellular hairs of varying lengths. Trichomes occur on both sides of leaflets, although many more are on the abaxial side. Adaxial trichomes are found mainly on the ribs, whereas abaxial trichomes occur on the ribs and scattered across the leaf surface.

Ivins and Milthorpe (1963) and Thornton and Sieczka (1980) provide a complete description of tuber structure. Potato tubers are simply enlarged portions of underground stems called stolons or rhizomes. The stolons closely resemble the above ground stems in having leaf scales located alternately on their surface. Tubers originate from stolon tips or along the stolon itself, and have characteristics of normal stems including dormant true buds (eyes) and leaf scars (eyebrows). Lenticels are conspicuous on most tubers and are similar to stem pores which allow air penetration deep into the stem interior. The single layer of cells on the surface of a potato tuber is called the epidermis. The red and blue pigment of some potato skins, anthocyanin, is often located in the periderm, which consists of several layers of corky cells immediately below the epidermis. The skin of a mature tuber is comprised of the hardened, corky periderm after the epidermis has been sloughed off. In a few varieties, the anthocyanin is located in the outer layers of the cortex, the region inside the periderm that extends inwardly to the vascular ring. The fleshy portion of the tuber is called the medullary area and is divided into outer and inner regions. The outer medulla is relatively dense, while the inner medulla is watery and translucent. The inner medulla extends towards each eye, so forming a continuous tissue network among all eyes of the tuber.

Buds are located on the exterior of a potato tuber, and are arranged in a spiral fashion. They are concentrated at the seed end, which is the portion of the tuber furthest away from the stem. Apical dominance is a characteristic in which the eyes of the seed end are the first to sprout. When whole tubers are planted, the effect of apical dominance is important as only one to three large, productive stems per hill usually emerge. The effect of apical dominance is lessened when tubers are cut into seed pieces, but differences between stem-end and seed-end sprouts still exist.

Propagation and Growth

Ewing (1981) discusses several factors concerning potato plant propagation. Reproduction in the potato plant is clonal in nature. The plant is notoriously heterozygous not only because of its asexual reproduction, but also because it is tetraploid. As a consequence of asexual propagation, bacterial, fungal, and viral diseases and the potato cyst nematode are readily spread from generation to generation through the tubers. Disease transmission by seed tubers still remains a problem in potato production. The North American practice of cutting seed tubers can lead to the dissemination of disease from infected to healthy tubers. Furthermore, cut tuber pieces are more susceptible to infection by soil-borne pathogens.

The initiation of tubers at stolon tips usually occurs when plants are 15-24 cm high or 5-7 weeks after planting (Thornton and Sieczka 1980). Tuber initiation is controlled by a tuberization stimulus (Gregory 1956), which is assumed to be a chemical substance. Formation of the stimulus is favoured by photoperiods shorter than a genetically determined critical photoperiod and by cool temperatures (Epstein 1971). In contrast to a commonly accepted notion, tuberization is independent of flowering. As Ewing (1981) states, the chemical nature of the stimulus is unknown, but it is suspected that the ratio of cytokinin(s) to gibberellin(s) affects the stimulus. However, other researchers feel that the stimulus is not cytokinin-like (Jameson et al. 1985). Upon receiving the tuberization stimulus the main shoot ceases development, leaves enlarge and form wide angles with the stem, internodes become short, stems thicken and aboveground axillary branching is suppressed. Below the soil, the stimulus restricts root growth and causes tubers to form on very short stolons. Very high ratios of tuber to total plant weight result in association with high levels of tuberization stimulus (Ewing 1981).

Growth of *S. tuberosum* and the yield of plants are affected by many environmental factors. The greatest single abiotic factor affecting the yield of potato plants is water stress (Burton 1981). For a high quality yield, an adequate water supply is necessary from tuber initiation until near maturity (Epstein and Grant 1973). Yield reduction due to water stress is attributable to reduced leaf area and reduced photosynthesis per unit leaf area (van Loon 1981). Water stress during maximum foliage growth, between emergence and tuber bulking, leads to a decrease in foliage weight and reduces the elongation of stems, leaves and roots (Gandar and Tanner 1976; Hang and Miller 1986).

Potato Flea Beetle

Description and Life History

The eggs of *E. cucumeris* are elliptical and white when first laid, and turn greyish when older. They are deposited in shaded moist soil near a host plant, at depths up to 2.5 cm. Length of eggs may vary from 0.44 to 0.50 mm and width may vary between 0.19 to 0.21 mm (Jewett 1929). The average egg incubation period in Manitoba is 5 days (Cole 1951).

The larval potato flea beetle, as described by Jewett (1929), is less than 1 mm long at hatching and, after four larval instars, reaches 3.5 to

4.5 mm in length. The larvae are thread-like in appearance, have three pairs of short thoracic legs and a pair of pro-legs on the last abdominal segment. The larva is mainly white; the head is light brown, with reddish mouthparts, and the thoracic and anal shields are faintly brown. Larvae have subtriangular mandibles with four blunt teeth, and short subcylindrical antennae (Johannsen 1913). The abdomen has nine segments, and on each segment are approximately 24 setae. Larvae feed on the roots, tubers and below ground portions of stalks of potato plants (Jewett 1929). After feeding has ceased, larvae become shorter and thicker, and then enter a quiescent prepupal stage (Cole 1951). In Manitoba, the average larval period lasts 24 days, which is then followed by a 7 day prepupal period; after this time, larvae construct earthen cells in which to pupate (Cole 1951).

Epitrix cucumeris pupae are white when newly formed, but darken as they mature. The abdomen is bifurcate, with slender incurved forks, and a transverse line of setae on the last segment (Johannsen 1913). Pupae can be found in soil around potato plants at depths of 1.25 to 7.5 cm (Jewett 1929). Potato flea beetles, in Manitoba, have a pupal stage that lasts an average of 10 days (Cole 1951).

Adult potato flea beetles are ovate, and 1.15 - 2 mm long. They are shiny black with antennae and legs of reddish-yellow, except that the enlarged hind femora are black (Jewett 1929). The surface of the elytra is finely and sparsely punctured and is covered in fine setae giving it a pubescent appearance. In Manitoba, overwintered adults begin collecting on potato plants in late May or early June (Senanayake 1987). The adult beetles characteristically jump, but do not fly when disturbed (Cannon 1949); however, potato flea beetle flight has been observed in the laboratory (Cole 1951). The summer generation of adults typically may be found on plants during late July in Manitoba, and continue to feed until the weather becomes cold or the food source diminishes (Senanayake 1987). In the fall after heavy frosts, *E. cucumeris* adults collect under litter or vines in fields and field margins. The insects then enter the soil to overwinter (Anderson and Walker 1936). Development from egg to adult in Manitoba requires approximately 46 days (Cole 1951), and in eastern Canada requires 28-42 days to complete (Hodgson et al. 1977).

Geographical Distribution and Host Plants

The potato flea beetle is found in all Canadian provinces except British Columbia (Hodgson et al. 1977). This species can also be collected as far south as Florida and, at the time of the revision of this genus, extended as far west as North Dakota, South Dakota and Kansas in the United States (Gentner 1944). Prior to this revision, many reports had been published of *E. cucumeris* being found in the western United States. However, it is likely that these were erroneously identified specimens of another species, the tuber flea beetle, *E. tuberis*. In general, the tuber flea beetle is confined to the west of the Rocky Mountains, nonetheless, specimens of *E. tuberis* have been collected in Alberta and Saskatchewan (Kelleher 1983). This suggests that an overlap in the distribution of *E. cucumeris* and *E. tuberis* could also exist in Manitoba, however there are no recorded specimens of *E. tuberis* in Manitoba (Cole 1951), nor have any been found in my identifications of

Epitrix spp.

Johannsen (1913) lists a range of plants as possible hosts for the potato flea beetle. The insect prefers to feed on members of the Solanaceae or nightshade family, including the potato (*Solanum tuberosum* L.), wonder berry (*S. nigrum var.* L.), bittersweet (*S. dulcamara* L.), Jerusalem cherry (*S. pseudo-capsicum* L.), horse nettle (*S. carolinense* L.), black or common night shade (*S. nigrum* L.), eggplant (*S. melogena* L.), tomato (*Lycopersicum esculentum* Mill.), Cayenne pepper (*Capiscum frutescens* L.), ground cherry (*Physalis pubescencs* L.), petunia (*Petunia axillaris* BSP.), tobacco (*Nicotiana tobacum* L.) and jimsonweed (*Daturia stramonium* L.). The wonder berry is noted as being the preferred host for the pest (Johannsen 1913).

Phenology

Two studies of potato flea beetle phenology have been completed in Manitoba: those by Cole (1951) and Senanayake (1987). These indicate that *E. cucumeris* undergoes one generation per year. Overwintered adults emerge in late May and move directly, or from an alternate host, onto emerged potato plants. These adults remain in low numbers from mid-June to mid-July, during which time they feed and mate and females oviposit in the soil. By mid- to late July, these adults die and the new generation of flea beetles has sufficiently developed to start emerging from the soil. The population of new beetles builds rapidly, and a large sustained population is established on the crop in early August. Numbers sharply decline towards the end of the August. Beetles feed until cold weather arrives in September or the food supply diminishes, at which time they move to overwintering sites in litter or soil.

Feeding Injury and Related Host Effects

Injury to potato plants by *E. cucumeris* is primarily done during the adult stage. The adult is a foliage feeder which chews small round holes in leaflets of potato plants (Johannsen 1913; Jewett 1929; Anderson and Walker 1936; Wolfenbarger 1940; Cannon 1949; Pond et al. 1970; Hodgson et al. 1977; Thompson 1987). The appearance of potato leaflets which are defoliated by potato flea beetle is that of being, "peppered with fine shot" (Cannon 1949). Feeding produces round scars 0.1 - 5 mm in diameter, which may or may not penetrate the entire thickness of the leaf (Senanayake 1987). Ladd (1963) performed precise measurements on feeding holes and determined the mean feeding hole diameter to be 0.9846 mm and the area of the standard hole to be 0.7612 mm^2. Typically, the area surrounding the feeding puncture desiccates and turns brown. Amalgamations of punctures on a leaflet may cause severe desiccation and leaflet death. If extensive defoliation by overwintered adults occurs in the early summer, growth of the young potato plant may be retarded (Jewett 1929). However, in Manitoba, this does not normally occur because early season control measures against Colorado potato beetles also kill potato flea beetles. Heavy defoliation by the new generation of *E. cucumeris* in late summer, in addition to causing potential yield loss, may lead to premature senescence (Thompson 1987). On Norland potatoes in Manitoba, late season defoliation caused economic yield reduction only when there were more than 65 feeding punctures per lower leaflet (Senanayake 1987).

Larvae of *E. cucumeris* usually feed on rootlets, but occasionally they may bore tunnels into tubers (Anderson and Walker 1936; Hodgson et al. 1977; Thompson 1987). These tunnels seldom extend beyond 6 mm into the tuber and can generally be removed by processing (Thompson 1987). Small raised bumps and worm trails on the surface of the tuber may also occur. Tunnels often are filled with corky, sliver-like structures with a pimple or depression on the outside (Cannon 1949). In severe instances, the whole outer surface of the tuber can be covered with pimples or depressions. Larval feeding injury rarely occurs in Manitoba.

Potato flea beetles may aid in the dissemination of several potato diseases. Tubers damaged by larval feeding may be infected with a pathogen such as common scab (*Streptomyces spp.*). Senanayake (1987) found an increase in the frequency and severity of common scab infection with increasing densities of potato flea beetles on plants. Mechanical transmission of bacterial diseases, spindle tuber viroid and early blight can occur directly by adult feeding (Hodgson et al. 1977; Thompson 1987). Preliminary studies have also shown that adult beetles may carry aggressive plant pathogens (*Fusarium* spp. and *Verticillium* spp.) as they emerge from the soil, and that infection of plants by these and other disease agents may be enhanced by their feeding (Thompson 1987).

Most Canadian investigations of yield loss in potatoes, due to potato flea beetles, have been conducted in the Maritimes. Thompson (1987) reported that from 1983-86, significant yield losses occurred in all years with the cv. Superior and in three out of the four years with cv. Russet Burbank. On average over this four year period, there was a loss of 19% for Superior and 14% for Russet Burbank exposed to normal field densities of potato flea beetle, with all other insect pests controlled. Similar research, involving plots of sprayed and unsprayed potatoes, showed significant differences in yield for such varieties as Russet Burbank, Kennebek, Superior, Pontiac, Shepody and Sebago. In these tests, reductions in yield caused by potato flea beetles ranged from 6% to 32% (Thompson 1984, 1985). Anderson and Walker (1936) found reductions in yield up to 25% in eastern Virginia during severe outbreaks of the pest. In Manitoba, Senanayake (1987) determined that normal field densities of potato flea beetle were not sufficient to cause significant yield reduction in cv. Norland potatoes.

Management and Control

The control of potato flea beetle by chemical compounds began early this century. Currently, many insecticides are registered against *E. cucumeris*, but the timing of insecticide applications is crucial for maximum effectiveness. Early season injury by the overwintering generation is usually controlled by applications of insecticide against Colorado potato beetle. In Manitoba, a foliar application of insecticide (carbofuran, endosulfan or deltamethrin) is sometimes made in late July to suppress the new generation of potato flea beetles. However, since new flea beetles are continually emerging from pupation, a single application of insecticide may have little influence on peak population densities (Senanayake 1987). Most tuber growth in a late maturing potato variety like Russet Burbank starts in early August; hence, early season defoliation by potato flea beetles may have little effect on yield, but mid- to late season defoliation can cause significant loss, unless the insects are controlled (Thompson 1987).

Decisions concerning the application of insecticide against potato flea beetles in Prince Edward Island have been based on the total number of holes on the fourth terminal leaflet down from the apex of the plant. If the number of holes exceeds 15, control has been warranted. This threshold is now being reexamined, as the number of holes per leaflet is known to be extremely variable from year to year (Thompson 1987). In Manitoba, Senanayake (1987) determined that on cv. Norland, at two weeks past first bloom, the economic injury level is 65-75 holes per lower terminal leaflet.

Little research has been done to develop effective biological controls against potato flea beetle. Parasitoids (Hymenoptera: Braconidae) have been recorded from *E. cucumeris* (Chittenden 1899; Forbes 1900, both cited by Johannsen 1913), but no studies since this time have reported their occurrence. Cultural practices can reduce the severity of potato flea beetle outbreaks. Uncultivated areas adjoining fields cropped in potatoes provide favourable conditions for flea beetles to accumulate and feed during periods in which the crop has not yet emerged from the soil (Wolfenbarger 1940). Then, potato flea beetle adults move from uncultivated areas to growing crops. Proper sanitation of weeds and volunteer alternate hosts of this pest eliminates possible overwintering shelter or early spring food sources.

Colorado Potato Beetle

The Colorado potato beetle, *L. decemlineata*, is a very well studied insect and consequently has a large quantity of literature associated with it. In the following section of this chapter, a brief review of the relevant literature, with respect to the overall objectives of this thesis, is provided. The reader is directed to the general reviews by Ferro and Voss (1985) and Hare (1990) for further information about this pest.

Life History

The adults of Colorado potato beetle overwinter in the soil. They may be found at depths up to 43 cm in loose soil, but are much nearer the surface in compacted soils (Gibson et al. 1925). Typically, the overwintering site is near the base of the previous year's host plant. Adults emerge in spring and disperse by walking or flying. In Manitoba this activity occurs in late May or early June. After 5-10 days, females oviposit masses containing 20-60 eggs on the lower surfaces of leaves; total fecundity can exceed 4000 eggs per female (Brown et al. 1980). Adults mate often and females may mate before and/or after entering diapause (Tauber et al. 1988a).

All eggs within an egg mass hatch simultaneously and larval feeding then begins (Hare 1990). The larvae pass through four instars in 10-20 days and like the adults, feed on the leaves. The larval feeding is generally continuous with the larvae remaining near the top of the plant (Gibson et al. 1925). First instars are responsible for 3% of the total leaf consumption, second instars 5%, third instars 15% and fourth instars 77% (Tamaki and Butt 1978; Ferro et al. 1985; Logan et al. 1985). After the fourth instar larvae have finished feeding, each burrows into the soil and pupates near the base of the plant. About 10 days later, the adults emerge from the soil, walk to a host and feed (Hare 1990). In Canada, adults that have emerged from pupation may feed and then enter overwintering diapause, or, in mild climates, may give rise to a second generation (Gibson et al. 1925). Factors inducing diapause are poor host plant condition, low temperatures and short photoperiod (Tauber et al. 1988b).

The host range of Colorado potato beetle is fairly narrow and is confined to 20 species of the Solanaceae family (Hsiao 1988). The principal host of the insect is the cultivated potato (*S. tuberosum*), but others suitable hosts include the beetle's original host plants, buffalobur (*S. rostratum*) and *S. angustifolium* Lam.

Management and Control

On a world-wide basis, the Colorado potato beetle is the most devastating defoliator of potato plants. Without control these insects can completely defoliate potato plants prior to tuber initiation, thereby causing total yield loss (Hare 1990). Numerous studies have developed sampling procedures (Martel et al. 1986; Wright et al. 1987; Senanayake and Holliday 1988) and injury levels (Zehnder 1986; Hare and Moore 1988; Wright et al. 1987; Senanayake and Holliday 1990; Mailloux et al. 1991) for the insect, but no single scheme is suitable for all regions. Most treatment guidelines limit defoliation to 10-25% during the period after first bloom, while higher levels of the pest are tolerated in the latter part of the growing season (Shields and Wyman 1984; Hare 1987). Simple predictive models for Colorado potato beetle populations in commercial potato fields have also been developed (Logan 1981).

Most control of Colorado potato beetle is achieved through the use of chemical insecticides. Granular systemic insecticides can be used at planting and have the added advantage of providing control from emergence to mid-season. However, they are expensive, must be applied before insect populations are assessed and may leave residues. Foliar insecticides are cheaper, less persistent and may be applied as spot treatments to areas of high beetle density. In Manitoba, control of the Colorado potato beetle is achieved through the use of foliar insecticide sprays, which are usually applied aerially or by ground equipment. An application is usually made in early July against early larval instars of the developing summer generation. This single application of insecticide is usually sufficient to control the pest, but if injurious levels of the pest reoccur, a subsequent spray may be applied in mid- to late July.

Case histories of insecticide use support the hypothesis that application of insecticides on a calendar-based spray schedule have lead to the development of pesticide resistance; many areas of the eastern United States presently have populations of Colorado potato beetles resistant to most currently registered insecticides (Forgash 1981). Resistance has not yet developed to synthetic pyrethroids in Manitoba, and many registered, effective insecticides exist. For further information about the management and control of Colorado potato beetle by chemical and non-chemical means, the reader is referred to the review by Casagrande (1987).

Common Scab Disease

Pathogenic Agent

The causal organism of common scab disease, *Streptomyces scabies*, is described by Hooker (1981). Streptomycetes are considered to be more closely related to bacteria than fungi because they are akaryotic and have cell wall characteristics more closely resembling bacteria. These organisms do resemble fungi in their filamentous morphology, but have notably smaller vegetative filaments. *Streptomyces scabies* has barrel shaped conidia 0.8-1.7 μm x 0.5-0.8 μm in size. Conidiophores of this pathogen are branched, septate and have long spirally coiled terminal branches. The organism is aerobic, produces colourless vegetative filaments and has pale grey aerial mycelia. Light reflection for *S. scabies* colonies is different from that of most bacteria because of the radiating filaments that are produced. Optimal temperature for culture development is 20-25° C with a range between 5-40° C.

Symtomology

As described by Rich (1983), *S. scabies* usually produces circular tuber lesions. Most are 5-8 mm in diameter and may coalesce, to produce a russetted appearance. Affected parts of the tuber may contain a superficial corklike layer (russet scab), an erumpent or cushion-like scab 1-2 mm high (raised scab), or may extend into the tuber itself (pitted scab) (Hooker 1981). Infected areas originate at the lenticels as elongate lens-shapes lesions; the tissue beneath them becomes a translucent straw-like colour.

Epidemiology and Vectoring

The pathogen survives in the soil and is primarily spread from one locale to another by the planting of infected tubers. Dissemination by infested soil is also possible when carried by water, by wind or mechanically (Rich 1983). *Streptomyces scabies* is predominantly found in soils with a pH range of 5.5 to 7.5 and is generally not a problem at soil pH's between 5.0 and 5.3 (Rich 1983). Continuous cropping of potatoes greatly increases the severity of common scab. Crop sequence has a marked effect on the presence or absence of scab (Rouatt and Atkinson 1950).

Several organisms have been evaluated as possible vectors of *S. scabies*. Tamaki et al. (1976) revealed that the scab gnat, *Pnyxia scabiei* (Hopkins), was not the causative agent of deep-pitted scab but, fed on the dead and infected tissue of scabby tubers. Various *Streptomyces* spp. have been isolated from the bodies of Collembola and mites and these have been implicated as vectors (Storch et al. 1978; Manzer et al. 1984). Infection of the disease occurs in young tubers through stomata or lenticels (Hooker 1981) and tubers are most susceptible when stomata are developing into lenticels (Lapwood and Adams 1973).

Other hosts of *S. scabies* include the fleshy roots of red beets, sugar beets, rutabaga, turnip, carrot, radish and parsnip (Hooker 1981).

Control

The most effective procedure to use in controlling the incidence and severity of common scab disease of potatoes is to plant resistant varieties and use non-scabby seed. The most resistant cultivars are those which are russet-skinned. Some of these include Early Gem, Russet

Burbank, Russet Sebago and Russet Rural. A complete listing of the many scab resistant cultivars available is provided in Rich (1983).

Many chemical controls have been developed to combat common scab disease. In the early 1970's, the only effective soil incorporated pesticide for this purpose was quintozene (McIntosh 1973). Other soil incorporated fungicides are effective against common scab as well. These include captafol - a phthalimide, 4-tert-butyl catechol, as well as unsubstituted and phenyl-, chloro-, 2,5 and 2,6 dichloroquinone compounds (McIntosh 1973, 1976). Ethione foliar sprays can also be successfully used against the disease; they are systemic fungicides, which move in phloem (McIntosh and Burrell 1980; Burrell 1981). In the early 1980's foliar sprays of 3,5 dichlorophenoxyacetic acid (3,5-D) were developed, which decrease scab incidence by 90%, however, a slight reduction in yield, an increase in the number of tubers set and some tuber deformity also result from their use (McIntosh et al. 1981). Subsequently developed pesticides have included 2,5 dichlorobenzoic acid, which has few undesirable side effects on plant yield (McIntosh et al. 1985, 1988).

Inorganic constituents of soil also have an effect on the expression of scab disease. Low soil pH, between 5.0 and 5.3 is enough to suppress *S. scabies* altogether (Rich 1983). The levels of calcium and phosphate in potato tubers also affect scab development. High levels of tuber calcium make periderm cells more susceptible to infection, but the application of phosphate, by neutralizing calcium ions, reduces scab severity (Davis et al. 1976). Organic manuring of potato fields to reduce scab infection has also been attempted. Manganese is reduced into a soluble form, which is toxic to *S. scabies*, after applications of green manure (Rogers 1969). Davis et al. (1976) also found a negative correlation between common scab severity and the amount of manganese in the soil.

Literature concerning soil moisture and its effect on common scab development indicates that the disease thrives in conditions of low soil moisture (Sanford 1923; Wellings and Rosser 1968; Lapwood et al. 1970, 1971, 1973; Lewis 1970; Lapwood 1972; Lapwood and Adams 1973, 1975; Davis et al. 1976; Adams and Lapwood 1978). Wellings and Rosser (1968) suggested that moist soil conditions for 2-3 weeks after the crop had achieved 20% ground cover could give significant scab control. Even brief periods of rainfall during an otherwise dry growing season can temporarily halt scab development (Lapwood and Adams 1973). This streptomycete infects young internodes on actively growing tubers when soils are dry (Lapwood et al. 1970). The pattern of infection is commercially important as the first 4 or 5 internodes formed expand more than those formed later, thereby causing greater scab blemishing. Potato tubers grown in soils with high moisture have greater populations of bacteria than actinomycetes on their lenticels. The reverse is true in dry soil conditions. Hence, it has been suggested that irrigation may diminish the populations of *S. scabies* in tuber lenticels by increasing the populations of antagonistic bacteria (Lewis 1970). It is not known whether these bacteria halt scab growth by competition or antibiosis (Adams and Lapwod 1978).

Grasshopper Feeding on Potatoes

The twostriped grasshopper, *Melanoplus bivittatus* (Say), and the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), are widespread and destructive pests of crops in the Canadian prairies (Smith and Holmes 1977; Hardman and Smoliak 1980). These insects are univoltine and feed on both grassy and broadleaved plants (Philip and Mengersen 1989). Although they are generalist feeders, *M. bivittatus* and *M. sanguinipes* are only considered to be potential potato pests during hot dry summers when numbers reach outbreak levels (Cole 1951; Hodgson et al. 1977; University of California 1986). There are very few, if any, published records recording grasshopper defoliation of potato crops, nor have any studies quantified yield loss in potatoes caused by these insects. Hence, research is needed to determine the potential detrimental effects of these species on potato crops.

Although the quantity of literature concerning these grasshopper species is large, it will not be further reviewed because of its lack of pertinence to the primary objectives of this thesis.

CHAPTER III

PART 1

Economic injury levels for the potato flea beetle, *Epitrix cucumeris* (Harris), on cv. Russet Burbank potatoes in Manitoba

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Abstract

In 1989 and 1990, cv. Russet Burbank potato plants were grown in cages in field plots, and potato flea beetles, *Epitrix cucumeris* (Harris), and Colorado potato beetles, *Leptinotarsa decemlineata* (Say), were introduced in different multiples of naturally occurring densities. Colorado potato beetles were introduced only in the early part of the growing season, but potato flea beetles were introduced for the duration of the season. In 1989, severe aphid infestations confused results, but plant yield was still found to be negatively correlated with flea beetle density. In 1990, without early season injury by Colorado potato beetle, plants had no yield loss up to 290 flea beetles per plant; above this density, yield was inversely proportional to flea beetle density. Based on current economic conditions, the level of economic damage for these plants ranged between 0.43-1.87%, equivalent to a peak density of 300-335 flea beetles per plant. For plants which sustained early season Colorado potato beetle injury, yield reduction was linear and inversely proportional to flea beetle density over the entire response. For these plants, the level of economic damage ranged between 0.40-1.88%, equivalent to a peak density of 4-19 potato flea beetles per plant.

The economic injury level for plants without Colorado potato beetle defoliation is best suited for use in the centre of commercial potato fields where densities of this pest are very low. The injury level for plants that sustained Colorado potato beetle defoliation should be used near field margins where relatively high numbers of the insect exist in early season. The economic injury levels are preliminary, but suggest

that, in most years, the only necessary insecticide applications for potato flea beetles in Manitoba are those along field margins.

Introduction

The potato flea beetle, *Epitrix cucumeris* (Harris), is a common pest of potatoes in Manitoba. This insect undergoes one generation per year (Senanayake 1987), and adults overwinter under litter or vines, or in the soil (Anderson and Walker 1936). Adults are the most injurious stage; they chew small round holes in the leaflets of potato plants (Thompson 1987). This feeding produces noticeable scars which sometimes penetrate the entire thickness of the leaf. Larvae feed mainly on the fine rootlets of plants; they may occasionally attack tubers, but the damage they cause is slight and is easily removed by peeling (Thompson 1987).

In Manitoba, overwintered adult Colorado potato beetles, *Leptinotarsa decemlineata* (Say), and potato flea beetle adults move onto newly emerged potato crops in mid- to late June (Senanayake and Holliday 1989). Here both species feed, mate and oviposit; eggs of Colorado potato beetle are laid on the underside of leaflets and those of potato flea beetle are laid in the soil. Populations of Colorado potato beetle larvae increase until the second week of July, when they are usually controlled by an insecticide spray. A single insecticide application is usually sufficient to reduce densities of Colorado potato beetle below economically injurious levels for the remainder of the growing season (Senanayake and Holliday 1990). Overwintered potato flea beetle adults remain on potato plants in low densities until first bloom, at which time the summer generation of adults starts to emerge from pupal cells in the soil. The population peak of new potato flea beetles occurs in early August and densities subsequently decline to zero by mid-September (Senanayake and Holliday 1989). In Manitoba, an application of insecticide against potato flea beetles is occasionally made in late July; however, it often reduces the August population peak only slightly, owing to the continual emergence of new adults (Senanayake 1987). Hence, potato crops in Manitoba face a regime of early season defoliation by Colorado potato beetle and late season defoliation by potato flea beetle.

There has been little research on the effect of potato flea beetles on the yield of cv. Russet Burbank potatoes. In Prince Edward Island, normal field densities of potato flea beetle can reduce yield of Russet Burbank plants by up to 15%, but economic injury levels have not been determined (Thompson 1984, 1985, 1987). In Manitoba, the economic injury level on cv. Norland is a peak density of 89 adult potato flea beetles per plant; this density reduces yield by 2.5% (Senanayake 1987). An economic injury level for crops suffering early season defoliation by Colorado potato beetle and late season defoliation by potato flea beetle would provide the best control decisions for commercial potato production. Therefore, the purpose of this study was to estimate an economic injury level for *E. cucumeris* on cv. Russet Burbank potatoes and examine how such an injury level is affected by early season defoliation by *L. decemlineata*.

Materials and Methods

1989

Design of Plots. In 1989, three plots of cv. Russet Burbank potatoes were planted using 50 g seed pieces. Immediately before planting, seed pieces were hand-cut from certified seed tubers, with all cutting utensils being disinfected in a 0.06% solution of quaternary ammonium compounds (HY-X®). All plots received 397 kg/ha of blended granular fertilizer (22.6/N; 14.1/P; 14.1/K; 2.8/S): if plots were machine-planted, fertilizer was banded; if plots were manually planted, an equivalent amount of fertilizer was applied beneath and around seed pieces.

One plot was located at the University of Manitoba Plant Science Research Farm in Portage la Prairie, Manitoba. This plot, known as the "Portage plot", was machine-planted on 27 May. It was 50 X 62.5 m with 51 rows of plants; rows were 1 m apart. In the centre section of the plot, plants were 81.2 cm apart within rows; in the peripheral 8 m all around the plot, within-row spacing was 40.6 cm. Extra spacing between plants in the centre of the plot facilitated sampling. The central area was divided into 15 subplots, each 10 X 10 m. Subplots were separated from each other by a single buffer row; every second plant within each subplot was considered a sampling candidate.

The "experimental plot" was located at the University of Manitoba Fort Garry Campus and was manually planted on 29 May. The plot was 30 X 30 m, with 11 rows of plants at 3 m spacing between and within rows. A pre-emergent spray of glyphosate (801 g A.I./ha) was applied on 30 May to control weeds.

The "reservoir plot" was also located at the University of Manitoba Fort Garry Campus and was machine-planted on May 30. It was 26 X 37 m, with 27 rows 1 m apart and plants 40.6 cm apart within rows.

<u>**Experimental Treatments**</u>. Selected plants in the experimental plot were individually caged with wood-framed cages covered in Tergal® drapery lining material (28 holes/cm) (Fig. 1). Cages were 1.26 m X 1.34 m X 1.22 m high. At 0.5 m above the ground on two opposite sides of each cage were 13 cm diameter holes with fabric sleeves to permit access to plants without moving the cage. Cages were anchored with guy lines, and earth was banked around the base of each cage to prevent insect movement in or out. Cages were placed over plants at emergence (18 June).

Of the 121 available plants in the experimental plot, 30 were caged for experimental treatments. There were ten treatments, each with three replicates. Treatments were arranged in rows in the centre of the experimental plot, with either two or three treatments being located in one row. All plants within an individual treatment were located immediately adjacent to each other. Treatments were different multiples of average field densities of Colorado potato beetle and potato flea beetle (Table 1). Field density was the average density of the insects in the Portage plot in the same week.

Field density was estimated at the beginning of each week throughout the summer, starting on 27 June, using both visual and whole-plant bag sampling at the Portage plot (Byerly et al. 1978). One plant per subplot was sampled by each method weekly, using a randomized design in which no plant was sampled twice. Using whole-plant bag sampling, Colorado potato beetle eggs, larvae and adults, and potato flea beetle adults were collected. In this method, two weeks prior to the date of sampling, a cylindrical nylon bag with open ends (1 m in diameter and 1.5 m long) was placed over a plant and flattened and covered with five shovelfuls of soil. On the sampling date, bags were rapidly drawn up over the plants and draw strings, located at both open ends of the bags, were cinched. Plants were then cut off at soil level and removed to a laboratory cold room to determine insect numbers. Visual sampling was used only to estimate numbers of Colorado potato beetle eggs, larvae and adults per plant. The height of plants sampled by both methods was also recorded.

During the latter part of each week, starting on 5 July, numbers of larval and adult Colorado potato beetles and adult potato flea beetles were manipulated in cages at the experimental plot. Manipulations were in accordance with the previously defined experimental treatments (Table 1), and involved the removal of cages from plants and examining the number and stadia of insects present. The numbers of Colorado potato beetles and potato flea beetles were then adjusted to the density required per plant in a given treatment. The reservoir plot was the source of insects for the experimental treatments.

Numbers of insects (Table 2) in each experimental treatment were initially based on the weekly average field density as determined by whole-plant bag sampling. However, in late July, Colorado potato beetles threatened to destroy plants in the Portage plot, and so applications of deltamethrin (7.5 g A.I./ha) were made on 21 July, 28 July and 8 August. Consequently, insect densities in the Portage plot were no longer "natural" and so, after the third week in July, treatment densities of potato flea beetle were based on published data from insecticide-free plots of cv. Norland potato plants (Senanayake and Holliday 1989). To compensate for the larger size of cv. Russet Burbank plants, average numbers for Norland were multiplied by four. Densities of Colorado potato beetle were based on unpublished sampling data from insecticide-free plots of Russet Burbank potatoes (N.J. Holliday, pers. comm.).

Also located at the experimental plot, were five uncaged plants, called the "cleared row", and five more uncaged plants called the "non-cleared row". The cleared row was picked clean of all insects twice a week while the non-cleared row was left undisturbed for the duration of the summer.

Harvesting. All experimental plants, and those in the cleared and non-cleared rows were harvested on 19 September. On 20 September, 30 randomly chosen plants from the Portage plot, and 30 plants from a nearby commercial potato field, were harvested. Fifteen plants from the reservoir plot were harvested on 22 September. Harvesting was done manually and tubers from each plant were kept separate to obtain yields from individual plants. Tubers were washed, weighed and graded in accordance with discrete size range classes used in both commercial and table grading schemes (B. Geisal, S. Prokopchuk, pers. comm.). Tubers were also scored for shape, material defects and the presence of disease.

1990

Design of Plots. In the second growing season, four plots of cv. Russet Burbank potatoes were planted. One day prior to planting, 50 g seed pieces were hand-cut from certified seed tubers. All cutting utensils and potato sacks were disinfected in a 0.06% solution of quaternary ammonium compounds (HY-X®). For overnight storage, seed pieces were bagged and placed in a room (16° C, 80% R.H.) which provided forced air circulation through the piles of seed pieces. Two plots, an experimental plot, and an adjacent reservoir plot, were located at the Agriculture Canada Research Station in Morden, Manitoba. These plots received 269 kg/ha of blended granular fertilizer (28/N; 26/P; 0/K): fertilizer was broadcast in the reservoir plot, but in the experimental plot an equivalent amount of fertilizer was applied beneath and around seed pieces. The Morden experimental plot was 36 X 36 m with 13 rows of plants spaced at 3 m intervals between and within rows; it was manually planted on 22 May. The Morden reservoir plot was mechanically planted on 22 May, and was 36 X 95 m with 37 rows, 1 m apart. Plants were spaced within rows at 45.7 cm intervals. On 10 July, a postemergent spray of metribuzin (261 g A.I./ha) and sethoxydim (809 g A.I./ha) was applied to suppress volunteer broadleaf and grassy weeds.

The remaining two plots also consisted of an experimental and an adjacent reservoir plot, and were located 8 km west of the town of Winkler, Manitoba. These plots received 168 kg/ha of blended granular fertilizer (18.2/N; 16.7/P; 16.7/K): fertilizer was banded in the reservoir plot, but in the experimental plot an equivalent amount of fertilizer was applied beneath and around seed pieces. The Winkler experimental plot was manually planted on 25 May and was 30 X 30 m, with plants spaced at intervals of 3 m between and within the 11 rows. The

Winkler reservoir plot was mechanically planted on 24 May, and was 30 X 60 m with 31 rows, 1 m apart. Plants were spaced within rows at 45.7 cm intervals. On 4 June, a pre-emergent spray of glyphosate (1.246 kg A.I./ha) was applied to both plots to control volunteer wheat. On 5 July, a post-emergent application of metribuzin (261 g A.I./ha) and sethoxydim (809 g A.I./ha) was made to control volunteer grassy and broadleaf weeds.

Experimental Treatments. Cages (Fig. 2) for the Morden experimental plot were constructed of Nitex® monofilament bolting cloth (12.5 holes/cm). Inside cage dimensions were 0.90 m X 0.90 m X 1.15 m high. Cages were supported by four 1.22 m lengths of 1.8 cm (O.D.) thin-walled steel conduit. Conduit was inserted through loops attached to the outside of the vertical edges of the cages and was driven into the ground. Strings on the upper four vertices of each cage were tied to the conduit to keep the roof of each cage well supported and taut. One side of each cage contained an 80 cm zipper to allow plants to be examined without removal of the cage. The bottom 5 cm of each cage was reinforced with 28 gauge galvanized steel sheeting, rivetted on each side of the Nitex® bolting cloth. Earth was banked around the base of each cage to prevent insects from entering or leaving. At the Winkler experimental plot, the previously described wooden cages were used.

At the Morden experimental plot, there were eight treatments replicated six times (Table 3); two treatments, each replicated six times were used at the Winkler experimental plot. Treatments were arranged in rows in the centre of each experimental plot. Each row was comprised of six plants, immediately adjacent to each other, and represented a single experimental treatment. As in 1989, one cage was used per plant in each treatment, but unlike that year, no treatments used late season infestations of Colorado potato beetle. Cages were put in place as plants emerged on 19 June and remained there until harvest.

Experimental Activities. Manipulations of potato flea beetle densities in experimental treatments were based on published data from insecticide-free plots of cv. Norland potatoes (Senanayake and Holliday 1989). Averages from these data were multiplied by four to account for the larger size of Russet Burbank plants; however in any given week, the ultimate densities per cage were governed by the abundance of potato flea beetles in the reservoir plot. Unlike July 1989, potato flea beetle abundance was very low during July 1990; hence, early season infestations of this pest on caged plants were not possible. Manipulations for Colorado potato beetle were based on unpublished sampling data from insecticide-free plots of Russet Burbank potatoes (N.J. Holliday, pers. comm.), which are analogous to peak numbers found at the periphery of commercial potato fields (Morris 1990).

Each week, all the cages at the Morden experimental plot were unzipped, cleared of insects and then the appropriate number of insects (Table 4) was introduced. Plant height was also recorded. At the Winkler experimental plot, similar methods were used, but the wooden cages were completely removed to facilitate manipulations. Insects introduced into cages were obtained by sweep-netting in the reservoir plots. As a biological control against aphids, 10 larval and 15 adult coccinellids were maintained in all cages from 1 August onward.

In the Morden experimental plot, a row of six uncaged plants, called the "cleared row" were picked clean of all insects, twice a week. An uncaged row of six plants in the Morden experimental plot was left undisturbed, but was surveyed weekly for Colorado potato beetle larvae and adults. In the Winkler experimental plot, an uncaged row of six plants was also left undisturbed, but insects on these plants were not monitored. The undisturbed rows were both referred to as "non-cleared rows".

Harvesting. All experimental plants, the cleared and non-cleared rows, and fifteen randomly chosen plants from each reservoir plot and from a nearby commercial field were harvested. Harvesting at the Winkler plots and commercial field was done on 22 September; all remaining plants were harvested on 23 September. Methods of harvesting and yield assessment were the same as in 1989.

Analysis

For both 1989 and 1990, only the weight of marketable tubers 4.4 cm or larger in diameter were considered in the analysis of marketable yield, hereafter referred to as yield. Data were analyzed by linear regression, analysis of covariance (ANCOVA) and analysis of variance (ANOVA) (Wilkinson 1990).

Results

The reader is referred to the appendices for detailed data on seasonal abundance of potato flea beetle and Colorado potato beetle in 1989 (Appendix 1), weekly numbers of Colorado potato beetles on the non-cleared row at Morden in 1990 (Appendix 2), heights of plants (Appendices

3,4 and 5) and tuber sizes from individual plants (Appendices 6 and 7).

1989

From the 1989 yield data (Table 5) no discernable trends can be seen, probably because of aphids, *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer), which fed on the experimental plants late in the season. During mid- to late August, the level of aphid infestation was visually ranked for each plant (Table 5) and was negatively correlated with yield (r=-0.75; d.f.=1,28; P<0.001). To minimize the detrimental effect of aphid feeding on the analysis of yield, plant yields were corrected by ANCOVA with aphid injury ranking as the independent variable (Table 6). However, because of the interaction of terms in the mathematical model representing early season and late season densities of Colorado potato beetle, the "110" treatment could not be included in this analysis or compared to other treatments with early season Colorado potato beetle injury. After correction for aphids, yield was found to be negatively correlated with peak densities of potato flea beetles (r=-0.69; d.f.=1,19; P<0.01), but the effect of Colorado potato beetle was still undiscernible (Fig. 3).

Average plant yield from the Portage plot (Table 7) was significantly smaller (t=11.0; d.f.=1,43; P<0.001) than in the commercial field or the "000" treatment in the experimental plot (t=10.5; d.f.=1,31; P<0.001). Plants in the Portage plot were in poor condition because of Colorado potato beetle feeding and weed competition. Average yield from the reservoir plot was also significantly smaller than that of the "000" treatment (t=2.9; d.f.=1,16; P<0.05).

1990

In the Morden experimental plot, yields were strongly influenced by the densities of both Colorado potato beetle and potato flea beetle (Table 8). Plants which sustained low levels of potato flea beetle injury, with no Colorado potato beetle injury, had slight increases in yield, but with this exception, increased insect density resulted in reduced yield (Fig. 4).

To model the linear portion of the yield response for plants without Colorado potato beetle injury, the "000" treatment was ignored. All four treatments were used to model the yield response for plants which did sustain Colorado potato beetle injury. The combined linear response for all seven treatments was analyzed by ANCOVA (Fig 4). Plant yield was significantly affected by the density of potato flea beetles (F=129.2; d.f.=1,3; P<0.01) and by the presence of early season Colorado potato beetles (F=25.8; d.f.=1,3; P<0.05). The slope of the linear portion of the response to potato flea beetle was significantly steeper when there had been early season defoliation by Colorado potato beetle (F=10.4; d.f.=1,3; P<0.05). In the absence of potato flea beetles, the difference between the means of the two control treatments shows that early season defoliation by Colorado potato beetle reduced yield by 0.408 kg. With no Colorado potato beetles, in the region where the response to potato flea beetles was linear, the reduction in yield for peak potato flea beetle densities was 1.625 g/flea beetle. However, when there had been early season Colorado potato beetle injury, this increased to 2.922 g/flea beetle.

The average yield of the "000" treatment in the Morden experimental plot (Table 8) was significantly larger (t=5.0; d.f.=1,10; P<0.001) than that in the cleared row, suggesting that caging has an effect on yield. The yield in the non-cleared row was 80% of that in the cleared row; in experimental treatments, the yield of the "100" treatment was 90% of the "000" treatment, and that in the "101" treatment was 75%. The average yield in the Morden reservoir plot was significantly smaller than that in the non-cleared row (t=-4.0; d.f.=1,19; P<0.001) but was larger than that in the commercial field (t=-2.7; d.f.=1,28; P<0.05). The commercial field suffered greatly from inadequate rainfall, and the yield was well below that typical for dryland potato production for Manitoba.

At Winkler, treatments were restricted because of a shortage of flea beetles; treatments which were carried out had smaller numbers of flea beetles than the corresponding treatments at Morden (Table 4). By ANOVA, no significant difference was found among yields of the two experimental treatments and non-cleared row at the Winkler site. The average yield from the Winkler reservoir plot was significantly larger than that from the commercial field (t=-2.9; d.f.=1,28; P<0.01), but did not differ significantly from that of the Morden reservoir plot.

Economic Injury Level

To obtain an economic injury level (EIL) for potato flea beetles, yields were converted to percent yield of the "000" treatment for plants without Colorado potato beetle injury, and percent yield of the "100" treatment for plants with Colorado potato beetle injury. Based upon the significance of the previous ANOVA, least squares regressions were used to calculate percent marketable yield reduction with varying peak numbers of potato flea beetles per plant (Figs. 5,6).

Two different approaches were used to fit regressions for Figs. 5 and 6. The response of plant yield to peak densities of potato flea beetles, as shown in Fig. 5, appears to be curvilinear. However, after exploratory analyses, the "000" treatment was ignored and the remaining treatments were fit by linear regression. This procedure best modelled plant response to flea beetle defoliation in the area where economic yield loss occurred. A linear regression that did not ignore the "000" treatment would greatly underestimate the yield of plants defoliated by normal field densities of flea beetles. An injury level calculated from such a regression would be far too low, because it would not adequately account for increased plant yield at low levels of potato flea beetles. In Fig. 6, all four experimental treatments were easily modelled by linear regression, with the regression being forced through 100% on the Y axis. Although the fit of the model was slightly compromised by forcing through 100%, the calculation of a practical injury level necessitated that the relationship showed no yield loss when no insects were present. The two relationships determined were:

Without early season Colorado potato beetle injury:
Percent Yield = 111.935 - (0.0412 x peak potato flea beetle density)

With early season Colorado potato beetle injury:
Percent Yield = 100.000 - (0.0988 x peak potato flea beetle density)

The economic injury levels, derived in a fashion similar to that of

Senanayake and Holliday (1990), are given in terms of peak numbers of potato flea beetles per plant:

Without early season Colorado potato beetle injury:

$$\text{EIL} = \left(\frac{100C}{vy} + 11.934\right) \div 0.0412$$

With early season Colorado potato beetle injury:

$$\text{EIL} = \frac{C}{0.000988vy}$$

where C = control cost ($ Canadian/ha), v = market price ($ Canadian/kg), and y = expected yield in absence of insect injury (kg/ha).

Economic injury levels depend on the price of pesticides, the cost of application, market price for the crop and potential yield of the crop and, in Manitoba, there is a range of expected yield depending on soil type and whether potato crops are irrigated or not. Furthermore, the market price for Russet Burbank potatoes is not fixed but varies depending on contractual obligations with processors. Hence, it would be inappropriate to produce a single, fixed economic injury level, and so a range of economic injury levels was calculated, based on the varying conditions faced by Manitoba producers (Table 9).

Discussion

The 1989 field season produced data which were difficult to interpret and showed few clear effects; several reasons may account for these problems. First, was the large infestation of Colorado potato beetles at the Portage plot, which caused severe defoliation and dictated the use of insecticide to save the crop. Insecticide applied against Colorado potato beetles had the undesirable effect of severely reducing potato flea beetle numbers. Secondly, weeds at the Portage plot caused severe competition for growing potato plants. These two factors created conditions atypical of a commercial potato field, and as manipulations at the experimental plot were based on average numbers from sampling of the Portage plot, half of the seasons's experimental manipulations did not reflect the typical densities of insects found in commercial potato fields. A further problem was the presence of aphids in cages late in the season. Correction for the effect of aphid feeding on yield was difficult, because aphid ranks were non-orthogonal with treatments. After correction a negative yield response to potato flea beetles was demonstrated, but the effect of Colorado potato beetle feeding was still undiscernible. As both potato flea beetles and aphids tended to predominate in late season, it is likely that aphid injury had the single greatest effect in confusing the results of this field season.

In 1990, problems were encountered at the Winkler site. Insufficient numbers of potato flea beetles, particularly during the bloom phase when plants are most sensitive to yield loss (Cranshaw and Radcliffe 1980; Hare 1980; Shields and Wyman 1984), probably was the primary reason for the absence of significant effects of treatments. Also, birds destroyed the tops of some of the cages in this experimental plot, thus allowing potato flea beetles to escape.

In the Morden experimental plot, plant heights shortly after plant emergence were slightly larger for non-Colorado potato beetle treatments than those with Colorado potato beetles (Appendix 4). This is attributed to the low-lying, poorly drained area in which the plants for the Colorado potato beetle treatments were planted, which resulted in slightly delayed germination and growth. However, among treatments with Colorado potato beetle, no difference in plant height was found by 43 days after planting when tested for the effect of potato flea beetle. Prior to this time, the only insect manipulations that took place were those for Colorado potato beetle, at a density of only one adult per plant, starting in the previous week. Plant height in the "105" treatment remained marginally lower than all other treatments throughout the season, but this is not surprising as it received the severest defoliation. Since the economic injury levels were based on percentage yield reductions of the "000" treatment for plants without Colorado potato beetles, and of the "100" treatment for plants with Colorado potato beetles, any potential yield discrepancy that may exist between the two groups of treatments would not affect the calculation of the economic injury levels. Therefore, early season variation in plant size between treatments was relatively small, and had negligible effect on injury level determination.

The only way by which a realistic economic injury level for potato flea beetle can be developed is by conducting an experiment under conditions found in a commercial potato field. However to maintain specific densities of insects on a plant grown under these conditions, and to have the ability to manipulate these densities to model natural population increases and decreases, plants must be caged. Cages were designed so that plants had about the same area for foliage as their field-grown counterparts. However, non-caged plants were slightly smaller than caged plants. In the Morden experimental plot, the cleared row was significantly smaller (t=5.0; d.f.=1,10; P<0.001) than the caged "000" experimental treatment, which had no insects introduced. Because spacing between plants was the same in both groups of plants, it is unlikely that competition for root space or nutrients could account for this difference. Differences in plant size and yield are probably attributable to the shade and protection from wind that the cages provided.

The percent yield reduction of experimental treatments from that of the "000" treatment is comparable to the percent yield reduction of plants in the cleared and non-cleared rows. In Morden, the yield of the non-cleared row was 80% of the cleared row. For experimental treatments, the "100" treatment was 90% of the "000" treatment, and that in the "101" treatment was 75%. No treatment in the Morden plot, owing to the fact that experimental treatments had no late season Colorado potato beetles, can be directly compared to the non-cleared row. However, the early season defoliation in the "101" treatment was higher than the densities in the field, and the level of potato flea beetles in the "101" treatment was probably much higher than the non-cleared row. Hence, the relationship of the 75% in the "101" treatment to the 80% in the field is a reasonable result.

If caging affects plant response to defoliation, then the economic injury levels would be affected. Senanayake and Holliday (1990) explored this possibility when developing an economic injury level for Colorado potato beetle on Norland potatoes. They attributed any discrepancies between observed yield loss in the field and predicted yield loss to the differential response of caged plants to defoliation. They found that the magnitude of the differences was small compared to the precision of field sampling, and concluded that no adjustments were necessary to the injury level. Senanayake and Holliday (1990) attributed all differences between predicted and observed yields to the effect of caging; no doubt caging was not the only reason for these differences, and so the real effect of caging on the yield response to defoliation is probably even less than their estimate. Another potential source of error may be brought by caging. When densities of insects are expressed on a per plant basis, caged plants, because of their larger size and increased foliage area, have fewer insects per unit foliage area than plants that are commercially grown. The result of such an effect is uncertain, but may lead to a slight exaggeration of economic injury levels.

In my studies of Russet Burbank, in the absence of early season Colorado potato beetle injury, there appeared to be an overcompensatory response to low densities of potato flea beetles: yield was increased when the peak density of potato flea beetles was between 0 and 290 flea beetles per plant. Artificial defoliation studies have also shown overcompensation in Russet Burbank potatoes, when leaf removal was at mid-season (Cranshaw and Radcliffe 1980). A similar overcompensatory response to potato flea beetles occurs in Norland potato plants (Senanayake 1987), but here yield increases between 0 and 77 beetles per plant. When considering flea beetle injury alone, Russet Burbank plants are about four times more tolerant of injury than is Norland. This difference in sensitivity to injury is similar to that of the same potato cultivars when defoliated by Colorado potato beetle alone (Holliday 1988). Such a differential response is probably related to the much larger foliage area of Russet Burbank potato plants (Holliday unpubl.).

Overcompensation is a plant response to insect feeding that occurs early in the generalized damage curve (Fenemore 1982), and is more evident in plant stands than in individual plants (Pedigo et al. 1986). Hence, if such an overcompensatory response does exist, as seen from the 1990 experimental data, it may occur even more intensely in a commercial field.

Several reasons may account for overcompensatory yield responses in individual plants. Damage early in the growing season, particularly to a vigorously growing terminal, inhibits apical dominance in plants (Harris 1974), so that new shoots are formed, and foliage area and yield increase. Harris (1974) suggested that such a mechanism was responsible for increased yield in moderately defoliated potatoes in Czechoslovakia (Skuhravy 1968). Limited defoliation may also optimize leaf area index. The optimum leaf area index is the ratio of leaf area to ground covered at which the balance of photosynthesis over respiration is at a maximum value (Harper 1963). Excess foliage, which shades lower leaves, causes carbohydrate synthesis in lower leaves to be less than their respiratory requirements, therefore, removal of leaves higher on the plant may increase overall photosynthetic efficiency (Harper 1963). Under certain environmental conditions, plants are limited either by their capacity to produce photosynthate ("source limitations") or by their ability to use it ("sink limitations"). Plants are more likely to become more source-limited as more sinks, such as fruits or tubers, develop (Wareing and

Patrick 1975). Early August, when most potato flea beetle defoliation occurs, is a period in which potato plants are likely source-limited. Low levels of defoliation, by reducing the effect of apical dominance and optimizing the leaf area index, may reduce the source limitation of plants, and allow more photosynthate to be allocated to tubers.

When plants are grown under optimal conditions, assimilate production in leaves is below its potential maximum, and when the source-sink ratio is decreased by defoliation, assimilate production may be optimized in the remaining leaves (Wareing and Patrick 1975). Such increases in the rate of assimilate production have been shown to occur with reductions in source-sink ratios by partial defoliation (Wareing et al. 1969; Dwelle 1990) or by grafting larger root sinks onto plants (Thorne and Evans 1964). The photosynthetic efficiency of undefoliated potato plants changes over the course of the growing season. Maximum efficiencies are found during the period of tuber bulking, while reduced efficiencies are found before tuber initiation and after plants have produced about 60-70% of their maximum yield (Moorby 1968; Moll 1980). Therefore, it is plausible that low levels of potato flea beetle feeding may increase photosynthetic efficiency to compensate for a decreased source-sink ratio. For this process to occur, photosynthesis may have to be regulated by hormonal factors which are synthesized in sink regions, such as tubers (Wareing and Patrick 1975).

The level of economic damage for previously uninjured Russet Burbank plants was between 0.43-1.87%, which is equivalent to a peak of 300-335 potato flea beetles per plant. Such high numbers of potato flea beetles may be withstood by plants because of their overcompensatory ability. Russet Burbank plants which have been exposed to early season defoliation by Colorado potato beetle lose their ability to compensate for injury by potato flea beetles. The level of economic damage for these plants ranged between 0.40-1.88%, equivalent to a peak density of 4-19 potato flea beetles per plant. The period of potato plant growth which is two weeks past first bloom (approximately 70 days after planting) is the most sensitive to injury in both short term insect defoliation (Hare 1980) and artificial defoliation studies (Cranshaw and Radcliffe 1980; Shields and Wyman 1984). Hence, for plants which have lost their overcompensatory ability, the low number of potato flea beetles necessary to cause economic injury is probably due to the sensitivity of plants to defoliation during this period.

Russet Burbank plants are sensitive not only to mid-season defoliation, but also to defoliation for a short period after emergence (Shields and Wyman 1984). During this period, removal of tissue from the lower leaves may disrupt the hormones involved in tuber initiation; these hormones are concentrated in older leaves (Cutter 1978). This delays the onset of tuberization which, in late maturing cultivars like Russet Burbank, often does not affect yield as plants have enough time to recover before maturity. However, added late season injury by potato flea beetle may hinder this recovery, and consequently reduce yield.

In many years in Manitoba, Colorado potato beetles are concentrated around the periphery of potato fields, up to approximately 50 m in from the edge (Holliday and Parry 1987), while densities in the centres of fields are often near zero (Morris 1990). Because of this distribution of this pest, I feel that the injury level determined for plants without Colorado potato beetle defoliation is most applicable to the centre of fields, and the injury level determined for plants with Colorado potato beetle injury is applicable to field margins. Potato flea beetle populations in Manitoba rarely exceed the economic injury level for no previous defoliation, but regularly do exceed the injury level for previous defoliation (Holliday unpubl.). Current control practices against potato flea beetle in Manitoba are therefore justified if confined to field margins of Russet Burbank potato fields where there were previous populations of Colorado potato beetles.

In order to allow for the proper timing of insecticide applications, based on previously calculated economic injury levels, an index must be developed which relates damage by potato flea beetles to absolute numbers per plant. Such an index can be developed from an examination of how feeding punctures accumulate on leaflets over the course of the growing season. This will be explored in Part 2 of Chapter III.

In conclusion, the responses of Russet Burbank potato plants to potato flea beetle defoliation closely parallel findings by Senanayake (1987) for Norland potatoes. In particular, an overcompensatory yield response may exist in both cultivars for low levels of potato flea beetle feeding. However, sequential defoliation by Colorado potato beetles in early season followed by potato flea beetles in late season eliminates the overcompensatory ability of plants, and greatly lowers the economic injury level for potato flea beetle. The economic injury levels developed herein are sensitive to the conditions of Manitoba potato production. They should be considered preliminary, and require additional field seasons of data to be refined.

Acknowledgements

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Table 1. Treatments in the experimental plot, 1989. Densities of each insect are expressed as multiples of average field densities (insects/plant) per week. Each treatment contained three replicates. (CPB = Colorado potato beetle; PFB = potato flea beetle).

Density of early season CPB	Density of late season CPB	Density of PFB	Treatment name
0	0	0	000
0	0	1	001
0	0	3	003
1	0	0	100
1	0	1	101
1	0	3	103
2	0	0	200
2	0	1	201
2	0	3	203
1	1	0	110

Table 2. Numbers of insects/plant introduced into cages at the experimental plot, each week in 1989. (DAP = days after planting; CPB = Colorado potato beetle; I-IV = CPB instar number; A = CPB adults; PFB = potato flea beetle adults).

			Treatment									
Date	DAP	Insects	000	001	003	100	101	103	200	201	203	110
5 July	37	CPB I	0	0	0	4	4	4	8	8	8	4
		II	0	0	0	3	3	3	6	6	6	3
		PFB	0	8	25	0	8	25	0	8	25	0
13 July	45	CPB I	0	0	0	7	7	7	14	14	14	7
		II	0	0	0	11	11	11	21	21	21	11
		III	0	0	0	8	8	8	17	17	17	8
		IV	0	0	0	6	6	6	13	13	13	6
		PFB	0	8	24	0	8	24	0	8	24	0
19 July	51	CPB I	0	0	0	3	3	3	6	6	6	3
		II	0	0	0	11	11	11	22	22	22	11
		III	0	0	0	10	10	10	20	20	20	10
		IV	0	0	0	20	20	20	40	40	40	20
		PFB	0	6	18	0	6	18	0	6	18	0
27 July	59		No Insects									
3 Aug.	66	CPB A	0	0	0	0	0	0	0	0	0	11
		PFB	0	5	16	0	5	16	0	5	16	0
11 Aug.	74	CPB A	0	0	0	0	0	0	0	0	0	11
		PFB	0	17	50	0	17	50	0	17	50	0
16 Aug.	79	CPB A	0	0	0	0	0	0	0	0	0	8
		PFB	0	100	300	0	100	300	0	100	300	0
23 Aug.	86	CPB A	0	0	0	0	0	0	0	0	0	8
		PFB	0	200	600	0	200	600	0	200	600	0
31 Aug.	94	CPB I	0	0	0	0	0	0	0	0	0	10
		II	0	0	0	0	0	0	0	0	0	10
		III	0	0	0	0	0	0	0	0	0	1
		A	0	0	0	0	0	0	0	0	0	4
		PFB	0	100	300	0	100	300	0	100	300	0
7 Sep.	101		No Insects									

Table 3. Experimental treatments used in the experimental plots at Morden and Winkler, Manitoba, 1990. Densities (insects/plant) are multiples of average field density for each week. Each treatment contained six replicates. (CPB = Colorado Potato Beetle; PFB = Potato Flea Beetle).

Density of early season CPB	Density of PFB	Treatment name
	Morden Site	
0	0	000
0	1	001
0	3	003
0	5	005
1	0	100
1	1	101
1	3	103
1	5	105
	Winkler Site	
0	0	000
0	5	005

Table 4. Numbers of insects introduced into cages at the Morden and Winkler experimental plots, each week in 1990. Dates are for Morden; those for Winkler generally followed by two days. (DAP = days after planting; CPB = Colorado potato beetle; I-IV = CPB instar number; A = CPB adults; PFB = potato flea beetle adults).

			Treatment									
			Morden								Winkler	
Date	DAP	Insects	000	001	003	005	100	101	103	105	000	005
25 June	34	CPB A	0	0	0	0	1	1	1	1	0	0
4 July	43	CPB I	0	0	0	0	3	3	3	3	0	0
		II	0	0	0	0	2	2	2	2	0	0
9 July	48	CPB I	0	0	0	0	5	5	5	5	0	0
		II	0	0	0	0	5	5	5	5	0	0
		III	0	0	0	0	10	10	10	10	0	0
		IV	0	0	0	0	10	10	10	10	0	0
16 July	55	CPB II	0	0	0	0	1	1	1	1	0	0
		III	0	0	0	0	3	3	3	3	0	0
		IV	0	0	0	0	5	5	5	5	0	0
23 July	62		No Insects									
30 July	69	PFB	0	0	0	0	0	10	30	50	0	50
7 Aug.	77	PFB	0	50	150	250	0	50	150	250	0	0
13 Aug.	83	PFB	0	100	300	500	0	100	300	500	0	500
20 Aug.	90	PFB	0	140	420	700	0	140	420	700	0	500
28 Aug.	98	PFB	0	50	150	250	0	50	150	250	0	250
3 Sep.	104	PFB	0	25	75	125	0	25	75	125	0	0
10 Sep.	111		No Insects									

Table 5. Marketable yield from plants in experimental treatments in 1989. Aphid rankings are from visual assessments of aphid infestation in cages during the latter part of the growing season. (0 = no aphids; 5 = highest density of aphids).

Treatment	Plant	Aphid rank	Yield (kg/plant)	Treatment yield (kg/plant)[1]
000	A	2	1.965	1.614 ± 0.380
000	B	1	2.021	
000	C	5	0.855	
001	A	3	1.082	1.301 ± 0.124
001	B	4	1.310	
001	C	4	1.511	
003	A	0	2.086	1.905 ± 0.314
003	B	0	2.335	
003	C	1	1.293	
100	A	3	1.134	1.788 ± 0.340
100	B	1	1.951	
100	C	3	2.278	
101	A	5	0.545	1.223 ± 0.416
101	B	1	1.144	
101	C	2	1.981	
103	A	3	1.230	1.035 ± 0.159
103	B	5	0.720	
103	C	2	1.154	
200	A	3	1.396	1.574 ± 0.249
200	B	3	1.261	
200	C	1	2.066	
201	A	1	1.662	1.640 ± 0.386
201	B	0	2.298	
201	C	5	0.961	
203	A	2	1.864	1.715 ± 0.302
203	B	4	1.133	
203	C	1	2.148	
110	A	0	1.837	1.964 ± 0.298
110	B	0	1.524	
110	C	0	2.531	

[1] N=3, Mean ± S.E.

Table 6. Marketable yield of plants in experimental treatments, corrected by analysis of covariance for the effect of aphids, 1989.

Treatment	Plant	Yield (kg/plant)	Treatment yield (kg/plant)[1]
000	A	1.693	
000	B	1.726	1.672
000	C	1.595	
001	A	1.502	
001	B	1.545	1.531
001	C	1.545	
003	A	1.481	
003	B	1.481	1.477
003	C	1.470	
100	A	1.564	
100	B	1.629	1.586
100	C	1.564	
101	A	1.492	
101	B	1.319	1.391
101	C	1.362	
103	A	1.353	
103	B	1.332	1.349
103	C	1.363	
200	A	1.725	
200	B	1.725	1.746
200	C	1.790	
201	A	1.480	
201	B	1.437	1.523
201	C	1.652	
203	A	1.524	
203	B	1.503	1.520
203	C	1.534	

[1] N=3, Mean

Table 7. Marketable yield of non-experimental plants, 1989.

Source of plants	N	Yield (kg/plant)[1]
Cleared Row	5	1.782 ± 0.125
Non-Cleared Row	5	1.503 ± 0.210
Reservoir Plot	15	0.892 ± 0.450
Portage Sampling Plot	30	0.176 ± 0.044
Commercial Field	30	1.877 ± 0.202

[1] Mean ± S.E.

Table 8. Marketable yield of all experimental and non-experimental plants, 1990.

Source of plants	N	Yield (kg/plant)[1]
Morden		
Experimental treatments:		
000	6	3.945 ± 0.194
001	6	4.247 ± 0.338
003	6	3.616 ± 0.521
005	6	3.337 ± 0.532
100	6	3.537 ± 0.881
101	6	2.968 ± 0.777
103	6	2.371 ± 0.945
105	6	1.408 ± 0.604
Cleared row	6	1.944 ± 0.352
Non-cleared row	6	1.560 ± 0.161
Reservoir plot	15	1.015 ± 0.059
Winkler		
Experimental treatments		
000	6	2.076 ± 0.268
005	6	2.227 ± 0.337
Non-cleared row	6	1.401 ± 0.255
Reservoir plot	15	1.094 ± 0.090
Commercial field	15	0.767 ± 0.069

[1] Mean ± S.E.

Table 9. Calculated economic injury levels for yields and control costs typical in Manitoba. Injury levels are expressed as peak numbers of potato flea beetles per plant over the growing season. (CPB = Colorado potato beetle).

Control costs[1] ($/ha)	Early season injury by CPB	Expected Yield[2] (t/ha) 15	18	21	24	27	30
17	No	311	307	305	303	301	300
	Yes	9	7	6	5	5	4
27	No	323	317	313	310	308	306
	Yes	14	12	10	9	8	7
37	No	335	327	322	318	315	312
	Yes	19	16	14	12	11	9

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[1] Includes costs of insecticides ($ Canadian/ha) and cost of aerial application ($9.26-11.12/ha).

[2] Assuming market value of $132/t.

Figure 1. Experimental cage at University of Manitoba Campus, Winnipeg, Manitoba, 1989.

Figure 2. Experimental cage at Agriculture Canada Research Station, Morden, Manitoba, 1990.

Figure 3. Relationship between mean marketable yield and peak numbers of potato flea beetles per plant (Y=1.619-0.000325X) for caged plants in the experimental plot, 1989. (CPB = Colorado potato beetle; 0X, 1X, 2X = multiples of naturally occurring field densities of Colorado potato beetles).

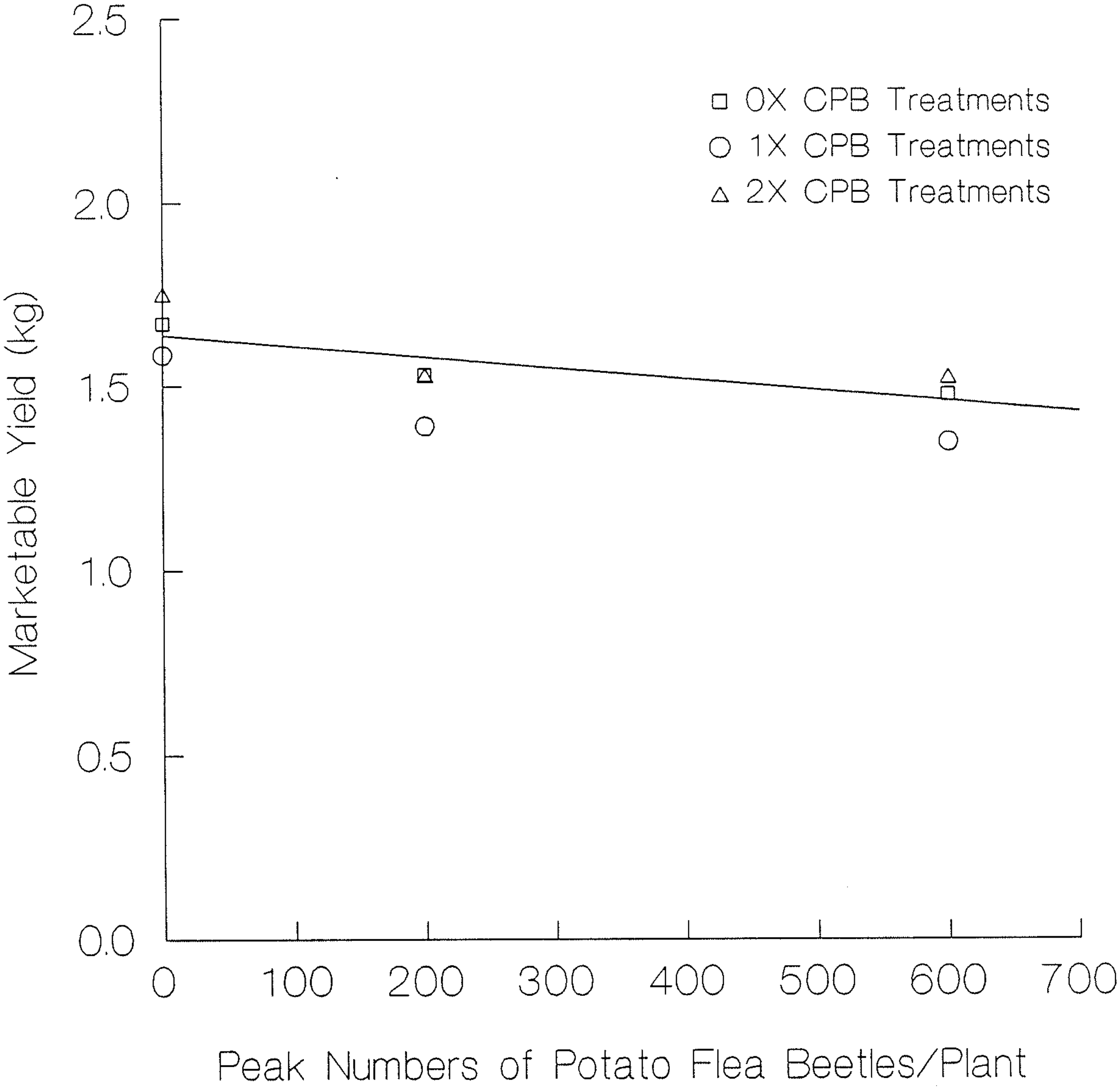

2.5
2.0
1.5
1.0
0.5
0.0
Marketable Yield (kg)
□ 0X CPB Treatments
○ 1X CPB Treatments
△ 2X CPB Treatments
0
100
200
300
400
500
600
700
Peak Numbers of Potato Flea Beetles/Plant

Figure 4. Relationship between marketable yield (mean ± s.e.) and peak numbers of potato flea beetles [Y=4.422-0.00163X (upper line); Y=3.488-0.00292X (lower line)] for caged plants at the Morden experimental plot, 1990. Note: point for treatment with 0 potato flea beetles and 0 Colorado potato beetles was omitted from the analysis. (CPB = Colorado potato beetle).

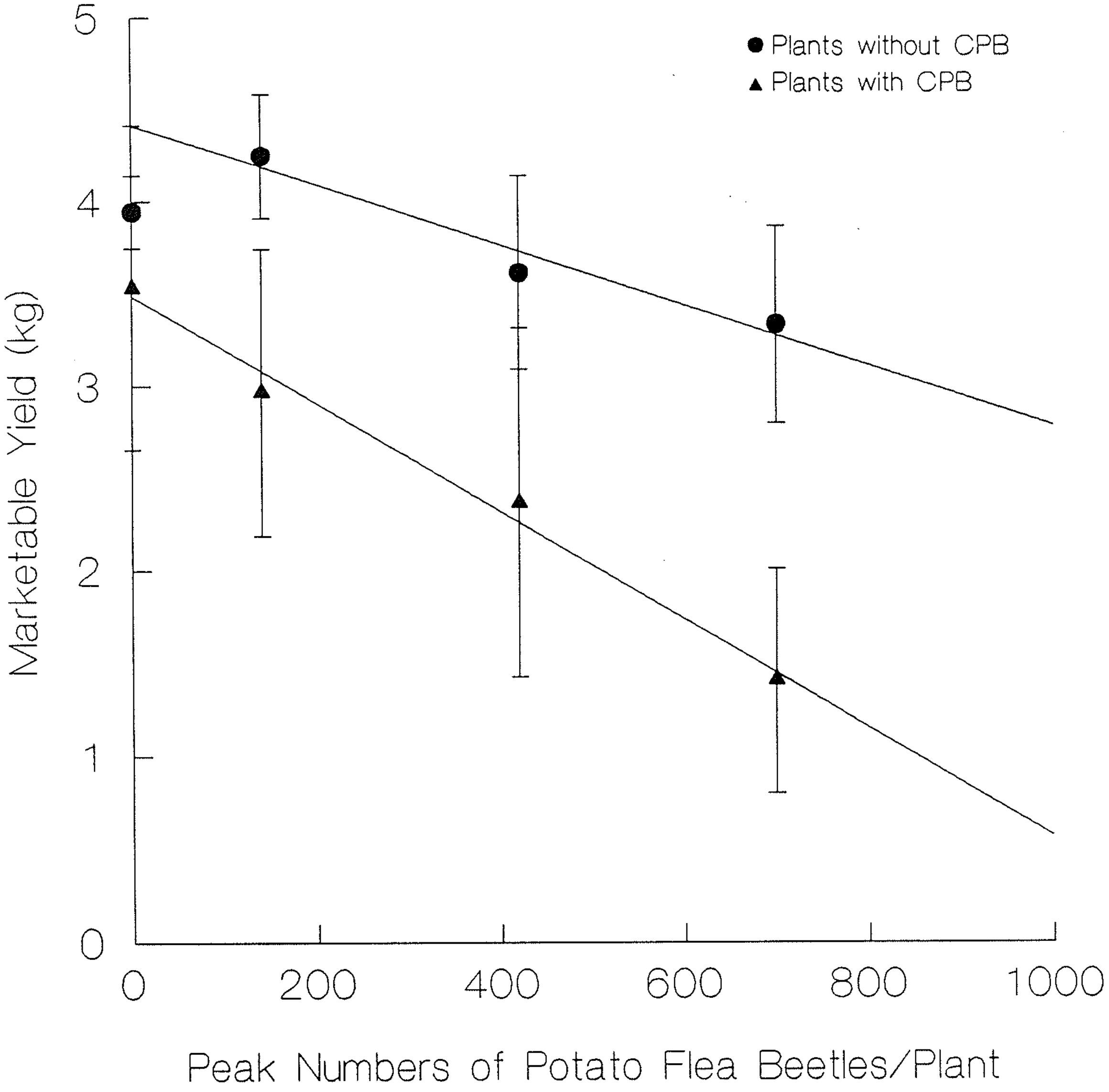

● Plants without CPB
▲ Plants with CPB
Marketable Yield (kg)
0
1
2
3
4
5
0
200
400
600
800
1000
Peak Numbers of Potato Flea Beetles/Plant

Figure 5. Relationship between marketable yield, as a percentage of control yield (mean ± s.e.) and peak numbers of potato flea beetles ($Y=111.935-0.0412X$) for plants with no early season Colorado potato beetle injury. Plants were grown in cages at the Morden experimental plot, 1990. Note: point for treatment with 0 potato flea beetles was not included in the calculation of the regression.

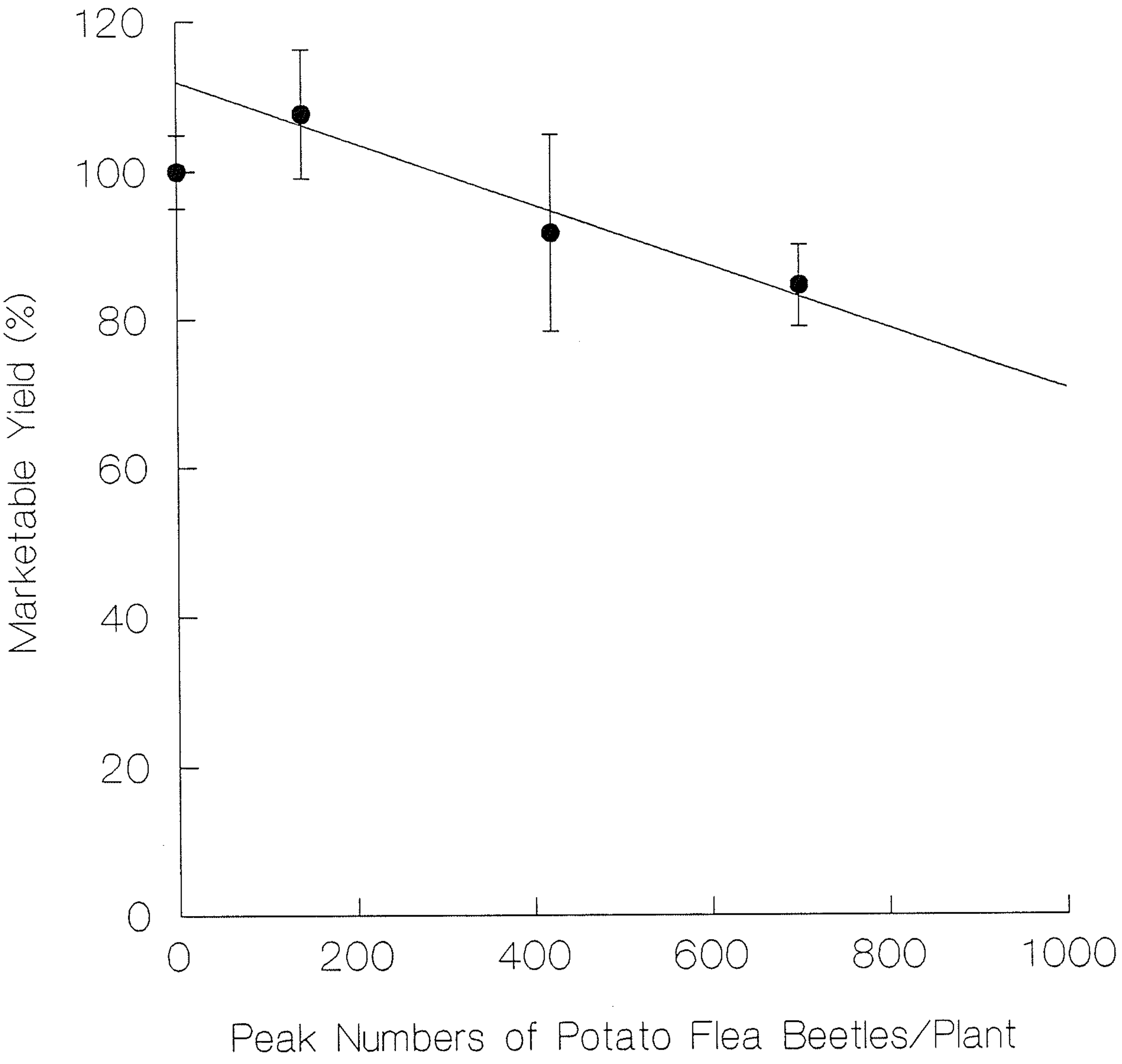
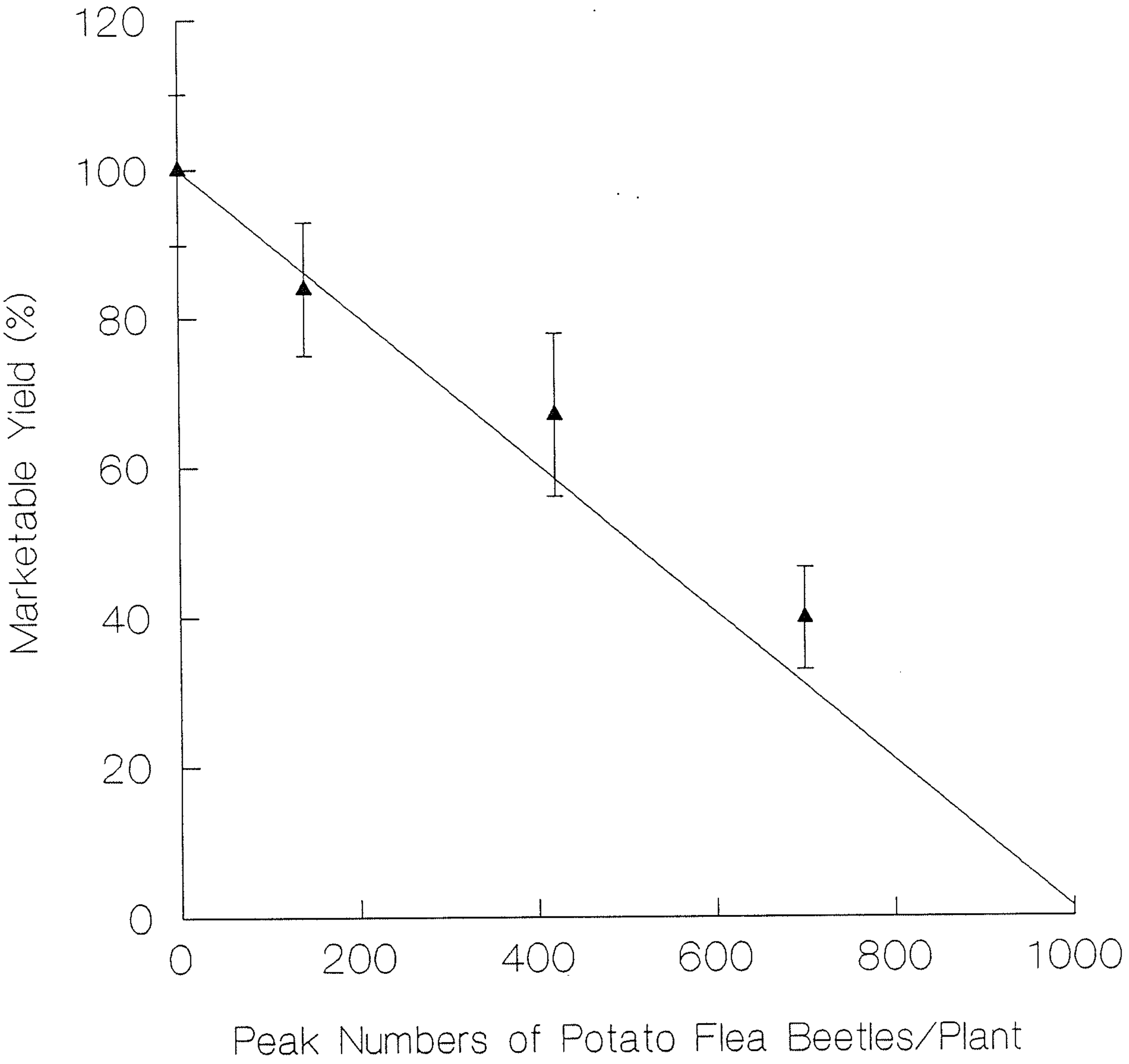

Marketable Yield (%)
0
20
40
60
80
100
120
0
200
400
600
800
1000
Peak Numbers of Potato Flea Beetles/Plant

Figure 6. Relationship between marketable yield, as a percentage of control yield (mean ± s.e.) and peak numbers of potato flea beetles (Y=100.000-0.09878X) for plants with early season Colorado potato beetle injury. Plants were grown in cages at the Morden experimental plot, 1990.


120
100
80
60
40
20
0
Marketable Yield (%)
0
200
400
600
800
1000
Peak Numbers of Potato Flea Beetles/Plant

Appendix 1. Mean (± S.E.) numbers of insects in the Portage sampling plot located at Portage la Prairie, Manitoba, 1989. (DAP = days after planting; WPBS = whole-plant bag sampling; I-IV = instar number; PFB = potato flea beetles).

			Colorado potato beetles/plant						PFB /plant
Date	DAP	Sample type	I	II	III	IV	Adults	Egg masses	Adults
27 June	31	Visual[1]	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	1.4 ± 0.3	-[2]
		WPBS[1]	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2	1.1 ± 3.9	9.7 ± 1.5
3 July	37	Visual	5.6 ± 3.3	0.5 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	1.5 ± 0.4	-
		WPBS	4.0 ± 2.4	2.9 ± 1.7	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	1.7 ± 0.4	8.3 ± 1.4
10 July	44	Visual	12.3 ± 4.3	26.5 ±12.9	10.2 ± 2.5	8.9 ± 3.0	0.1 ± 0.1	0.4 ± 0.2	-
		WPBS	6.9 ± 5.1	11.0 ± 4.8	8.3 ± 2.8	6.5 ± 2.1	0.1 ± 0.1	0.5 ± 0.2	5.9 ± 1.1
17 July	51	Visual	3.0 ± 1.5	11.7 ± 3.5	7.8 ± 1.6	16.5 ± 3.5	0.1 ± 0.1	0.1 ± 0.1	-
		WPBS	2.9 ± 1.8	10.8 ± 4.3	9.5 ± 2.7	20.3 ± 3.1	0.1 ± 0.1	0.1 ± 0.1	6.4 ± 2.1
24 July	58	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.4 ± 1.4	0.7 ± 0.2	0.7 ± 0.2	-
		WPBS	0.0 ± 0.0	0.2 ± 0.1	0.3 ± 0.2	4.9 ± 1.4	1.1 ± 0.7	0.1 ± 0.1	0.3 ± 0.2
31 July	65	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	8.9 ± 1.4	0.0 ± 0.0	-
		WPBS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.2	11.1 ± 2.8	0.1 ± 0.1	5.3 ± 0.9
8 Aug.	73	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	15.5 ± 2.1	0.8 ± 0.3	-
		WPBS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	10.6 ± 2.4	1.1 ± 0.3	16.6 ± 4.3
14 Aug.	79	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	18.4 ± 2.9	1.1 ± 0.5	-
		WPBS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.2 ± 0.6	0.6 ± 0.2	1.1 ± 0.3
21 Aug.	86	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	15.3 ± 2.6	0.2 ± 0.1	-
		WPBS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	5.1 ± 1.0	0.1 ± 0.1	1.7 ± 0.5
28 Aug.	93	Visual	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.3 ± 1.5	0.0 ± 0.0	-
		WPBS	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.6 ± 1.8	0.0 ± 0.0	5.7 ± 1.2

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[1] N=15

[2] Potato flea beetle adults were not sampled by this technique.

Appendix 2. Mean (± S.E.) numbers of Colorado potato beetles/plant from weekly inspections of the non-cleared row at the Morden experimental plot, 1990. (DAP = days after planting; I-IV = instar number).

		Colorado potato beetles/plant[1]					
Date	DAP	I	II	III	IV	Adults	Egg masses
25 June	34	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	0.3 ± 0.2
4 July	43	5.2 ± 3.2	1.7 ± 1.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2
9 July	48	0.7 ± 0.5	1.7 ± 0.9	2.7 ± 2.7	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2
16 July	55	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	1.8 ± 0.5
23 July	62	0.5 ± 0.3	0.7 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.3	0.5 ± 0.5
30 July	69	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.6	0.7 ± 0.3
6 Aug.	76	3.2 ± 2.2	1.5 ± 1.3	1.3 ± 0.9	0.3 ± 0.3	4.0 ± 0.7	0.5 ± 0.2
13 Aug.	83	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	1.0 ± 0.6	3.0 ± 1.3	1.7 ± 0.9
20 Aug.	90	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.7	4.2 ± 2.2	0.0 ± 0.0
27 Aug.	97	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
3 Sep.	104	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
10 Sep.	111	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

[1] N=6

Appendix 3. Mean (± S.E.) height of potato plants at the Portage sampling plot in 1989.

Date	Days after planting	Height(cm)[1]
27 June	31	12.0 ± 1.0
2 July	37	23.0 ± 1.1
10 July	44	34.5 ± 0.9
17 July	51	41.4 ± 0.9
24 July	58	43.9 ± 1.7
31 July	65	45.8 ± 1.4
8 Aug.	73	48.1 ± 1.6
14 Aug.	79	47.0 ± 1.9
21 Aug.	86	47.9 ± 2.3
28 Aug.	93	45.9 ± 1.6

[1] N=30

Appendix 4. Mean height (cm ± S.E.) of plants in experimental treatments, cleared and non-cleared rows at the Morden experimental plot, 1990. (DAP = days after planting; CLR = cleared row; NCLR = non-cleared row).

		Experimental treatment[1]									
Date	DAP	000	001	003	005	100	101	103	105	CLR	NCLR
25 June	34	26.0 ± 1.3	18.3 ± 1.6	19.3 ± 1.3	15.3 ± 2.0	19.0 ± 2.0	18.2 ± 1.7	15.5 ± 1.1	11.5 ± 1.4	20.5 ± 3.3	18.3 ± 2.0
4 July	43	39.2 ± 1.5	34.3 ± 1.6	34.5 ± 2.1	29.0 ± 1.5	31.5 ± 2.4	30.8 ± 4.4	30.5 ± 2.2	26.8 ± 2.5	32.2 ± 3.0	30.0 ± 1.7
9 July	48	45.0 ± 0.9	44.0 ± 2.7	42.7 ± 1.0	37.0 ± 2.0	41.5 ± 2.7	38.3 ± 4.2	36.2 ± 1.6	30.7 ± 2.5	36.8 ± 2.6	35.5 ± 1.5
16 July	55	53.0 ± 1.2	52.5 ± 1.7	51.7 ± 1.5	48.3 ± 2.6	48.7 ± 2.5	44.0 ± 2.8	43.8 ± 2.9	31.8 ± 1.4	45.8 ± 1.9	44.0 ± 2.1
23 July	62	62.3 ± 4.3	55.0 ± 4.0	59.0 ± 2.7	55.3 ± 3.8	55.2 ± 3.4	52.7 ± 3.7	48.2 ± 3.0	39.0 ± 1.8	51.2 ± 2.0	47.5 ± 3.0
30 July	69	63.5 ± 2.1	61.8 ± 3.9	64.8 ± 2.3	58.0 ± 2.5	59.2 ± 2.3	52.2 ± 3.5	50.2 ± 1.6	45.3 ± 1.5	57.8 ± 3.0	55.0 ± 2.5
6 Aug.	76	62.5 ± 1.8	65.5 ± 3.4	65.5 ± 2.9	59.5 ± 1.3	54.0 ± 1.9	54.3 ± 2.8	47.7 ± 3.0	47.2 ± 1.1	56.0 ± 2.2	49.7 ± 3.7
13 Aug.	83	74.5 ± 4.2	72.0 ± 3.0	61.7 ± 4.3	56.2 ± 2.1	60.5 ± 1.9	53.2 ± 4.5	59.7 ± 3.8	54.7 ± 1.5	60.5 ± 3.3	57.5 ± 4.0
20 Aug.	90	65.7 ± 2.8	72.3 ± 3.5	59.3 ± 3.2	52.2 ± 2.9	56.5 ± 3.1	50.7 ± 3.7	54.7 ± 4.0	49.0 ± 1.9	58.3 ± 2.3	53.7 ± 3.2
27 Aug.	97	67.3 ± 3.7	63.5 ± 5.9	59.3 ± 3.6	59.8 ± 2.6	60.7 ± 4.6	54.7 ± 4.2	61.5 ± 4.7	49.8 ± 1.8	54.3 ± 3.4	56.0 ± 3.7
3 Sep.	104	60.3 ± 4.8	55.3 ± 4.6	53.8 ± 2.1	47.0 ± 1.9	49.8 ± 2.8	48.7 ± 4.5	50.8 ± 3.0	46.0 ± 1.1	51.7 ± 3.8	52.5 ± 3.6
10 Sep.	111	61.0 ± 4.9	60.2 ± 6.2	60.0 ± 3.1	51.0 ± 3.5	57.5 ± 2.2	54.0 ± 6.0	52.3 ± 4.6	46.7 ± 2.1	54.0 ± 2.6	52.8 ± 3.1

[1] N=6/Treatment

Appendix 5. Mean height (cm ± S.E.) of plants in experimental treatments at the Winkler experimental plot, 1990.

Date	Days after planting	Experimental treatment[1]	
		000	005
26 June	32	11.7 ± 2.1	12.5 ± 2.1
4 July	40	29.8 ± 1.4	30.2 ± 2.5
10 July	46	43.3 ± 2.0	41.5 ± 3.3
17 July	53	57.3 ± 2.3	55.8 ± 4.6
24 July	60	62.7 ± 2.0	45.2 ± 5.9
31 July	67	58.2 ± 1.8	53.8 ± 3.8
9 Aug.	76	46.5 ± 2.0	59.3 ± 3.9
15 Aug.	82	53.7 ± 3.3	61.0 ± 2.7
22 Aug.	89	64.3 ± 1.5	53.2 ± 4.0
29 Aug.	96	50.7 ± 3.1	39.7 ± 3.6
3 Sep.	101	41.5 ± 2.8	41.3 ± 2.6
10 Sep.	108	40.0 ± 2.4	40.3 ± 3.6

[1] N=6/Treatment

Appendix 6. Numbers of tubers and their total mass (g), by size grade, for individual plants, 1989.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Experimental Plot					
000A	No.:	3	2	0	2	4	6	0	0	17
	Mass:	57.9	126.8	0	259.6	613.2	1092.5	0	0	2150.0
000B	No.:	3	1	0	1	2	2	1	1	11
	Mass:	40.8	40.4	0	132.0	348.4	438.2	612.4	489.9	2102.5
000C	No.:	4	0	0	2	3	1	0	0	10
	Mass:	159.1	0	0	206.6	428.2	220.1	0	0	1014.0
001A	No.:	3	0	0	2	6	0	0	0	11
	Mass:	26.5	0	0	236.9	845.2	0	0	0	1108.6
001B	No.:	5	0	0	1	3	2	0	0	11
	Mass:	67.7	0	0	259.5	542.5	508.5	0	0	1378.2
001C	No.:	3	2	2	1	3	3	0	0	14
	Mass:	22.6	114.4	218.8	172.3	417.9	702.0	0	0	1648.0
003A	No.:	2	2	0	0	4	4	1	0	13
	Mass:	55.3	83.4	0	0	636.8	1105.2	344.4	0	2225.1
003B	No.:	5	0	3	1	2	5	3	0	19
	Mass:	86.5	0	223.5	81.0	280.9	954.1	795.1	0	2421.1
003C	No.:	3	1	2	1	1	3	0	0	11
	Mass:	34.4	42.4	226.5	182.8	102.4	781.8	0	0	1370.3
100A	No.:	0	0	0	0	0	0	2	1	3
	Mass:	0	0	0	0	0	0	669.9	464.0	1133.9
100B	No.:	2	2	1	3	2	4	1	0	15
	Mass:	16.1	87.3	64.8	299.3	215.1	1071.0	301.3	0	2054.9
100C	No.:	0	0	0	0	0	3	3	1	7
	Mass:	0	0	0	0	0	846.7	1003.3	427.5	2277.5
101A	No.:	3	1	1	3	1	0	0	0	9
	Mass:	51.3	61.7	74.2	356.3	114.4	0	0	0	657.9
101B	No.:	0	0	0	0	2	2	1	0	5
	Mass:	0	0	0	0	342.4	374.8	426.8	0	1144.0
101C	No.:	0	1	0	0	1	3	2	0	7
	Mass:	0	44.1	0	0	143.4	867.3	969.8	0	2024.6
103A	No.:	0	0	0	0	1	2	0	1	4
	Mass:	0	0	0	0	189.4	365.6	0	675.3	1230.3
103B	No.:	3	0	1	3	2	0	0	0	9
	Mass:	86.6	0	69.9	355.8	294.2	0	0	0	806.5
103C	No.:	1	0	1	0	0	2	0	1	5
	Mass:	6.0	0	65.2	0	0	631.1	0	457.6	1159.9

Appendix 6. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Experimental Plot (Continued)					
200A	No.:	0	0	0	2	1	3	0	0	6
	Mass:	0	0	0	232.4	141.2	1022.2	0	0	1395.8
200B	No.:	2	0	0	0	2	1	2	0	7
	Mass:	58.4	0	0	0	252.2	145.4	863.2	0	1319.2
200C	No.:	2	1	0	0	3	4	2	0	12
	Mass:	21.3	78.6	0	0	478.6	854.7	733.2	0	2166.4
201A	No.:	4	0	2	1	2	4	0	1	14
	Mass:	41.5	0	99.9	95.2	226.4	801.6	0	438.5	1703.1
201B	No.:	4	0	0	0	1	4	3	0	12
	Mass:	57.4	0	0	0	111.1	1080.7	1106.3	0	2355.5
201C	No.:	1	2	1	0	3	2	0	0	9
	Mass:	10.5	112.1	87.0	0	437.6	436.0	0	0	1083.2
203A	No.:	11	0	0	1	3	3	2	0	20
	Mass:	168.3	0	0	106.4	458.8	777.7	521.5	0	2032.7
203B	No.:	2	4	2	0	5	1	0	0	14
	Mass:	22.0	320.6	149.6	0	686.0	297.8	0	0	1476.0
203C	No.:	0	0	0	0	2	3	1	0	6
	Mass:	0	0	0	0	433.9	1417.0	296.9	0	2147.8
110A	No.:	0	0	2	0	4	3	0	0	9
	Mass:	0	0	224.4	0	617.0	995.7	0	0	1837.1
110B	No.:	2	0	0	0	2	5	0	0	9
	Mass:	51.6	0	0	0	221.5	1302.5	0	0	1575.6
110C	No.:	2	2	1	3	0	4	0	3	15
	Mass:	38.7	113.3	56.5	296.1	0	860.3	0	1318.5	2683.4
CLEAR#1[a]	No.:	2	0	1	0	1	5	1	0	10
	Mass:	63.6	0	60.1	0	129.2	879.0	437.6	0	1569.5
CLEAR#2	No.:	1	0	0	0	1	3	2	0	7
	Mass:	37.3	0	0	0	218.9	503.4	1099.7	0	1859.3
CLEAR#3	No.:	12	3	2	3	8	3	0	0	31
	Mass:	141.7	109.1	111.8	313.4	931.1	582.8	0	0	2189.9
CLEAR#4	No.:	3	3	1	0	1	6	1	1	16
	Mass:	11.2	178.8	73.2	0	168.5	1187.3	401.0	313.6	2333.6
CLEAR#5	No.:	4	1	2	1	3	1	0	0	12
	Mass:	73.3	64.5	120.5	75.6	830.6	474.5	0	0	1639.0
NONCLR#1[b]	No.:	4	0	2	2	0	3	0	0	11
	Mass:	70.2	0	180.9	289.6	0	1055.5	0	0	1596.2

Appendix 6. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Experimental Plot (Continued)										
NONCLR#2	No.:	0	0	1	1	3	2	2	0	9
	Mass:	0	0	118.0	82.2	348.4	323.2	654.4	0	1526.2
NONCLR#3	No.:	3	3	4	1	1	1	1	0	14
	Mass:	85.5	149.4	355.5	60.3	164.2	265.2	181.5	0	1261.6
NONCLR#4	No.:	0	0	0	2	2	3	1	0	8
	Mass:	0	0	0	186.3	253.8	520.1	228.5	0	1188.7
NONCLR#5	No.:	1	2	1	1	0	6	1	0	12
	Mass:	5.4	57.5	89.6	145.9	0	1450.8	561.1	0	2310.3
Reservoir Plot										
RES#1[c]	No.:	7	3	1	0	3	0	0	0	14
	Mass:	88.6	163.7	89.5	0	399.3	0	0	0	741.1
RES#2	No.:	1	1	1	1	2	3	0	0	9
	Mass:	59.3	50.3	73.1	132.2	222.3	562.7	0	0	1099.9
RES#3	No.:	6	2	0	1	1	1	0	0	11
	Mass:	148.3	145.8	0	64.8	74.6	136.2	0	0	569.7
RES#4	No.:	4	1	2	2	3	1	0	0	13
	Mass:	150.4	99.8	143.2	198.4	318.6	282.6	0	0	1193.0
RES#5	No.:	2	1	3	1	7	0	0	1	15
	Mass:	21.5	41.1	253.2	292.8	1010.4	0	0	265.6	1884.6
RES#6	No.:	10	4	2	0	4	1	0	0	21
	Mass:	241.2	157.5	165.2	0	607.5	151.7	0	0	1323.1
RES#7	No.:	7	5	1	0	0	0	0	0	13
	Mass:	82.8	267.3	57.3	0	0	0	0	0	407.4
RES#8	No.:	6	1	0	2	2	0	0	0	11
	Mass:	97.2	68.1	0	160.2	246.9	0	0	0	572.4
RES#9	No.:	3	0	2	0	5	1	0	0	11
	Mass:	53.3	0	148.2	0	608.2	199.8	0	0	1009.5
RES#10	No.:	4	1	1	1	3	2	0	0	12
	Mass:	61.4	42.7	49.5	121.9	435.1	356.7	0	0	1067.3
RES#11	No.:	6	1	3	3	1	2	0	0	16
	Mass:	116.4	65.1	240.0	279.5	158.1	447.6	0	0	1306.7
RES#12	No.:	7	1	3	2	4	1	0	0	18
	Mass:	83.1	50.5	232.0	158.2	669.1	180.2	0	0	1373.1
RES#13	No.:	2	0	0	0	1	1	2	0	6
	Mass:	32.5	0	0	0	247.9	355.9	779.5	0	1415.8

Appendix 6. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Reservoir Plot (Continued)										
RES#14	No.:	4	1	2	1	2	1	1	0	12
	Mass:	49.1	52.3	132.2	154.6	240.8	259.7	278.0	0	1166.7
RES#15	No.:	7	2	1	4	2	0	0	0	16
	Mass:	124.5	115.3	73.9	345.6	317.5	0	0	0	976.8
Portage Sampling Plot										
A10[d]	No.:	5	2	0	0	0	0	0	0	7
	Mass:	69.2	94.5	0	0	0	0	0	0	163.7
A14	No.:	8	4	0	0	0	0	0	0	12
	Mass:	160.6	149.4	0	0	0	0	0	0	310.0
B3	No.:	2	1	2	0	1	0	0	0	6
	Mass:	26.7	54.6	127.9	0	170.1	0	0	0	379.3
B6	No.:	1	1	2	3	0	0	0	0	7
	Mass:	9.4	40.3	135.6	288.5	0	0	0	0	473.8
C2	No.:	5	5	0	0	0	0	0	0	10
	Mass:	213.3	100.0	0	0	0	0	0	0	313.3
C15	No.:	0	2	1	1	0	0	0	0	4
	Mass:	0	120.8	70.7	73.9	0	0	0	0	265.4
D14	No.:	2	1	1	0	1	0	0	0	5
	Mass:	18.4	48.6	57.2	0	116.7	0	0	0	240.9
D25	No.:	0	1	2	1	3	0	0	0	7
	Mass:	0	47.6	110.9	128.1	328.6	0	0	0	615.2
E3	No.:	1	2	1	0	0	0	0	0	4
	Mass:	35.3	115.6	51.8	0	0	0	0	0	202.7
E10	No.:	0	0	1	0	0	0	0	0	1
	Mass:	0	0	93.8	0	0	0	0	0	93.8
F23	No.:	2	3	0	0	0	0	0	0	5
	Mass:	33.3	140.0	0	0	0	0	0	0	173.3
F24	No.:	1	2	0	3	0	0	0	0	6
	Mass:	20.5	91.1	0	267.3	0	0	0	0	378.9
G17	No.:	3	1	0	0	1	0	0	0	5
	Mass:	64.6	40.9	0	0	137.1	0	0	0	242.6
G21	No.:	3	1	0	0	0	0	0	0	4
	Mass:	63.6	67.0	0	0	0	0	0	0	130.6
H1	No.:	2	1	2	0	0	0	0	0	5
	Mass:	70.3	34.1	111.1	0	0	0	0	0	215.5

Appendix 6. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Portage Sampling Plot (Continued)					
H5	No.:	6	4	0	0	0	0	0	0	10
	Mass:	118.7	218.5	0	0	0	0	0	0	337.2
I9	No.:	1	2	0	1	0	0	0	0	4
	Mass:	3.7	102.8	0	88.6	0	0	0	0	195.1
I14	No.:	0	3	0	0	1	0	0	0	4
	Mass:	0	240.0	0	0	86.4	0	0	0	326.4
J1	No.:	3	4	0	1	0	0	0	0	8
	Mass:	91.3	229.0	0	76.9	0	0	0	0	397.2
J16	No.:	4	1	0	0	0	0	0	0	5
	Mass:	92.2	70.4	0	0	0	0	0	0	162.6
K2	No.:	1	2	1	0	1	0	0	0	5
	Mass:	20.8	64.6	60.3	0	76.9	0	0	0	222.6
K14	No.:	8	0	0	0	0	0	0	0	8
	Mass:	109.6	0	0	0	0	0	0	0	109.6
L16	No.:	9	1	0	1	0	0	0	0	11
	Mass:	118.3	41.0	0	54.7	0	0	0	0	214.0
L17	No.:	2	2	0	1	1	0	0	0	6
	Mass:	13.0	104.5	0	87.2	89.1	0	0	0	293.8
M1	No.:	2	1	0	3	1	1	0	0	8
	Mass:	30.2	31.5	0	631.8	238.2	216.0	0	0	1147.7
M16	No.:	6	2	0	0	0	0	0	0	8
	Mass:	112.6	104.3	0	0	0	0	0	0	216.9
N4	No.:	2	5	2	0	0	0	0	0	9
	Mass:	36.0	240.9	184.1	0	0	0	0	0	461.0
N11	No.:	0	2	1	1	0	0	0	0	4
	Mass:	0	96.0	130.2	105.8	0	0	0	0	332.0
O1	No.:	0	0	1	0	2	2	0	0	5
	Mass:	0	0	71.3	0	295.0	326.1	0	0	692.4
O3	No.:	3	2	0	2	0	0	0	0	7
	Mass:	66.4	106.9	0	245.3	0	0	0	0	418.6
					Commercial Field					
COM#1[a]	No.:	8	2	2	3	5	4	1	0	25
	Mass:	148.8	69.2	183.1	267.4	885.9	1122.2	459.4	0	3136.0
COM#2	No.:	0	0	1	2	3	4	1	0	11
	Mass:	0	0	84.4	208.9	412.7	929.2	430.5	0	2065.7

Appendix 6. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
		Commercial Field (Continued)								
COM#3	No.:	2	4	5	5	11	2	0	0	29
	Mass:	51.3	192.3	409.5	319.6	1600.0	428.0	0	0	3000.7
COM#4	No.:	0	0	0	3	4	1	0	0	8
	Mass:	0	0	0	289.7	547.6	186.3	0	0	1023.6
COM#5	No.:	2	3	3	6	4	10	0	0	18
	Mass:	23.0	172.0	260.3	644.0	546.7	1655.3	0	0	3301.3
COM#6	No.:	3	2	1	3	6	3	0	0	18
	Mass:	97.0	101.4	57.0	306.3	898.7	667.4	0	0	2127.8
COM#7	No.:	1	0	1	0	2	3	1	1	6
	Mass:	16.8	0	65.0	0	239.1	603.5	319.8	437.4	1681.5
COM#8	No.:	1	1	4	3	4	6	0	0	19
	Mass:	10.4	29.3	274.8	319.3	573.5	1123.0	0	0	2330.3
COM#9	No.:	0	0	0	0	0	6	0	0	6
	Mass:	0	0	0	0	0	1725.7	0	0	1725.7
COM#10	No.:	1	0	0	1	1	4	1	0	8
	Mass:	29.2	0	0	63.4	343.9	825.9	308.9	0	1571.3
COM#11	No.:	0	0	0	1	0	5	0	0	6
	Mass:	0	0	0	66.1	0	1473.8	0	0	1539.9
COM#12	No.:	1	0	1	1	1	1	0	0	5
	Mass:	30.0	0	41.5	97.8	114.7	304.9	0	0	588.9
COM#13	No.:	1	0	0	0	0	2	1	0	4
	Mass:	20.4	0	0	0	0	602.3	442.0	0	1064.7
COM#14	No.:	1	1	0	1	5	2	0	0	10
	Mass:	8.9	48.2	0	60.8	629.7	442.4	0	0	1190.0
COM#15	No.:	1	2	0	2	5	4	2	0	16
	Mass:	9.6	131.1	0	160.4	833.3	901.1	973.1	0	3008.6
COM#16	No.:	3	2	1	0	10	0	0	0	16
	Mass:	35.6	100.3	93.6	0	1498.8	0	0	0	1728.3
COM#17	No.:	0	2	2	0	3	4	2	0	13
	Mass:	0	128.3	122.9	0	416.3	1449.6	811.0	0	2928.1
COM#18	No.:	2	2	2	0	8	3	0	0	17
	Mass:	42.4	128.4	175.6	0	1240.5	754.4	0	0	2341.3
COM#19	No.:	3	3	2	1	6	7	0	0	22
	Mass:	23.7	173.5	117.5	71.8	886.9	1635.1	0	0	2908.5
COM#20	No.:	1	0	0	1	3	5	1	1	12
	Mass:	6.6	0	0	89.8	489.3	1237.2	431.6	531.4	2785.9

Appendix 6. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Commercial Field (Continued)					
COM#21	No.:	0	0	2	0	2	3	0	3	10
	Mass:	0	0	142.4	0	348.6	944.2	0	1451.0	2886.2
COM#22	No.:	7	1	2	1	7	9	0	0	27
	Mass:	115.0	47.2	109.5	100.6	972.4	1598.0	0	0	2942.7
COM#23	No.:	1	0	0	1	0	1	2	1	6
	Mass:	15.1	0	0	103.7	0	107.9	583.3	496.9	1369.9
COM#24	No.:	3	3	1	0	6	5	0	0	18
	Mass:	67.9	132.6	117.9	0	929.8	1102.3	0	0	2350.5
COM#25	No.:	5	5	3	2	4	2	0	0	21
	Mass:	92.5	237.3	275.2	236.2	533.1	437.5	0	0	1811.8
COM#26	No.:	0	3	0	3	4	3	1	2	16
	Mass:	0	184.2	0	318.7	511.8	453.7	440.2	999.1	2907.7
COM#27	No.:	0	1	0	1	6	3	0	0	11
	Mass:	0	42.8	0	108.7	989.8	831.9	0	0	1973.2
COM#28	No.:	2	0	3	2	6	10	1	0	24
	Mass:	53.1	0	236.1	198.4	892.7	2157.3	407.1	0	3944.7
COM#29	No.:	0	0	0	1	0	6	1	1	9
	Mass:	0	0	0	90.9	0	1735.7	413.6	416.6	2656.8
COM#30	No.:	0	0	0	0	0	3	2	2	7
	Mass:	0	0	0	0	0	703.7	575.8	1368.2	2647.7

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[a]Cleared Row, Plant #1
[b]Non-Cleared Row, Plant #1
[c]Reservoir Plot, Plant #1
[d]A-O = subplot label; 1-25 = within subplot plant numbering.
[e]Commercial Field, Plant #1

Appendix 7. Numbers of tubers and their total mass (g), by size grade, for individual plants, 1990.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Morden Experimental Plot					
000A	No.:	4	1	0	1	3	3	2	2	16
	Mass:	80.8	66.5	0	85.8	525.6	636.2	879.0	1879.7	4153.6
000B	No.:	2	0	0	3	3	4	3	0	15
	Mass:	23.5	0	0	261.1	331.7	1403.2	1290.7	0	3310.2
000C	No.:	4	3	1	2	2	3	0	4	19
	Mass:	68.8	155.5	93.2	119.9	286.0	2017.2	0	2027.2	4767.8
000D	No.:	2	3	2	1	4	7	0	3	22
	Mass:	46.7	127.4	144.1	100.5	364.9	1603.0	0	1877.5	4264.1
000E	No.:	6	5	1	1	3	6	1	2	25
	Mass:	102.7	172.1	71.3	138.7	380.9	1186.8	306.5	2176.7	4535.7
000F	No.:	19	3	5	2	3	2	0	2	36
	Mass:	401.2	129.3	259.8	179.6	353.9	1009.2	0	1681.0	4014.0
001A	No.:	8	7	5	4	7	6	1	2	40
	Mass:	185.9	381.4	314.3	249.8	704.7	1362.4	214.6	588.3	4001.4
001B	No.:	2	4	2	2	4	3	0	4	21
	Mass:	29.3	165.8	144.9	180.3	427.4	241.4	0	2823.3	4012.4
001C	No.:	0	0	0	2	2	7	3	3	17
	Mass:	0	0	0	156.0	268.1	2279.9	923.7	1472.8	5100.5
001D	No.:	3	2	1	3	6	5	1	4	25
	Mass:	81.5	73.0	49.5	254.0	911.8	1705.5	643.9	1908.1	5627.3
001E	No.:	3	0	1	1	4	3	3	1	16
	Mass:	38.7	0	186.3	120.4	656.5	813.8	1488.9	557.6	3862.2
001F	No.:	3	0	2	0	3	5	2	1	16
	Mass:	42.3	0	146.5	0	369.2	1553.2	1312.9	451.0	3875.1
003A	No.:	5	1	1	0	5	2	1	5	20
	Mass:	25.0	46.4	63.0	0	904.0	649.6	588.2	2819.2	5095.4
003B	No.:	6	2	0	2	2	4	4	0	20
	Mass:	92.9	116.6	0	259.5	290.0	1057.9	2017.4	0	3834.3
003C	No.:	10	5	0	1	7	6	0	2	31
	Mass:	166.3	203.5	0	81.7	1398.8	1546.3	0	1047.4	4444.0
003D	No.:	8	5	1	4	2	2	0	0	22
	Mass:	52.2	211.1	130.0	353.5	375.5	549.3	0	0	1571.6
003E	No.:	9	12	0	1	3	7	1	0	33
	Mass:	134.4	594.8	0	149.0	353.2	2197.0	612.7	0	4041.0
003F	No.:	0	4	1	1	1	0	0	7	14
	Mass:	0	173.9	184.4	66.3	131.4	0	0	3973.5	4529.5

Appendix 7. Continued.

		Maximum tuber diameter (D cm)								
Plant		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Morden Experimental Plot (Continued)										
005A	No.:	0	0	0	0	1	1	2	1	5
	Mass:	0	0	0	0	122.8	365.7	1130.2	962.4	2581.1
005B	No.:	1	1	1	1	1	0	2	3	10
	Mass:	42.2	41.4	61.3	109.6	189.8	0	679.2	2117.5	3241.0
005C	No.:	3	1	1	4	0	6	2	0	17
	Mass:	64.2	32.0	68.6	619.3	0	1368.0	1761.5	0	3913.6
005D	No.:	1	1	0	1	4	2	0	2	11
	Mass:	49.0	32.2	0	64.5	575.8	832.4	0	1928.3	2482.2
005E	No.:	3	0	0	0	1	5	2	1	12
	Mass:	56.0	0	0	0	147.0	889.9	1630.6	1365.3	4088.8
005F	No.:	4	3	0	1	4	5	1	1	19
	Mass:	85.9	126.7	0	117.0	461.1	1190.1	394.1	869.2	3244.1
100A	No.:	3	2	1	0	7	4	2	1	20
	Mass:	51.3	125.4	52.7	0	858.7	546.8	620.0	945.4	3200.3
100B	No.:	0	0	0	0	0	2	0	1	3
	Mass:	0	0	0	0	0	1433.8	0	611.7	2045.5
100C	No.:	2	1	0	1	1	5	1	3	14
	Mass:	30.7	51.6	0	57.6	96.9	1294.7	406.5	1871.1	3809.1
100D	No.:	1	0	0	0	2	7	0	6	16
	Mass:	11.3	0	0	0	326.5	1433.4	0	2794.2	4565.4
100E	No.:	3	0	0	0	0	5	2	2	12
	Mass:	360.4	0	0	0	0	1364.3	1676.9	938.4	4340.0
100F	No.:	7	1	1	1	5	8	0	3	26
	Mass:	112.6	80.4	59.6	59.7	554.9	1631.3	0	1587.4	4085.9
101A	No.:	6	4	3	3	6	2	1	1	26
	Mass:	94.7	187.8	353.6	238.1	818.6	638.8	551.0	778.6	3661.2
101B	No.:	1	0	5	3	0	2	1	3	15
	Mass:	11.2	0	381.2	240.9	0	782.0	459.5	1582.1	3456.9
101C	No.:	0	0	0	0	0	1	1	2	4
	Mass:	0	0	0	0	0	135.1	426.3	1722.0	2283.4
101D	No.:	4	2	1	1	1	5	0	1	15
	Mass:	101.7	96.6	107.7	93.0	112.4	1139.8	0	325.4	1976.6
101E	No.:	8	0	2	3	2	3	0	2	20
	Mass:	162.3	0	102.6	241.6	137.8	727.6	0	2606.9	3978.8
101F	No.:	7	3	2	2	2	3	2	2	23
	Mass:	158.4	124.7	100.3	179.0	220.3	563.8	1090.6	951.9	3389.0

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Morden Experimental Plot (Continued)					
103A	No.:	1	1	0	0	1	5	1	0	9
	Mass:	18.0	46.2	0	0	110.7	2169.3	905.0	0	3249.2
103B	No.:	1	1	0	0	2	0	2	0	6
	Mass:	9.4	155.4	0	0	368.4	0	960.7	0	1493.9
103C	No.:	7	1	2	1	1	2	0	0	14
	Mass:	150.7	61.2	128.4	78.2	89.8	1038.3	0	0	1546.6
103D	No.:	1	2	0	0	4	4	2	1	14
	Mass:	14.3	106.2	0	0	739.9	1195.0	1055.4	331.2	3442.0
103E	No.:	7	3	3	0	8	7	0	0	28
	Mass:	116.0	172.1	252.2	0	1164.1	1700.3	0	0	3404.7
103F	No.:	5	5	1	1	0	1	0	2	15
	Mass:	97.2	310.2	59.3	93.0	0	100.1	0	1686.1	2345.9
105A	No.:	3	2	0	1	1	5	0	0	12
	Mass:	71.0	75.7	0	134.6	94.0	1099.3	0	0	1474.6
105B	No.:	4	2	0	1	2	4	0	0	13
	Mass:	112.4	115.1	0	146.8	378.0	764.5	0	0	1516.8
105C	No.:	3	5	2	2	2	1	1	0	16
	Mass:	46.4	170.0	179.8	282.4	165.8	244.4	373.8	0	1462.6
105D	No.:	2	1	0	2	3	1	0	0	9
	Mass:	23.7	31.3	0	186.4	457.7	123.2	0	0	822.3
105E	No.:	8	3	0	1	2	3	1	0	18
	Mass:	144.1	141.5	0	97.2	238.6	605.7	308.6	0	1535.7
105F	No.:	2	1	0	4	1	7	0	1	16
	Mass:	41.2	38.1	0	311.0	164.1	1533.5	0	558.2	2646.1
CLEAR#1[a]	No.:	2	2	0	2	4	1	2	0	13
	Mass:	35.6	108.3	0	248.9	787.5	166.5	989.2	0	2336.0
CLEAR#2	No.:	5	3	1	0	3	2	0	0	14
	Mass:	125.6	110.1	90.7	0	392.0	1007.7	0	0	1726.1
CLEAR#3	No.:	3	1	0	1	0	7	0	1	12
	Mass:	66.8	55.0	0	69.4	0	2166.1	0	464.1	2821.4
CLEAR#4	No.:	2	1	2	0	2	4	1	1	13
	Mass:	25.7	52.4	144.9	0	256.0	763.3	618.1	707.6	2568.0
CLEAR#5	No.:	0	1	0	0	1	2	0	0	4
	Mass:	0	70.1	0	0	96.7	303.2	0	0	470.0
CLEAR#6	No.:	1	1	2	1	1	5	2	1	14
	Mass:	11.0	50.0	121.9	93.6	80.8	1107.8	624.4	363.2	2452.7

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Morden Experimental Plot (Continued)										
NONCLR#1^b	No.:	0	1	1	0	2	4	2	0	10
	Mass	0	52.5	132.6	0	223.9	567.4	639.7	0	1616.1
NONCLR#2	No.:	0	1	0	0	2	1	1	1	6
	Mass:	0	78.6	0	0	544.5	142.8	688.0	426.6	1880.5
NONCLR#3	No.:	3	0	0	3	1	2	0	0	9
	Mass:	38.9	0	0	300.2	64.5	412.2	0	0	815.8
NONCLR#4	No.:	0	5	1	2	4	2	0	0	14
	Mass:	0	243.4	86.9	221.9	502.1	867.9	0	0	1922.2
NONCLR#5	No.:	3	0	0	1	0	3	3	0	10
	Mass:	42.6	0	0	65.5	0	651.0	1115.7	0	1874.8
NONCLR#6	No.	3	0	0	2	3	6	0	0	14
	Mass:	63.0	0	0	136.6	394.3	1175.6	0	0	1769.5
Morden Reservoir Plot										
RES#1^c	No.:	0	0	0	1	2	1	1	0	5
	Mass:	0	0	0	104.0	293.2	472.9	271.6	0	1141.7
RES#2	No.:	0	3	1	4	1	1	0	0	10
	Mass:	0	127.1	92.8	410.6	100.6	197.6	0	0	928.7
RES#3	No.	3	1	0	0	3	2	0	0	9
	Mass:	48.2	33.6	0	0	452.3	710.1	0	0	1244.2
RES#4	No.:	1	1	1	0	2	0	1	1	7
	Mass:	26.6	56.9	101.3	0	292.3	0	306.6	292.4	1076.1
RES#5	No.:	0	2	1	2	2	3	0	0	10
	Mass:	0	117.6	69.4	218.1	210.5	621.7	0	0	1237.3
RES#6	No.:	2	1	0	0	4	2	0	0	9
	Mass:	59.1	50.2	0	0	317.2	454.4	0	0	880.9
RES#7	No.:	3	1	3	2	2	1	0	0	12
	Mass:	41.5	38.4	204.5	218.6	193.0	123.2	0	0	819.2
RES#8	No.:	3	2	0	1	2	3	0	0	11
	Mass:	85.1	147.2	0	123.2	366.7	590.0	0	0	1312.2
RES#9	No.:	3	2	2	1	0	4	0	0	12
	Mass:	59.0	98.3	112.0	66.9	0	756.2	0	0	1092.4
RES#10	No.:	2	2	0	1	3	2	2	0	12
	Mass:	15.0	100.1	0	120.1	284.4	296.2	473.7	0	1289.5
RES#11	No.:	1	0	0	1	2	5	0	0	9
	Mass:	15.0	0	0	89.0	275.5	1214.8	0	0	1594.3

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Morden Reservoir Plot (Continued)										
RES#12	No.:	4	1	1	1	2	3	0	0	12
	Mass:	123.6	38.4	71.5	80.6	218.8	747.5	0	0	1280.4
RES#13	No.:	2	6	3	3	0	3	0	1	18
	Mass:	28.6	264.1	177.9	180.7	0	436.1	0	214.8	1302.1
RES#14	No.:	2	2	1	1	3	4	0	0	13
	Mass:	43.4	74.8	68.3	75.8	320.0	464.5	0	0	1046.8
RES#15	No.:	5	1	0	0	2	2	0	0	10
	Mass:	52.7	75.5	0	0	329.5	339.4	0	0	797.1
Winkler Experimental Plot										
000A	No.:	4	0	1	0	0	5	1	0	11
	Mass:	72.1	0	33.6	0	0	1788.3	659.1	0	2553.1
000B	No.:	5	5	0	0	0	0	1	1	12
	Mass	114.5	257.1	0	0	0	0	678.6	370.4	1420.6
000C	No.:	0	0	0	2	0	6	1	2	11
	Mass:	0	0	0	213.0	0	1328.5	391.8	853.8	2787.1
000D	No.:	0	0	1	0	0	4	2	0	7
	Mass:	0	0	109.9	0	0	942.3	787.9	0	1840.1
000E	No.:	1	0	0	0	0	5	1	0	7
	Mass:	6.3	0	0	0	0	1380.2	339.6	0	1726.1
000F	No.:	0	0	1	0	1	2	2	2	8
	Mass:	0	0	66.2	0	122.1	625.4	747.6	1014.4	2575.7
005A	No.:	0	0	0	2	2	2	0	3	9
	Mass:	0	0	0	280.5	444.2	329.7	0	1794.6	2849.0
005B	No.:	0	2	0	0	0	5	1	0	8
	Mass:	0	125.2	0	0	0	1627.0	430.4	0	2182.6
005C	No.:	0	0	0	0	0	3	0	1	4
	Mass:	0	0	0	0	0	815.0	0	911.6	1726.6
005D	No.:	0	0	1	0	7	1	0	0	9
	Mass:	0	0	93.5	0	1440.9	283.8	0	0	1818.2
005E	No.:	0	1	0	0	0	5	0	0	6
	Mass:	0	95.6	0	0	0	1343.8	0	0	1439.4
005F	No.:	3	0	0	0	2	6	2	1	14
	Mass:	19.5	0	0	0	300.2	1831.4	851.0	586.9	3589.0
NONCLR#1[d]	No.:	0	3	1	0	2	3	0	0	9
	Mass:	0	249.3	101.2	0	303.6	730.3	0	0	1384.4

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
Winkler Experimental Plot (Continued)										
NONCLR#2	No.:	1	0	0	0	1	0	2	0	4
	Mass:	34.4	0	0	0	246.4	0	1337.4	0	1618.2
NONCLR#3	No.:	2	1	1	1	0	5	0	0	10
	Mass:	43.6	36.8	54.9	57.0	0	1713.8	0	0	1906.1
NONCLR#4	No.:	1	3	1	1	1	0	0	0	7
	Mass:	29.6	132.0	84.8	80.1	80.9	0	0	0	407.4
NONCLR#5	No.:	0	2	3	2	4	1	0	0	12
	Mass:	0	77.9	320.9	320.6	751.4	365.4	0	0	1836.2
NONCLR#6	No.:	1	2	0	0	3	5	0	0	11
	Mass:	6.7	73.4	0	0	468.3	1389.3	0	0	1937.7
Winkler Reservoir Plot										
RES#1•	No.:	0	0	1	0	2	0	0	0	3
	Mass:	0	0	133.7	0	287.1	0	0	0	514.8
RES#2	No.:	0	0	0	0	1	3	1	0	5
	Mass:	0	0	0	0	132.4	660.4	338.8	0	1131.6
RES#3	No.:	0	0	0	1	2	2	0	0	5
	Mass:	0	0	0	95.3	297.1	370.5	0	0	762.9
RES#4	No.:	1	3	1	0	5	3	0	0	13
	Mass:	17.4	131.5	92.8	0	761.9	682.7	0	0	1686.3
RES#5	No.:	0	0	0	3	0	2	0	0	5
	Mass:	0	0	0	282.3	0	526.9	0	0	809.2
RES#6	No.:	3	2	1	0	1	3	0	0	10
	Mass:	52.5	96.7	49.2	0	82.1	488.8	0	0	769.3
RES#7	No.:	0	1	0	1	3	3	1	0	9
	Mass:	0	51.8	0	87.7	391.8	688.4	375.2	0	1594.9
RES#8	No.:	0	0	1	0	1	0	2	0	4
	Mass:	0	0	116.1	0	96.4	0	885.9	0	1098.4
RES#9	No.:	0	0	0	0	0	4	0	0	4
	Mass:	0	0	0	0	0	794.8	0	0	794.8
RES#10	No.:	1	1	2	1	5	1	0	0	11
	Mass:	37.2	64.2	160.6	154.3	781.5	249.6	0	0	1447.4
RES#11	No.:	0	0	0	0	0	1	1	1	3
	Mass:	0	0	0	0	0	292.1	227.8	726.0	1245.9
RES#12	No.:	0	2	1	3	1	0	1	1	9
	Mass:	0	108.4	91.8	271.6	80.0	0	236.4	423.6	1211.8

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								Total
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	
Winkler Reservoir Plot (Continued)										
RES#13	No.:	0	0	0	1	2	4	1	0	8
	Mass:	0	0	0	75.5	322.4	840.2	323.8	0	1561.9
RES#14	No.:	0	0	0	0	1	3	2	0	6
	Mass:	0	0	0	0	78.7	596.3	612.6	0	1287.6
RES#15	No.:	1	0	2	0	3	3	0	0	9
	Mass:	33.4	0	180.4	0	349.3	617.8	0	0	1180.9
Commercial Field										
COM#1[f]	No.:	0	1	0	5	3	1	0	0	10
	Mass:	0	51.4	0	524.2	392.4	208.5	0	0	1176.5
COM#2	No.:	1	1	2	3	1	0	0	0	8
	Mass:	8.0	89.5	201.2	346.9	122.7	0	0	0	768.3
COM#3	No.:	0	0	0	0	4	3	0	0	7
	Mass:	0	0	0	0	559.1	749.6	0	0	1308.7
COM#4	No.:	0	0	0	0	2	3	0	0	5
	Mass:	0	0	0	0	253.9	689.7	0	0	943.6
COM#5	No.:	0	0	0	0	2	2	0	0	4
	Mass:	0	0	0	0	339.0	531.9	0	0	870.9
COM#6	No.:	0	0	0	1	0	2	0	0	3
	Mass:	0	0	0	107.2	0	365.0	0	0	472.2
COM#7	No.:	6	1	2	4	1	0	0	0	14
	Mass:	146.0	56.6	119.4	335.4	112.9	0	0	0	770.3
COM#8	No.:	0	1	0	2	1	1	0	0	5
	Mass:	0	59.8	0	179.3	123.3	164.7	0	0	527.1
COM#9	No.:	0	0	0	0	1	1	0	0	2
	Mass:	0	0	0	0	206.3	252.6	0	0	458.9
COM#10	No.:	7	1	0	1	1	2	0	0	12
	Mass:	145.0	46.4	0	105.9	161.2	321.0	0	0	779.5
COM#11	No.:	2	0	0	2	1	0	1	0	6
	Mass:	54.5	0	0	147.8	162.5	0	497.9	0	862.7
COM#12	No.:	0	4	1	0	2	0	0	1	8
	Mass:	40.2	179.2	68.2	0	321.7	0	0	413.1	1022.5
COM#13	No.:	1	0	0	0	4	1	1	0	7
	Mass:	20.6	0	0	0	407.8	148.2	202.5	0	779.1
COM#14	No.:	2	1	0	0	2	2	1	0	8
	Mass:	27.2	34.9	0	0	336.3	578.5	221.9	0	1198.8

Appendix 7. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
					Commercial Field (Continued)					
COM#15	No.:	2	0	1	1	3	0	0	0	7
	Mass:	63.2	0	80.0	82.8	368.1	0	0	0	594.1

[a] Morden Experimental Plot, Cleared Row, Plant #1
[b] Morden Experimental Plot, Non-Cleared Row, Plant #1
[c] Morden Reservoir Plot, Plant #1
[d] Winkler Experimental Plot, Non-Cleared Row, Plant #1
[e] Winkler Reservoir Plot, Plant #1
[f] Commercial Field, Plant #1

CHAPTER III

PART 2

Accumulation of feeding punctures by the potato flea beetle, *Epitrix cucumeris* (Harris), on leaflets of cv. Russet Burbank potatoes

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Abstract

In 1989 and 1990, cv. Russet Burbank potato plants were grown in cages in field plots, and potato flea beetles, *Epitrix cucumeris* (Harris), and Colorado potato beetles, *Leptinotarsa decemlineata* (Say), were introduced in different multiples of naturally occurring field densities. Colorado potato beetles were introduced only in the early part of the growing season, but potato flea beetles were introduced for the duration of the season. Feeding punctures were counted each week in terminal leaflets from the lower, middle and upper third of plants; in addition, punctures were counted in non-terminal leaflets from the upper third of plants. Behavioral models were developed to describe the spatial and temporal pattern of flea beetle feeding. Results indicate that a switch in feeding preference from lower to middle and upper leaflets occurred after the period of peak flea beetle abundance. High densities of flea beetles reduced the rate of feeding per individual and may alter the pattern of feeding preference by causing beetles to disperse more evenly throughout the plant. Disruptions to the generalized upward feeding movement may further be related to changes in plant microenvironment.

A preliminary population model was also derived, which established a relationship between average feeding punctures per leaflet and accumulated flea beetle weeks. This relationship enables the estimation of flea beetle numbers per plant, but is very sensitive to the accuracy of feeding puncture counts.

Introduction

The potato flea beetle, *Epitrix cucumeris* (Harris), is a common pest of potatoes in Manitoba and undergoes one generation per year (Senanayake 1987). Injury to potato plants is primarily caused by the adults, which chew small round holes in the leaflets. Larvae feed on the fine rootlets of plants and, on rare occasions, the tubers (Cole 1951; Thompson 1987). Adult feeding punctures usually penetrate the entire thickness of the leaflet often giving them the appearance of being "peppered with fine shot" (Cannon 1949). Feeding punctures are approximately 1 mm in diameter and are generally encircled by an area of necrotic tissue (Ladd 1963). Amalgamation of punctures, in extreme cases, causes severe leaflet desiccation and death. In the Canadian Maritime Provinces, the summer generation of potato flea beetle, if uncontrolled, may cause significant yield losses in cv. Russet Burbank potatoes (Thompson 1987).

A preliminary economic injury level has been developed for the potato flea beetle feeding on cv. Russet Burbank potatoes (Chapter III, Part 1 of this thesis); this injury level was expressed as numbers of beetles per plant. However, densities of potato flea beetles per plant are extremely difficult to determine in the field because of the small size and extreme mobility of the adults. Accurate estimates can be obtained only by whole-plant bag sampling, but this technique is too complex for use in routine monitoring (Senanayake and Holliday 1988). Visual sampling and sweep-net sampling lack sufficient precision or accuracy, or have seasonal changes in efficiency (Senanayake and Holliday 1988). An alternative method for obtaining an index of potato flea beetle density might be derived from counting feeding punctures per leaflet. However, without knowledge about the way in which feeding punctures accumulate, such an index of damage is of little use.

Very little research has been done on the potato flea beetle, particularly with respect to how feeding punctures per leaflet relate to population numbers or reductions in yield. According to Thompson (1987), the old recommendation in the Canadian Atlantic Provinces stated that, if an average of 15 feeding punctures per fourth terminal leaflet down from the apex of the plant can be found, an insecticide should be applied. However, studies from Prince Edward Island indicate that numbers of feeding punctures are extremely variable from year to year, but that there is little accompanying change in yield loss (Thompson 1984; 1985; 1987). In Manitoba, economic loss was found to occur in cv. Norland when densities of 65-75 feeding punctures per leaflet or greater were found on the bottom side of lower terminal leaflets at two weeks past first bloom (Senanayake 1987). This study correlated yield loss with feeding punctures at a time when effective control decisions could be made, but did not attempt to model how the accumulation of holes changed on various strata of the plant at various insect densities.

The objectives of this study were to examine the spatial and temporal patterns of accumulation of feeding punctures by potato flea beetle on cv. Russet Burbank potato plants, and determine if feeding punctures can be used to calculate actual population numbers of this insect.

Materials and Methods

Experiments took place in 1989 at Winnipeg and Portage la Prairie, Manitoba and in 1990 at Morden and Winkler, Manitoba. The design of plots, experimental treatments and experimental activities are described in the materials and methods section of Part 1 of this chapter.

In 1989, plants sampled for insects in the Portage sampling plot were also sampled for potato flea beetle feeding punctures. For this purpose, plants were stratified into three strata, corresponding to the lower, middle and upper third of foliage. One terminal leaflet from each of the lower, middle and upper strata of each plant was examined, and the potato flea beetle feeding punctures per leaflet was counted. In addition, punctures were counted on one upper non-terminal leaflet, located immediately adjacent to the already selected upper terminal leaflet. For plants sampled by whole-plant bag sampling, leaflets were randomly chosen and examined in the laboratory. Visually sampled plants had leaflets removed in the field for subsequent laboratory examination. Feeding punctures were counted only if they penetrated the entire thickness of the leaflet. The size of individual feeding punctures was considered to be 1 mm^2 or less (Ladd 1963; Senanayake 1987); larger lesions were assumed to be composed of a number of feeding punctures, and this number was estimated. Owing to the small size of plants early in the growing season, feeding punctures counted during the weeks of 27 June and 3 July were considered to be from the lower stratum. After this time all strata were sampled at weekly intervals until the week of 28 August.

Also in 1989, feeding punctures were counted from caged plants in the experimental plot in Winnipeg. Holes in leaflets were counted, as described above. The four leaflets to be sampled were removed from the experimental plants before the weekly manipulations of insect numbers (Chap. III, Part 1, Table 2). Leaflets were examined from all strata at weekly intervals from 12 July, one week following the introduction of insects, until the week of 7 September.

In 1990, feeding punctures per leaflet were counted from the Morden and Winkler experimental plots as in 1989; however, three terminal leaflets per stratum and three non-terminal leaflets were examined per plant. Each week, feeding punctures were counted from all experimental plants before numbers of potato flea beetles were manipulated (Chap. III, Part 1, Table 4). Leaflets were examined from 6 August, one week after the first introduction of potato flea beetles, until the week of 10 September.

Data were analyzed by analysis of variance (ANOVA), analysis of covariance (ANCOVA), linear regression, multiple regression and univariate and multivariate repeated measures analysis (Wilkinson 1990).

Results

The reader is referred to the appendices for detailed data about the numbers of feeding punctures per leaflet at the Portage sampling plot in 1989 (Appendix 8), feeding punctures in experimental treatments in 1989 (Appendix 9) and feeding punctures in experimental treatments in 1990 (Appendix 10).

At the Portage sampling plot in 1989, several problems were encountered over the course of the growing season. Potato plants faced severe competition from weeds, which reduced their foliage area and vigour. Also, large infestations of Colorado potato beetles necessitated the spraying of insecticide to prevent the crop from being totally defoliated (refer to Chap. III, Part 1, Materials and Methods section). Therefore, densities of potato flea beetles and their associated numbers of feeding punctures were not representative of a commercial field. Furthermore, a tendency to overestimate numbers of feeding punctures in early season, by scoring Colorado potato beetle injury as that of potato flea beetle, casts doubt on the reliability of this data set. For these reasons, the Portage sampling plot feeding puncture data have been omitted from any analyses in this study.

The data set from the experimental plot in Winnipeg, 1989, was modified prior to analyses. All feeding puncture data prior to 9 August (72 days after planting) were omitted from analyses because Colorado potato beetle injury was mistakenly scored as that of potato flea beetle. By two-way ANOVA, Colorado potato beetle (F=2.0; d.f.=2,191) and the interaction between Colorado potato beetle and potato flea beetle (F=1.0; d.f.=4,191) were found to have no significant effects on the numbers of feeding punctures produced. Hence, treatments were pooled over all Colorado potato beetle densities.

In general, the 1990 feeding puncture data from the Morden experimental plot was used for the development of models to describe both the nature of potato flea beetle feeding and to estimate potato flea beetle numbers from feeding punctures. Feeding puncture data from the Winkler experimental plot, were based on one density of flea beetles, and, owing to a lack of abundance, had fewer potato flea beetles per treatment than in Morden. For these reasons, the Winkler data were unsuitable to pool with the Morden data for the development of models. The 1989 data set was used only to validate findings from 1990 because plants in 1989 suffered late season injury by aphids, *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* (Sulzer), which may have altered potato flea beetle feeding responses.

Behavioral Modelling

The purpose of this modelling was to determine what factors affected the accumulation of feeding punctures and where feeding punctures accumulated on plants over the course of the growing season. The dependent variable in these models was the estimated number of feeding punctures produced in a sampled leaflet per week per flea beetle. This was termed the incremental number of holes per week per potato flea beetle (INC) and is:

$$\mathrm{INC} = \frac{P_{t+1} - P_t}{\mathrm{PFB}}$$

where P_t is the number of holes per leaflet at the beginning of the week and P_{t+1} is the number of holes per leaflet at the end of the week, and PFB is the number of potato flea beetles on the plant that week. Note that P_{t+1} and P_t are for different leaflets of the same stratum.

Preliminary analysis showed that it was preferable to pool the 1990 data into three time periods, corresponding to sampling dates preceding, during, or following the peak of flea beetle abundance. Hence, for 1990, data from the two weeks preceding and following the peak of flea beetle abundance were separately pooled prior to analysis. By ANCOVA, it was determined that:

$$INC = b_0 + b_1PFB + b_2STRATA$$

where INC = incremental holes per week per potato flea beetle; b_{0-2} = estimates of coefficients for regression variables; PFB = number of potato flea beetles that week; and STRATA = stratum where feeding punctures occurred. For this model, all treatments having zero potato flea beetles were not included, because INC would have zero as a denominator. From this relationship it was shown that, in 1990, the effect of flea beetles was significant at the peak (F=10.3; d.f.=1,19; $P<0.01$) and past the peak (F=5.6; d.f.=1,43; $P<0.05$) of potato flea beetle abundance (Table 10), and that the effect of leaflet stratum on the number of new feeding punctures per beetle was only significant during the week of peak insect abundance (F=16.0; d.f.=3,19; $P<0.001$) (Table 11). Examination of the least squares means indicates that no clear preference existed for any stratum prior to peak flea beetle abundance, but during this peak lower leaflets were preferred (Table 11). Although not significant, in the period following peak flea beetle abundance, all other leaflets were preferred over lower ones. Contrasts for the effect of leaflet strata on incremental holes per week per potato flea beetle show that lower leaflets were significantly more preferred than all others during the period of peak insect density (F=40.0; d.f.=1,19; $P<0.001$), but after this peak, beetles tended to prefer feeding on middle and upper leaflets, although this was not quite significant (F=3.7; d.f.=1,43; $P<0.1$). No other significant contrasts were found among leaflet types.

Because peak numbers of flea beetles occurred in different weeks in 1989 than 1990, it was not possible to pool the same number of weeks before and after the peak of flea beetle abundance for each year. The 1989 data subset contains average numbers of feeding punctures for the three weeks preceding, one week during and one week following peak flea beetle abundance. Therefore, data were pooled for the three weeks prior to peak abundance only.

The effect of flea beetles, in 1989, was not significant over the three time periods tested (Table 10), however, the effect of leaflet strata on the number of feeding punctures was significant before (F=5.1; d.f.=3,67; P<0.01) and after the period of peak insect abundance (F=5.2; d.f.=3,19; P<0.01) (Table 11). Examination of the least squares means for each stratum indicates that before the week of peak insect density, all non-lower leaflets, especially the upper non-terminals, were preferred over lower leaflets (Table 11). During peak flea beetle abundance, no obvious preference for any stratum was evident. After the peak, both upper and upper non-terminal strata seemed to be preferred over the lower and middle strata. Contrasts of leaflet strata on incremental holes per week per potato flea beetle showed that lower leaflets were significantly less preferred than all others during the period prior to peak insect density (F=12.2; d.f.=1,67; P<0.001). After peak abundance, beetles preferred feeding on upper and upper non-terminal leaflets over those in the lower and middle strata (F=9.7; d.f.=1,19; P<0.01).

A second behavioral model was developed to try to explain why potato flea beetles preferred to feed in different strata over the course of the season. It was found that the variability partitioned by the variable STRATA in the previous model could be explained by the number of feeding punctures in leaflets at the beginning of the week. By ANCOVA from the 1990 data, it was found that:

$$\text{INC} = b_0 + b_1\text{PFB} + b_2\text{PREVHOLE}$$

where INC = incremental holes per week per potato flea beetle; PFB = number of potato flea beetles in that week; and PREVHOLE = previous number of feeding punctures per leaflet. Again, the time periods preceding, during and following the peak abundance of potato flea beetles were examined. By ANCOVA, it was determined that the only weeks of the 1990 data which could be pooled for analyses were the two after the peak; the two weeks before the peak had significant interactions between PREVHOLE and a variable representing time and were therefore analyzed separately.

During the three time periods tested, the effect of potato flea beetles was significant to the model only during peak flea beetle abundance (F=8.2; d.f.=1,21; P<0.01) (Table 12). The effect of previous feeding punctures was highly significant from 6 August to 12 August (F=13.4; d.f.=1,21; P<0.01) and approached significance during (F=4.3; d.f.=1,21; P<0.1), and after (F=3.6; d.f.=1,45; P<0.1) peak potato flea beetle abundance. Coefficients for PFB show a decreasing trend for punctures per beetle over the season, while the effect of PREVHOLE is negative before and after peak abundance.

For the 1989 data subset, no pooling of weeks was done before the peak of potato flea beetle abundance, again due to the interaction of

PREVHOLE with a variable representing time. The effect of incremental potato flea beetles was significant only during the second of the three weeks preceding the peak of abundance, from 9 - 14 August ($F=5.8$; d.f.=1,21; $P<0.05$) (Table 12). The effect of PREVHOLE was significant in the first two of the three weeks preceding peak flea beetle abundance, from 1 - 8 August ($F=5.7$; d.f.=1,21; $P<0.05$) and 9 - 14 August ($F=8.5$; d.f.=1,21; $P<0.01$), as it was after peak abundance ($F=8.0$; d.f.=1,21; $P<0.05$). Coefficients for PFB show no particular trend, but are consistently negative for PREVHOLE throughout the season.

Population Modelling

A second type of modelling was employed to determine whether feeding punctures could be used to estimate numbers of potato flea beetles. The dependent variable in this model was accumulated potato flea beetle weeks (ACCUM), and was determined by cumulatively summing the number of potato flea beetles in a particular treatment each week, starting when insects were first introduced. One potato flea beetle week was therefore equivalent to one potato flea beetle feeding on a plant for one week. Although several combinations of strata were satisfactory for estimating accumulated potato flea beetle weeks, the average number of feeding punctures summed across the lower, middle and upper strata, not including upper non-terminal leaflets, was used. The relationship derived was:

$$\mathrm{ACCUM} = b_0 + b_1\mathrm{PUNCTURES}$$

where ACCUM = accumulated potato flea beetle weeks and PUNCTURES = the average number of feeding punctures summed across a combination of strata.

Numbers of feeding punctures per leaflet were a good indicator of the number of accumulated potato flea beetle weeks a plant had sustained in both 1990 (Fig. 7) and 1989 (Fig. 8). A linear relationship was significant for both the 1990 (F=224.4; d.f.=1,42; P<0.001) and 1989 (F=222.5; d.f.=1,48; P<0.001) data sets. In 1990, this relationship was not significantly affected by whether plants had early season Colorado potato beetle damage or not. For the 1989 data subset, as earlier described, all treatments were pooled over Colorado potato beetle treatments, thereby not enabling the effect of Colorado potato beetle to be tested.

The Y-intercepts of the regressions for 1990 and 1989 were -67.847 and -114.599, respectively (Figs. 7,8). For 1990, the Y-intercept was not significantly different from zero (t=-1.3, d.f.=42), but for 1989, a significant difference existed (t=-3.4, d.f.=48, P<0.01). This low intercept may be a consequence of Colorado potato beetle damage being mistakenly scored as that of potato flea beetle very early in the season.

In the previously defined population model, the variables ACCUM and PUNCTURES were cumulative measures whose value in week *n* were directly dependant on their values in week *n*-1. Therefore, the normal regression model, which assumes independence of samples, is not a valid means of assessing significance. In order to test the statistical validity of this relationship it was necessary to employ a univariate and multivariate repeated measures design. Therefore, the following model was designed and tested:

$$\text{PUNCTURES(1-5)} = b_0 + b_1\text{STRATA} + b_2\text{PFB} + b_3\text{CPB} + b_4\text{STRATA*PFB} + b_5\text{STRATA*CPB} + b_6\text{PFB*CPB} + b_7\text{STRATA*PFB*CPB}$$

where PUNCTURES(1-5) = number of feeding punctures for each of the five weeks tested; STRATA = leaflet stratum where feeding punctures occurred; PFB = number of potato flea beetles in that week; and CPB = number of Colorado potato beetles in that week. In 1990, testing all treatments, it was determined that a relationship existed in which PFB ($F=652.4$; d.f.=1,176; $P<0.001$), and the interactions of STRATA*PFB ($F=22.2$; d.f.=3,176; $P<0.001$), STRATA*CPB ($F=22.3$; d.f.=1,176; $P<0.001$) and STRATA*PFB*CPB ($F=3.0$; d.f.=3,176; $P<0.05$) were significant. Therefore, the number of feeding punctures for a given leaflet in a given week is primarily dependent on the density of potato flea beetles. Also, although a variable representing leaflet stratum is not necessary, the significance of the interaction between PFB and STRATA suggests that the calculated feeding punctures would best represent an average number summed across a set of strata. If the significant variables in the relationship are rearranged, the resulting equation is similar to the regression model of population. Hence, the repeated measures analysis of the 1990 data gives statistical validity to the population model.

For the 1989 data subset, no variable representing Colorado potato beetle was included in the model, because data were pooled over Colorado potato beetle treatments. Accordingly, interaction terms containing the CPB variable were dropped from the model as were the "110" treatment values (those plants with early and late season by Colorado potato beetle, but no potato flea beetle). From this repeated measures design analysis, it was shown that a relationship existed, and that the only significant variable in the model was PFB (F=78.516; d.f.=3,20; P<0.001). Although the STRATA*PFB interaction term was not significant, average feeding punctures for a combination of strata was determined as precisely as that for a single stratum. Hence, the process of summing across a set of strata to determine an average number of feeding punctures per leaflet was retained in the population model.

The regressions of accumulated potato flea beetle weeks versus feeding punctures in 1990 and 1989 (Figs. 7,8) were tested for coincidence (Berenson et al. 1983), and were not significantly different (F=0.4; d.f.=2,90). Hence, the regression coefficients derived from the 1990 data were used for all further calculations of accumulated potato flea beetle weeks, as this data set was free of the complicating effects of aphids which occurred in 1989.

The use of the population model allowed estimation of the number of accumulated potato flea beetle weeks a plant had sustained from the number of feeding punctures in a given week. From these potato flea beetle week values, the estimated number of potato flea beetles in a week was calculated by subtracting from the accumulated potato flea beetle weeks for a given week, the corresponding value for the previous week. If estimated potato flea beetle numbers were an exact match for the actual potato flea beetle numbers, all points would lie along a perfectly straight line with a slope of one. Although the estimated values are far from perfect, they provide a reasonable estimate of actual potato flea beetle populations over a wide range of densities (Figs. 9-11). In these plots, all points which were outliers or had great leverage were excluded. These points were also well above 300 potato flea beetles per plant, an area in which the economic injury is well exceeded. The regressions (Figs. 9-11) were tested to determine whether their slopes differed significantly from one and their Y-intercepts from zero. Figures 9 (t=-1.5, d.f.=12) and 11 (t=-2.8, d.f.=14) did not have slopes differing from one, but the slope in figure 10 was significantly less than one (t=-2.770, d.f.=14, P<0.01). None of the intercepts for the regressions in figures 9 (t=2.0; d.f.=12), 10 (t=1.8, d.f.=14) or 11 (t=0.5, d.f.=7) were significantly different from zero.

Discussion

The accumulation of feeding punctures on a potato plant is a very complex process for which the results of this study are a mere preliminary explanation. However, an attempt was made to understand the temporal and spatial accumulation of feeding punctures, to facilitate the use of economic injury levels for potato flea beetle.

The two behavioral models developed in this paper may aid in explaining the process by which beetles feed preferentially on different strata during the course of the growing season. From the results of the first behavioral model, it appears that a "switching" process is occurring between strata as the season progresses. In both 1990 and 1989, although statistical results vary, a shift of the preferred site of feeding seems to occur upwards on the plant from the time of peak flea beetle abundance to after the peak (Table 11). As a consequence of this switch, beetles feed on upper and upper non-terminal leaflets more preferentially than lower leaflets. It is also possible that prior to the peak, beetles may experience a shift in the preferred site of feeding from lower to middle leaflets, but such a trend is not well supported by these data.

Deviations from the upward movement on plants may be explained by other factors. In 1989, the lack of preference for any one stratum during the period of peak insect abundance may simply be an artifact of insect density. From the results of modelling, it was seen that reduced numbers of feeding punctures per beetle were associated with higher densities. The lack of stratum preference in 1989 may be indicative of a more uniform dispersion of insects over the plant in order to better allocate any unexploited food resources. Although no direct evidence from this study supports this contention, higher densities of beetles were observed, in the field, to cause more uniform damage among leaflets per plant than did lower densities.

In 1990, a uniform dispersion of insects was not seen for the week of peak abundance, but it is possible that other environmental factors specific to the environment of the plants may have caused beetles to concentrate on the lowest leaflets. To examine this hypothesis, average weekly comparisons of maximum ambient air temperature and stratum of feeding preference were made. However, no relationship was elucidated. The identity of such an environmental factor remains uncertain, and if pursued, must be investigated within the microenvironment of the plant.

If such an upward movement of beetle feeding occurs over the course of the growing season, it is necessary to determine what force is driving it. An answer may lie in the examination of the results of the second behavioral model. In this second model, much of the variability partitioned by the variable STRATA in the first model could be accounted for by the average number of feeding punctures in leaflets in the previous week (PREVHOLE). This interpretation of the relationship of PREVHOLE and STRATA is inferred because the sums of squares did not change greatly from the first to the second behavioral model. For 1989, 41-63% of the variability partitioned by STRATA was accounted for by PREVHOLE before the peak, 36% at the peak and 61% after the peak. In 1990, greater than 69% of the variability partitioned by STRATA was explained by PREVHOLE for all of the time periods examined. Therefore, it is likely that any switching between various leaflet strata over the course of the growing season is likely mediated through the condition of the leaflets having already been fed on. This is supported by observations of plant condition throughout the season. Lower leaflets, at the time of beetles switching away from them, are the oldest on the plant, have the most number of accumulated punctures, and are most shaded by the haulm of the potato plant thereby reducing their photosynthetic output and general efficiency (Harper 1963). All of these factors contribute to the decline of the general health of the leaflets and likely reduce their attractiveness to flea beetles as food.

The population model developed in this study is potentially of great use, but also has limitations. This study was the first to establish a quantitative relationship between feeding punctures in potato leaflets of different strata and actual population numbers of potato flea beetles for a wide range of densities with and without early season Colorado potato beetle injury. This may serve as a useful tool for trying to estimate flea beetle densities, by replacing the time-consuming use of whole-plant bag sampling with the simpler task of sampling leaflets. The technique of randomly choosing three terminal leaflets per lower, middle and upper stratum was chosen so that it would provide a good estimate of feeding punctures per plant. Such sampling would tend to average out any aggregations of feeding punctures in a certain area of the plant and provide the sampler with a technique that is easy to use.

Upon examination of the estimated versus actual population values for 1990 and 1989 (Figs. 9-11), it is seen that there is much scatter around the line of best fit for the regression. This variability may be attributable to the relatively large coefficient by which the number of feeding punctures per week is multiplied to obtain the value for accumulated potato flea beetle weeks. Thus, any slight inaccuracies in estimating feeding punctures are much exaggerated. In addition, the scatter of predictions are further affected because the value of accumulated potato flea beetle weeks for week *n* is subtracted from that of *n*-1. Therefore, a slightly inaccurate count of feeding punctures not only results in an exaggerated value for flea beetles during the current week, but, also reduces the value of the prediction in the following week. Most of the variability in estimated population values in Figs. 9-11 can be attributed to slight inaccuracies in estimating average feeding punctures per leaflet, particularly in the early season. Although slopes did not differ significantly from one and intercepts did not differ from zero (except in Fig. 10), it appears that the mean predicted value for potato flea beetles is consistently biased, being below that of actual numbers of flea beetles. Such bias is not easily explained from the results of this study, but may be reduced by better future modelling of this insect.

It is important to note that the relationship between potato flea beetle numbers and accumulated potato flea beetle weeks is consistent from 1989 to 1990. The regressions in figures 7 and 8 were previously shown to be coincident; however, the regression coefficients from 1990 (Fig. 7) or 1989 (Fig. 8) can also be used to produce coincident regressions of actual versus predicted potato flea beetles from 1989 feeding punctures (F=0.01; d.f.=2,14). This further exemplifies the consistency of the relationship between flea beetle numbers and accumulated flea beetle weeks and its robustness as a predictor from year to year.

Although the population model can be used to calculate actual numbers of potato flea beetles, these numbers can only be determined after the week in which they exist has already passed. In Part 1 of this chapter, the economic injury levels of 4-19 or 300-335 potato flea beetles per plant, correspond to an average of 3-4 or 16-17 feeding punctures per leaflet, respectively. The population model does not predict when in the season these numbers will be exceeded, nor when peak numbers of the pest will occur. Such information is necessary for effective control decisions to be made in order to time the application of insecticide such that it will depress the population peak of the insect. Although useful for post-hoc monitoring of populations of flea beetles, the population model is not capable of predicting what the population curve of the pest is likely to be, in order for proper control measures to be effected.

In conclusion, potato flea beetles tend to move their area of feeding preference upward during the latter part of the season, from the time of peak abundance to past this peak. This upward switching of strata may be obscured by responses of the beetles to population density or perhaps by other factors which may affect the microenvironment of the plant. The relationship is complex, which may explain the absence of a direct relationship between yield of plants and feeding punctures per leaflet (Thompson 1984, 1984, 1987).

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Table 10. Values for the coefficient b_1 in the model INC = $b_0 + b_1$PFB + b_2STRATA, prior to, during and after peak potato flea beetle abundance, 1990 and 1989. (INC=incremental feeding punctures per week per potato flea beetle; PFB=number of potato flea beetles; STRATA=leaflet stratum where feeding punctures occur).

Year	Dates	Relationship to peak	b_1	P^1
1990	6 Aug - 19 Aug	Before	-0.000024	n.s.
1990	20 Aug - 26 Aug	During	-0.000071	<0.01
1990	27 Aug - 9 Aug	After	-0.000622	<0.05
1989	1 Aug - 21 Aug	Before	0.001269	n.s.
1889	22 Aug - 29 Aug	During	-0.000020	n.s.
1989	30 Aug - 6 Sep	After	0.000078	n.s.

[1] Significance of PFB to the model.

Table 11. Adjusted least squares means for all strata in the model INC = $b_0 + b_1$PFB + b_2STRATA, prior to, during and after peak potato flea beetle abundance, 1990 and 1989. (INC=incremental feeding punctures per week per potato flea beetle; PFB=number of potato flea beetles; STRATA=leaflet stratum where feeding punctures occur; UpperNT=upper non-terminal).

			Stratum				
Year	Dates	Relationship to peak	Lower	Middle	Upper	UpperNT	P[1]
1990	6 Aug - 19 Aug	Before	0.020583	0.045250	0.022833	0.025000	n.s.
1990	20 Aug - 26 Aug	During	0.085333	0.033833	0.005500	-0.005333	<0.001
1990	27 Aug - 9 Sep	After	0.065583	0.160750	0.154667	0.110750	n.s.
1989	1 Aug - 21 Aug	Before	-0.762629	-0.015400	-0.088554	0.079335	<0.01
1989	22 Aug - 29 Aug	During	0.056246	0.057439	0.051167	0.040996	n.s.
1989	30 Aug - 6 Sep	After	0.037546	0.000047	0.109833	0.110491	<0.01

[1] Overall significance of all strata to the model.

Table 12. Values for the coefficients b_1 and b_2 in the model INC = b_0 + b_1PFB + b_2PREVHOLE, prior to, during and after peak potato flea beetle abundance, 1990 and 1989. (INC=incremental feeding punctures per week per potato flea beetle; PFB=number of potato flea beetles; PREVHOLE=previous number of feeding punctures per leaflet).

Year	Dates	Relationship to peak	Coefficient	Value	P[1]
1990	6 Aug - 12 Aug	Before	b_1	0.000113	n.s.
			b_2	-0.002336	<0.01
1990	13 Aug - 19 Aug	Before	b_1	-0.000052	n.s.
			b_2	-0.000377	n.s.
1990	20 Aug - 26 Aug	During	b_1	-0.000142	<0.01
			b_2	0.000701	<0.1
1990	27 Aug - 9 Sep	After	b_1	-0.000455	n.s.
			b_2	-0.000594	<0.1
1989	1 Aug - 8 Aug	Before	b_1	-0.016075	n.s.
			b_2	-0.005383	<0.05
1989	9 Aug - 14 Aug	Before	b_1	0.012172	<0.05
			b_2	-0.002120	<0.01
1989	15 Aug - 21 Aug	Before	b_1	0.000032	n.s.
			b_2	-0.000018	n.s.
1989	22 Aug - 29 Aug	During	b_1	-0.000008	n.s.
			b_2	-0.000060	n.s.
1989	30 Aug - 6 Sep	After	b_1	0.000243	n.s.
			b_2	-0.000311	<0.05

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[1] Significance of PREVHOLE or PFB to the model.

Figure 7. Relationship between accumulated potato flea beetle weeks and feeding punctures per leaflet (Y=-67.847+22.815X) for experimental plants, 1990. Each point represents the average feeding punctures per leaflet and accumulated potato flea beetle week values for individual treatments in a week. Feeding punctures per leaflet are averaged from terminal leaflets over the lower, middle and upper strata.

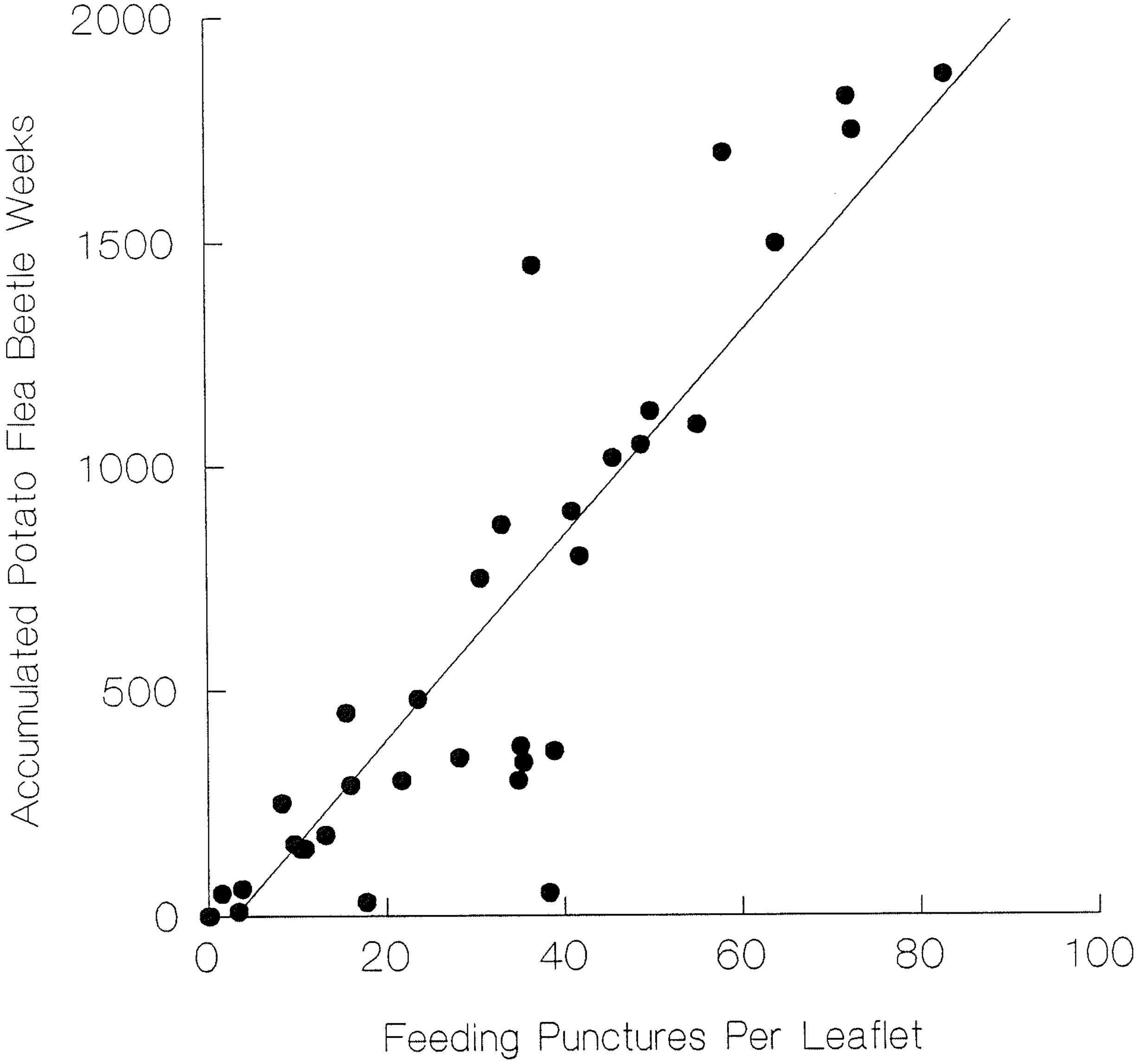
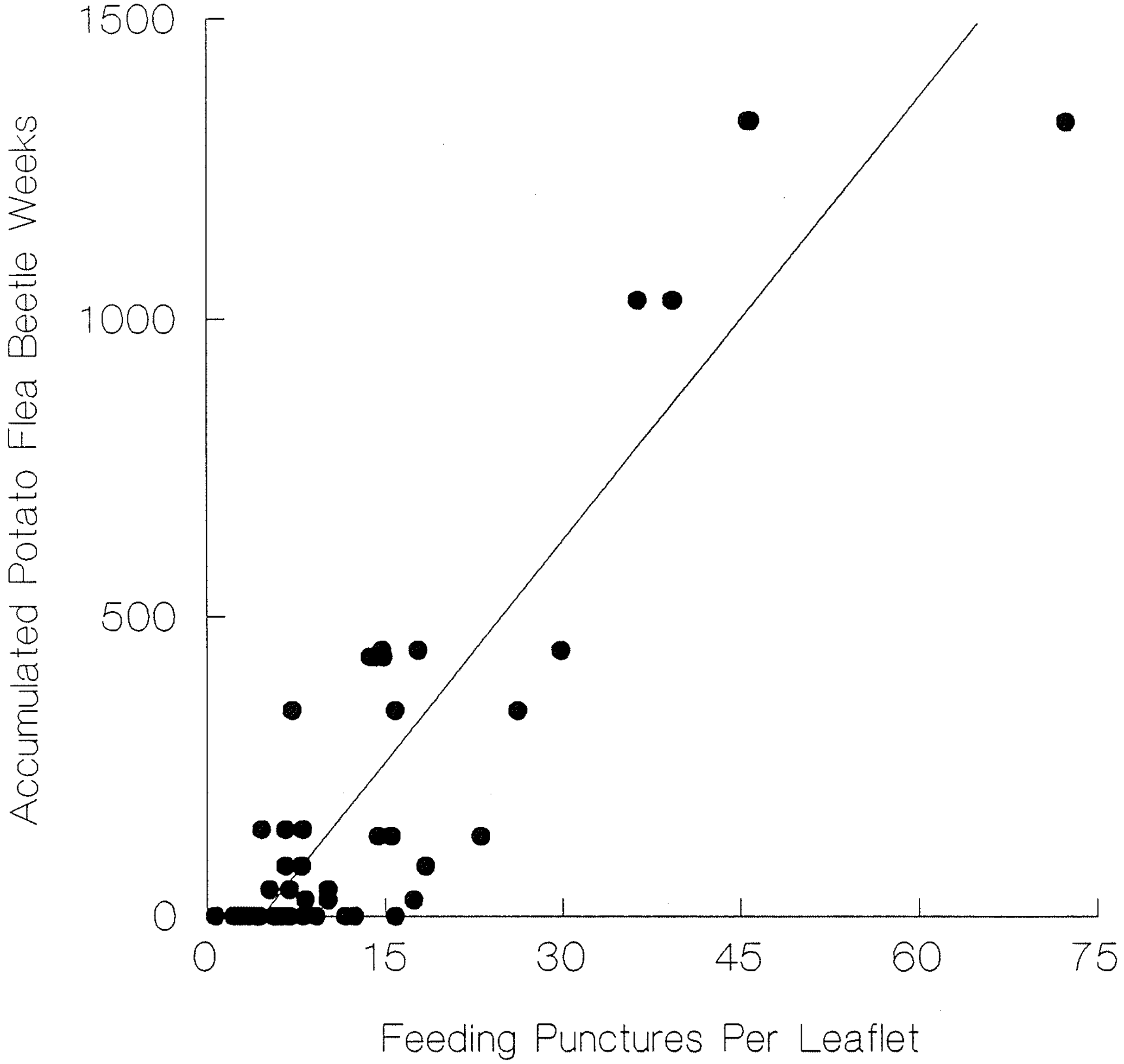

Accumulated Potato Flea Beetle Weeks
2000
1500
1000
500
0
0
20
40
60
80
100
Feeding Punctures Per Leaflet

Figure 8. Relationship between accumulated potato flea beetle weeks and feeding punctures per leaflet (Y=-114.599+24.819X) for experimental plants, 1989. Each point represents the average feeding punctures per leaflet and accumulated potato flea beetle week values for individual treatments in a week. Feeding punctures per leaflet are averaged from terminal leaflets over the lower, middle and upper strata.



Accumulated Potato Flea Beetle Weeks
1500
1000
500
0
0
15
30
45
60
75
Feeding Punctures Per Leaflet

Figure 9. Estimated versus actual numbers of potato flea beetles for experimental treatments without Colorado potato beetle in 1990 ($Y=135.924+0.596X$). The solid line is the line of best fit for all data points; the broken line represents perfect flea beetle estimates and has a slope of 1 and an intercept of 0. Estimated values are calculated with regression coefficients from Fig. 7.

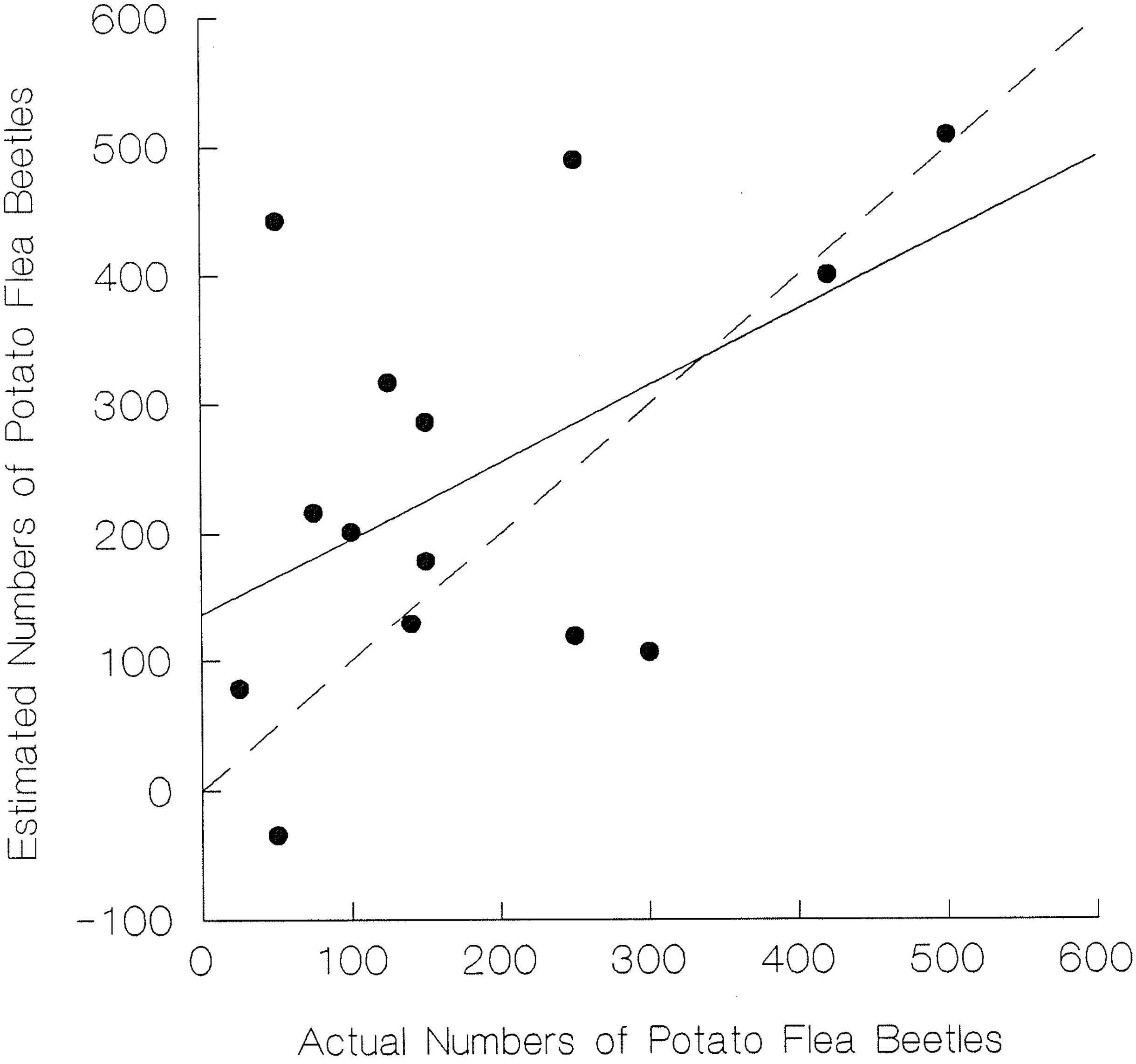

Estimated Numbers of Potato Flea Beetles
600
500
400
300
200
100
0
-100
0
100
200
300
400
500
600
Actual Numbers of Potato Flea Beetles

Figure 10. Estimated versus actual numbers of potato flea beetles for experimental treatments with Colorado potato beetle in 1990 (Y=97.919+0.285X). The solid line is the line of best fit for all data points; the broken line represents perfect flea beetle estimates and has a slope of 1 and an intercept of 0. Estimated values are calculated with regression coefficients from Fig. 7.

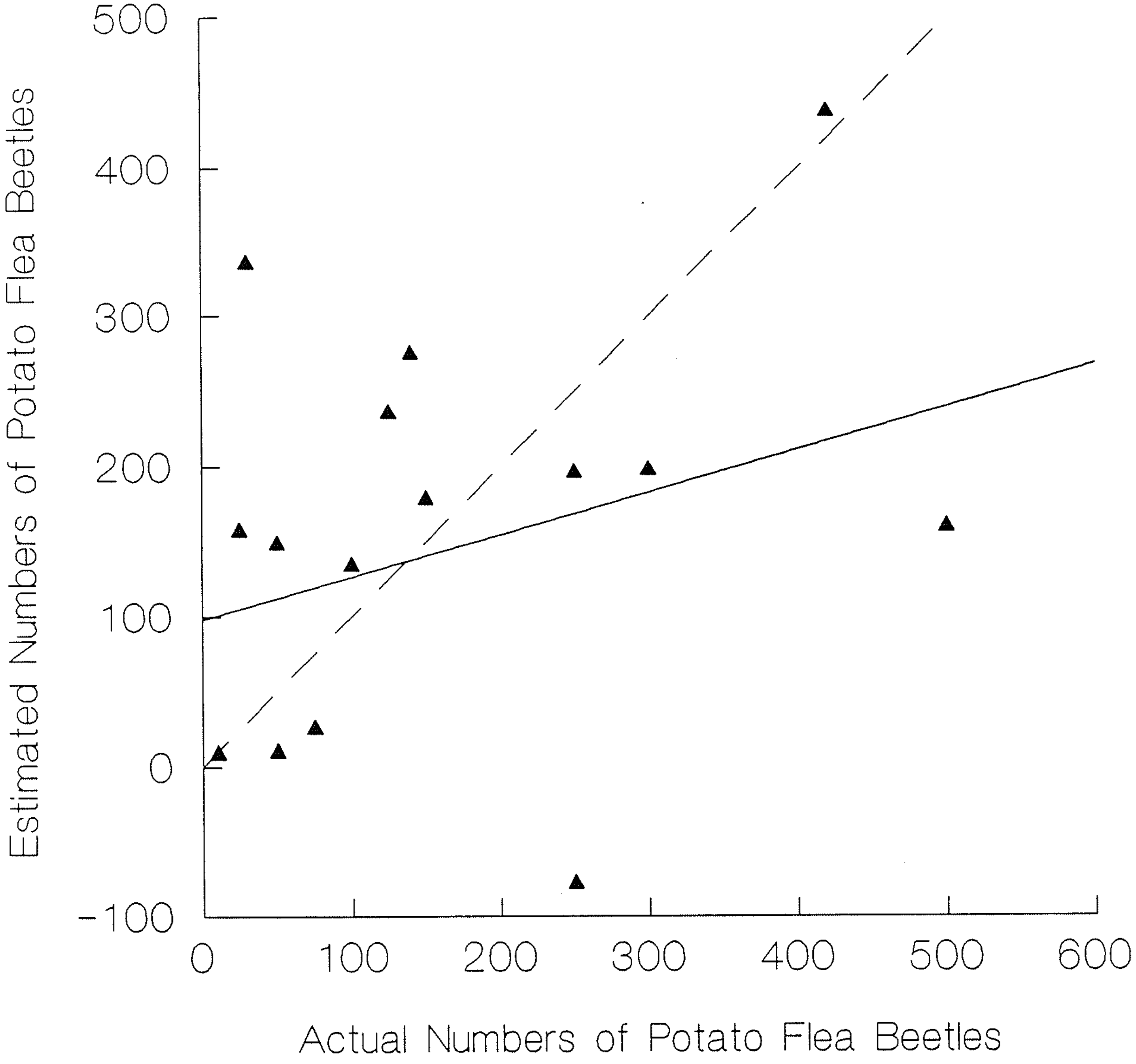
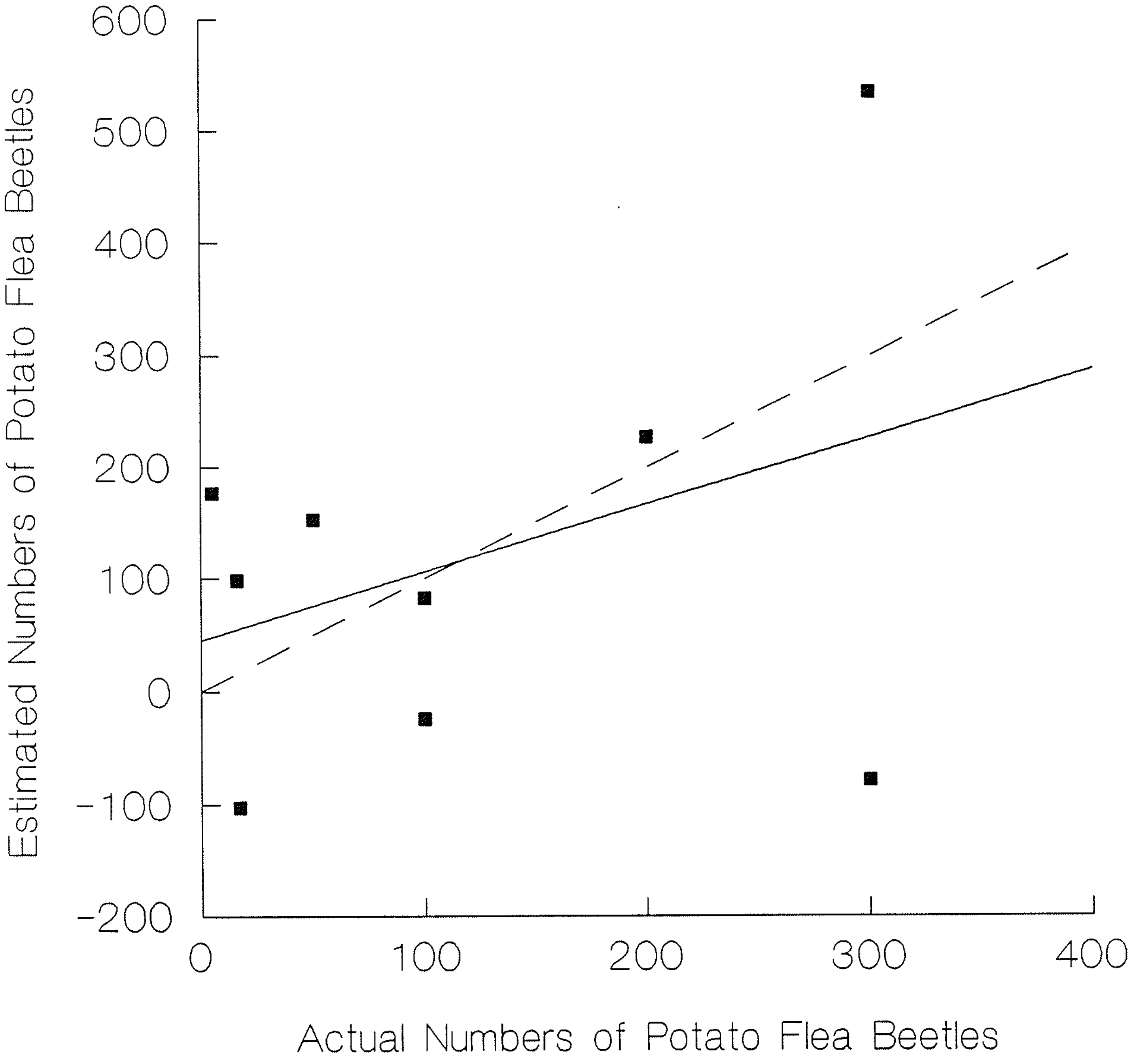

Estimated Numbers of Potato Flea Beetles
500
400
300
200
100
0
-100
0
100
200
300
400
500
600
Actual Numbers of Potato Flea Beetles

Figure 11. Estimated versus actual numbers of potato flea beetles for experimental treatments in 1989 (Y=45.314+0.608X). The solid line is the line of best fit for all data points; the broken line represents perfect flea beetle estimates and has a slope of 1 and an intercept of 0. Estimated values are calculated with regression coefficients from Fig. 7.


Estimated Numbers of Potato Flea Beetles
600
500
400
300
200
100
0
-100
-200
0
100
200
300
400
Actual Numbers of Potato Flea Beetles

Appendix 8. Mean (± S.E.) potato flea beetle feeding punctures per leaflet of plants sampled from the Portage sampling plot by either visual or whole-plant bag sampling, 1989. (Lower = lower terminal leaflets; Middle = middle terminal leaflets; Upper = upper terminal leaflets; UpperNT = upper non-terminal leaflets; DAP = days after planting).

Date	DAP	Sampling type	Leaflet			
			Lower	Middle	Upper	UpperNT
27 June	31	Visual[1]	63 ± 6	-[2]	-	-
		WPBS[1]	91 ± 8	-	-	-
3 July	37	Visual	88 ± 6	-	-	-
		WPBS	112 ± 4	-	-	-
10 July	44	Visual	184 ± 19	81 ± 9	30 ± 4	16 ± 2
		WPBS	171 ± 9	89 ± 5	41 ± 5	32 ± 4
17 July	51	Visual	121 ± 10	67 ± 6	33 ± 4	20 ± 3
		WPBS	140 ± 13	80 ± 11	38 ± 3	34 ± 4
24 July	58	Visual	113 ± 14	57 ± 9	33 ± 6	23 ± 4
		WPBS	111 ± 11	59 ± 6	33 ± 4	19 ± 4
31 July	65	Visual	88 ± 9	40 ± 8	8 ± 2	3 ± 1
		WPBS	110 ± 11	55 ± 6	9 ± 4	5 ± 3
8 Aug.	73	Visual	93 ± 8	56 ± 11	9 ± 3	6 ± 2
		WPBS	117 ± 14	67 ± 7	16 ± 5	8 ± 2
14 Aug.	79	Visual	111 ± 7	51 ± 8	18 ± 6	8 ± 2
		WPBS	97 ± 9	68 ± 11	16 ± 4	9 ± 3
21 Aug.	86	Visual	75 ± 14	24 ± 5	11 ± 4	5 ± 2
		WPBS	96 ± 8	47 ± 5	6 ± 1	3 ± 1
28 Aug.	93	Visual	107 ± 9	44 ± 5	18 ± 3	11 ± 2
		WPBS	85 ± 7	47 ± 4	13 ± 2	11 ± 2

[1] N=15
[2] Only lower leaflets were sampled because of small plant size.

Appendix 9. Weekly means (± S.E.) of potato flea beetle feeding punctures per leaflet in each plant stratum. Numbers listed are for each experimental treatment in 1989. (DAP = days after planting; Low = lower terminal leaflets; Mid = middle terminal leaflets; Up = upper terminal leaflets; UpNT = upper non-terminal leaflets).

Date	DAP	Plant stratum	Experimental treatment									
			000	001	003	100	101	103	200	201	203	110
12 July	44	Low[1]	73 ± 9.3	47 ± 21.4	121 ± 6.6	74 ± 40.6	73 ± 15.0	46 ± 21.1	136 ± 19.0	61 ± 20.0	145 ± 8.7	61 ± 22.9
		Mid[1]	33 ± 13.3	14 ± 5.2	66 ± 28.4	46 ± 9.0	30 ± 2.1	69 ± 23.1	61 ± 20.8	29 ± 8.9	60 ± 4.2	14 ± 2.6
		Up[1]	15 ± 7.5	14 ± 8.5	32 ± 8.5	8 ± 0.9	24 ± 15.5	66 ± 21.9	16 ± 4.3	14 ± 7.3	44 ± 18.2	12 ± 5.2
		UpNT[1]	10 ± 3.7	9 ± 3.3	28 ± 10.0	4 ± 1.2	33 ± 5.8	25 ± 13.2	3 ± 1.5	13 ± 6.6	29 ± 19.7	8 ± 6.7
18 July	50	Low	52 ± 16.3	63 ± 18.0	58 ± 26.9	56 ± 3.8	52 ± 10.0	122 ± 52.3	88 ± 31.6	101 ± 44.3	229 ± 12.3	146 ± 45.4
		Mid	28 ± 4.6	14 ± 5.0	71 ± 20.8	25 ± 9.4	50 ± 14.3	79 ± 30.5	40 ± 2.1	56 ± 10.7	56 ± 23.2	90 ± 35.7
		Up	8 ± 4.7	12 ± 6.0	30 ± 13.1	13 ± 8.7	12 ± 3.6	26 ± 15.3	8 ± 1.5	10 ± 3.8	7 ± 1.2	12 ± 3.8
		UpNT	5 ± 1.9	17 ± 14.3	21 ± 16.7	4 ± 2.1	8 ± 6.0	6 ± 5.0	4 ± 2.3	7 ± 5.5	5 ± 3.5	9 ± 4.2
25 July	57	Low	33 ± 17.4	40 ± 7.0	31 ± 18.1	48 ± 6.5	13 ± 2.9	42 ± 11.0	33 ± 4.7	57 ± 25.0	55 ± 26.9	42 ± 11.0
		Mid	11 ± 6.7	11 ± 5.2	16 ± 8.1	16 ± 9.5	5 ± 2.4	7 ± 3.2	15 ± 6.2	39 ± 24.8	22 ± 10.2	7 ± 3.2
		Up	2 ± 1.4	4 ± 3.5	13 ± 6.5	4 ± 3.5	9 ± 2.6	3 ± 1.5	2 ± 1.9	10 ± 5.5	12 ± 4.4	2 ± 1.5
		UpNT	1 ± 0.3	0 ± 0.3	7 ± 3.3	2 ± 1.2	7 ± 4.2	6 ± 5.0	2 ± 5.2	6 ± 2.5	8 ± 3.0	6 ± 5.0
1 Aug.	64	Low	20 ± 9.0	19 ± 4.7	87 ± 17.7	17 ± 3.5	31 ± 7.1	59 ± 17.1	21 ± 6.7	52 ± 14.0	25 ± 10.4	55 ± 35.0
		Mid	1 ± 0.7	7 ± 1.2	4 ± 0.3	9 ± 4.9	5 ± 1.5	26 ± 18.9	8 ± 5.4	6 ± 3.3	11 ± 4.4	5 ± 1.2
		Up	0 ± 0.0	0 ± 0.3	2 ± 1.9	3 ± 1.2	1 ± 0.7	2 ± 0.0	2 ± 1.2	4 ± 4.0	5 ± 2.0	0 ± 0.3
		UpNT	0 ± 0.0	1 ± 0.7	0 ± 0.3	0 ± 0.3	0 ± 0.0	2 ± 1.2	0 ± 0.0	0 ± 0.0	1 ± 0.3	0 ± 0.0
9 Aug.	72	Low	32 ± 11.4	19 ± 8.7	15 ± 4.7	7 ± 2.2	19 ± 5.0	45 ± 12.8	9 ± 1.5	42 ± 26.6	17 ± 4.4	8 ± 0.3
		Mid	4 ± 1.2	10 ± 3.0	3 ± 0.6	6 ± 3.4	3 ± 0.7	8 ± 2.3	6 ± 1.7	8 ± 2.4	5 ± 1.5	3 ± 0.7
		Up	1 ± 0.6	2 ± 0.0	2 ± 1.5	4 ± 1.7	2 ± 0.6	3 ± 0.3	4 ± 0.6	3 ± 1.2	2 ± 0.6	1 ± 0.3
		UpNT	0 ± 0.3	1 ± 0.3	1 ± 1.0	8 ± 6.2	1 ± 0.7	4 ± 2.4	1 ± 0.3	1 ± 0.7	2 ± 1.5	1 ± 0.3
15 Aug.	78	Low	3 ± 1.7	8 ± 1.7	23 ± 0.6	5 ± 1.5	7 ± 1.2	31 ± 18.7	36 ± 5.9	12 ± 2.7	20 ± 11.2	10 ± 3.9
		Mid	7 ± 4.6	8 ± 4.0	12 ± 5.8	5 ± 2.9	4 ± 0.6	12 ± 5.0	8 ± 3.9	14 ± 3.8	19 ± 16.8	3 ± 0.9
		Up	1 ± 0.7	4 ± 1.8	11 ± 2.6	6 ± 0.3	5 ± 3.3	26 ± 20.2	4 ± 1.2	5 ± 2.1	4 ± 1.5	4 ± 1.7
		UpNT	8 ± 6.2	5 ± 1.5	3 ± 2.4	3 ± 0.0	3 ± 0.7	6 ± 3.5	3 ± 0.7	7 ± 3.8	4 ± 0.3	5 ± 2.5
22 Aug.	85	Low	5 ± 2.0	4 ± 0.3	28 ± 14.2	4 ± 1.5	13 ± 5.5	18 ± 8.9	5 ± 2.7	9 ± 2.9	17 ± 3.8	3 ± 1.0
		Mid	2 ± 0.6	5 ± 0.9	10 ± 2.6	6 ± 1.3	7 ± 3.7	17 ± 2.9	6 ± 4.3	9 ± 5.7	6 ± 1.9	4 ± 2.2
		Up	3 ± 1.0	5 ± 1.2	4 ± 1.8	3 ± 1.7	4 ± 1.5	9 ± 3.5	3 ± 0.9	2 ± 0.9	18 ± 5.5	2 ± 1.7
		UpNT	1 ± 1.3	1 ± 0.7	4 ± 3.2	1 ± 0.3	5 ± 2.4	6 ± 0.7	2 ± 1.5	1 ± 0.0	5 ± 2.4	1 ± 0.7

Appendix 9. Continued.

Date	DAP	Plant stratum	Experimental treatment 000	001	003	100	101	103	200	201	203	110
30 Aug.	93	Low	4 ± 1.9	3 ± 0.9	24 ± 7.9	7 ± 1.8	35 ± 13.7	29 ± 13.3	10 ± 6.7	11 ± 2.7	39 ± 10.5	5 ± 0.0
		Mid	2 ± 0.6	5 ± 2.9	53 ± 25.8	15 ± 5.2	29 ± 6.3	38 ± 15.5	18 ± 7.8	20 ± 3.6	47 ± 14.3	12 ± 0.0
		Up	1 ± 0.6	13 ± 3.8	32 ± 19.0	6 ± 2.1	15 ± 1.5	50 ± 13.2	7 ± 6.0	17 ± 7.4	32 ± 10.3	0 ± 0.0
		UpNT	0 ± 0.0	8 ± 3.8	17 ± 8.1	6 ± 4.3	12 ± 3.0	41 ± 14.3	3 ± 1.5	13 ± 5.6	27 ± 13.3	0 ± 0.0
7 Sep.	101	Low	1 ± 0.7	11 ± 4.1	22 ± 7.4	9 ± 6.2	43 ± 15.5	58 ± 13.9	6 ± 3.2	15 ± 5.2	20 ± 2.2	3 ± 0.8
		Mid	0 ± 0.0	10 ± 2.0	53 ± 12.3	10 ± 3.0	28 ± 6.5	43 ± 7.9	10 ± 7.8	14 ± 3.4	49 ± 14.4	5 ± 0.0
		Up	1 ± 0.7	23 ± 12.5	62 ± 15.2	2 ± 0.9	19 ± 2.7	115 ± 20.5	9 ± 6.3	25 ± 6.3	68 ± 16.5	5 ± 3.3
		UpNT	1 ± 0.3	26 ± 20.0	74 ± 25.3	1 ± 0.0	23 ± 5.0	70 ± 18.5	2 ± 1.2	13 ± 3.6	55 ± 9.3	1 ± 0.6

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[1] N=3

Appendix 10. Weekly means (± S.E.) of potato flea beetle feeding punctures per leaflet in each plant stratum. Numbers listed are for each experimental treatment in Morden and Winkler, 1990. Dates listed are those for Morden; those for Winkler generally followed by two days. (DAP = days after planting; Low = lower terminal leaflets; Mid = middle terminal leaflets; Up = upper terminal leaflets; UpNT = upper non-terminal leaflets).

			Experimental treatments									
			Morden								Winkler	
Date	DAP	Plant stratum	000	001	003	005	100	101	103	105	000	005
6 Aug.	76	Low[1]	-[2]	-	-	-	0 ± 0.0	3 ± 1.3	27 ± 15.3	54 ± 20.2	0 ± 0.0	19 ± 3.2
		Mid[1]	-	-	-	-	0 ± 0.0	6 ± 3.0	8 ± 3.4	31 ± 14.9	0 ± 0.0	15 ± 4.5
		Up[1]	-	-	-	-	0 ± 0.0	1 ± 0.5	18 ± 18.5	29 ± 11.8	0 ± 0.0	11 ± 3.5
		UpNT[1]	-	-	-	-	0 ± 0.0	0 ± 0.2	11 ± 4.1	16 ± 4.4	0 ± 0.0	11 ± 3.5
13 Aug.	83	Low	0 ± 0.1	2 ± 0.7	8 ± 1.9	6 ± 0.8	0 ± 0.2	5 ± 0.5	12 ± 2.6	47 ± 12.1	0 ± 0.0	21 ± 1.5
		Mid	0 ± 0.0	1 ± 0.4	17 ± 3.5	10 ± 1.7	0 ± 0.1	3 ± 0.7	19 ± 5.2	38 ± 8.1	0 ± 0.0	15 ± 1.8
		Up	0 ± 0.2	1 ± 0.3	7 ± 1.6	9 ± 1.7	0 ± 0.0	3 ± 0.8	8 ± 1.1	20 ± 4.0	0 ± 0.0	11 ± 1.5
		UpNT	0 ± 0.0	1 ± 0.2	10 ± 2.9	9 ± 2.1	0 ± 0.0	3 ± 0.7	10 ± 1.9	12 ± 3.0	0 ± 0.0	11 ± 1.6
20 Aug.	90	Low	0 ± 0.0	12 ± 2.4	19 ± 2.6	28 ± 4.4	0 ± 0.1	7 ± 1.4	25 ± 4.3	40 ± 6.4	0 ± 0.1	31 ± 6.9
		Mid	0 ± 0.0	12 ± 2.9	17 ± 2.6	33 ± 2.9	0 ± 0.1	13 ± 2.8	26 ± 4.4	52 ± 7.2	0 ± 0.1	41 ± 5.6
		Up	0 ± 0.0	7 ± 1.2	11 ± 2.5	31 ± 4.2	0 ± 0.2	8 ± 1.3	19 ± 1.9	34 ± 5.9	0 ± 0.2	30 ± 3.7
		UpNT	0 ± 0.0	4 ± 0.7	9 ± 1.8	29 ± 3.2	0 ± 0.1	6 ± 1.3	19 ± 3.1	25 ± 3.8	0 ± 0.0	22 ± 1.8
27 Aug.	97	Low	0 ± 0.0	24 ± 4.8	48 ± 7.5	40 ± 4.9	0 ± 0.0	32 ± 6.0	58 ± 7.0	98 ± 10.9	0 ± 0.0	57 ± 9.1
		Mid	0 ± 0.0	16 ± 2.6	34 ± 4.5	47 ± 6.3	0 ± 0.0	20 ± 4.0	49 ± 7.3	64 ± 6.1	0 ± 0.0	52 ± 4.3
		Up	0 ± 0.0	8 ± 1.5	18 ± 2.7	23 ± 2.8	0 ± 0.0	13 ± 4.2	16 ± 2.9	31 ± 3.5	0 ± 0.0	49 ± 2.0
		UpNT	0 ± 0.0	7 ± 1.4	10 ± 1.6	17 ± 2.9	0 ± 0.0	7 ± 3.4	8 ± 1.7	13 ± 1.8	0 ± 0.0	34 ± 3.3
3 Sep.	104	Low	0 ± 0.0	34 ± 4.7	56 ± 4.2	72 ± 3.6	0 ± 0.0	31 ± 2.6	61 ± 7.0	88 ± 3.2	0 ± 0.0	67 ± 6.0
		Mid	0 ± 0.0	40 ± 5.3	47 ± 3.1	63 ± 2.6	0 ± 0.0	30 ± 2.4	56 ± 4.7	77 ± 9.8	0 ± 0.0	74 ± 4.8
		Up	0 ± 0.0	33 ± 3.9	33 ± 4.8	39 ± 2.1	0 ± 0.0	23 ± 2.0	29 ± 5.3	52 ± 2.7	0 ± 0.0	53 ± 3.0
		UpNT	0 ± 0.0	23 ± 22.9	22 ± 3.6	30 ± 1.6	0 ± 0.0	15 ± 1.6	19 ± 3.9	36 ± 2.5	0 ± 0.0	33 ± 2.4

Appendix 10. Continued.

			Experimental treatments									
			Morden								Winkler	
Date	DAP	Plant stratum	000	001	003	005	100	101	103	105	000	005
10 Sep.	111	Low	0 ± 0.0	43 ± 5.0	64 ± 4.6	86 ± 7.7	0 ± 0.0	32 ± 3.0	52 ± 5.4	86 ± 4.1	0 ± 0.0	62 ± 6.7
		Mid	0 ± 0.0	45 ± 4.6	56 ± 3.1	76 ± 8.8	0 ± 0.0	40 ± 4.1	57 ± 5.3	94 ± 6.4	0 ± 0.0	75 ± 5.1
		Up	0 ± 0.0	29 ± 3.4	45 ± 2.9	54 ± 5.4	0 ± 0.0	34 ± 4.2	40 ± 2.9	69 ± 3.8	0 ± 0.0	54 ± 4.4
		UpNT	0 ± 0.0	18 ± 2.1	30 ± 2.5	43 ± 3.0	0 ± 0.0	22 ± 2.9	27 ± 1.6	53 ± 4.3	0 ± 0.0	34 ± 3.0

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[1] N=18

[2] Potato flea beetles were not yet introduced into these treatments.

CHAPTER III

PART 3

The influence of potato flea beetle, *Epitrix cucumeris* (Harris), on the occurrence of common scab of potatoes

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Abstract

Potato tubers were examined to determine if any relationship existed between the incidence or severity of common scab and the density of adult potato flea beetles, *Epitrix cucumeris* (Harris), on plants. In 1989 and 1990, plants were grown in caged experimental treatments in field plots and varying densities of potato flea beetles and Colorado potato beetles, *Leptinotarsa decemlineata* (Say), were introduced throughout the season. Out of all plants harvested in both years, very few tubers exhibited symptoms of common scab; this was true even of tubers from a plot with a history of recurrent scab problems. The causal agent of common scab disease, *Streptomyces scabies* (Thaxter) Waksman and Henrici was isolated and identified from each scabby tuber. Soil core sampling from a commercial field in 1990 showed a positive correlation between the mean number of feeding holes per lower terminal leaflet and the number of potato flea beetle immatures. The lack of scab in this study suggests that the incidence of the disease is not greatly affected by potato flea beetle adult or larval densities. Abiotic factors such as varietal resistance to scab and the availability of soil moisture during tuber initiation appear to have far greater effects on the expression of this disease.

Introduction

Common scab is caused by the soil-borne actinomycete *Streptomyces scabies* (Thaxter) Waksman and Henrici, and is a blemishing disease of potato tubers (Burrell 1984). The main symptom of this disease, a brown scab, is produced by the infection of lenticels which are not fully suberised (Adams and Lapwood 1978). Lesions are usually 5-8 mm in diameter and may coalesce to form russetted areas (Rich 1983). Affected areas of the tuber may contain a superficial corklike area (russet scab), an erumpent or cushionlike scab 1-2 mm high (raised scab), or may extend into the tuber itself (pitted scab) (Hooker 1981). The disease has no above ground symptoms; affected tubers have reduced value and grade and are usually only detected at harvest (Martin 1969).

Streptomyces scabies survives in the soil and is spread from one locale to another primarily by the planting of infected tubers (Rich 1983). Collembola and mites and have been suggested to be vectors of this disease as *Streptomyces spp.* have been isolated from their bodies (Storch et al. 1978; Manzer et al. 1984). Several organisms have also been observed to be present on scab lesions, including: scab gnats, *Pnyxia scabiei* (Hopkins); oligochaetes and nematodes (Tamaki et al. 1976); and potato flea beetle, *Epitrix cucumeris* (Harris), larvae (Schaal 1934). Although a preliminary trend has been shown between the density of potato flea beetle adults and the occurrence of common scab in cv. Norland potatoes (Senanayake 1987), any quantitative relationship between potato flea beetle larvae and the occurrence of scab is unclear. The objective of this study was to determine whether the density of potato flea beetles has an effect on the incidence or severity of common scab disease on cv. Russet Burbank tubers.

Materials and Methods

Experiments took place during in 1989 at Winnipeg and Portage la Prairie, Manitoba, and in 1990 at Morden and Winkler, Manitoba. The design of plots, experimental treatments and harvesting procedures are described in the materials and methods section of Part 1 of this chapter. In 1990, the Winkler experimental and reservoir plots were situated in a field with a history of recurrent scab problems (H. Thiesen, pers. comm.). Any scabby tubers harvested were recorded, and the percent surface area covered by scab was estimated.

To establish whether the number of potato flea beetle adults feeding on a plant is associated with the number of larvae in the soil around its root system, soil core samples were taken on 25 July, 1990. Three groups of five plants were sampled in the commercial field; groups were comprised of plants with high (21-30), moderate (11-20) or low (1-10) numbers of feeding punctures per leaflet at the time of sampling. Feeding punctures were counted on three randomly-selected lower terminal leaflets per plant. Two - 10 cm diameter soil cores, on opposite sides of a plant, were taken to a depth of 15 cm. Each core was transferred to a plastic bag for subsequent counting of *E. cucumeris* immatures in the laboratory.

Methods for isolating *S. scabies* were based on Loria and Davis (1988). Any tubers exhibiting symptoms of common scab disease were disinfested in 1.5% aqueous sodium hypochlorite for 1 minute and rinsed with sterile water. A piece of tissue was removed from beneath one scab lesion per tuber and was macerated in a sterile plastic bag with 5 ml of water. A drop of this suspension was streaked onto nystatin-polymixin-penicillin-cyclohexamide (NPPC) water agar and was incubated for 14 days at 30° C. This antibiotic agar only allowed colonies of *Streptomyces* spp. to grow. Three serial dilutions, made from an isolated colony of the pathogen, were streaked in a cross-hatch pattern onto yeast malt extract (YME) agar and were incubated at 28° C for 14 days. Serial dilutions were also streaked onto peptone-yeast extract iron (PYI) agar and incubated at 28° C for four days. From colonies grown on YME and PYI agar, observations of aerial mass colour, reverse colour and spore-bearing hyphae were used confirm the presence of *S. scabies*.

Results

Few harvested tubers showed symptoms of common scab disease (Table 13). Plants with affected tubers had little or no flea beetle damage and generally did not come from fields with a history of common scab. Also, most affected tubers had less than five percent of their surface area covered by scab, which is insufficient to downgrade the yield for table stock (S. Prokopchuk, pers. comm.). Therefore, the effect of adult potato flea beetle densities on the occurrence and severity of scab on Russet Burbank tubers was undiscernible.

Streptomyces scabies was identified from at least one of the serial dilutions on YME or PYI agar made from each tuber exhibiting symptoms of common scab disease. The identification of colonies was based on diagnostic features from Loria and Davis (1988). On YME agar, the pathogen was identified by the presence of grey aerial mycelia with loose spiral spore chains, observed at 200-400X magnification. Only brown or black diffusible pigments are characteristic of *S. scabies*, and the reverse side of the colony is a golden-brown colour. On PYI agar, the pathogen characteristically produces a very dark melanoid pigment and has similar mycelial properties as on YME agar.

With increased numbers of feeding punctures per leaflet, an increase in the number of potato flea beetle immatures was found in soil core samples (Table 14). A significant linear relationship between mean feeding punctures per leaflet and the number of potato flea beetle immatures was found to exist ($Y=-0.025+0.128X$; $F=19.9$; d.f.=1,13; $P<0.01$). Since potato flea beetle adult densities are correlated with the number of feeding punctures per leaflet (Chapter III, Part 2), it can safely be assumed that densities of potato flea beetle larvae and pupae are related to numbers of adults.

Discussion

Two factors may account for the absence of common scab disease in this study. First, differences between potato cultivars must be considered. All russet-skinned varieties of potatoes are generally resistant to scab infection, and Russet Burbank is considered to be tolerant of scab under most conditions (Pavek et al. 1973; Hodgson et al. 1977; Rich 1983; Campbell et al. 1984). This varietal trait may explain why very little scab infection took place, even in the Winkler plots where there was a recurrent history of scab infection. Senanayake (1987) showed a relationship between densities of potato flea beetle adults and the occurrence of scab in the cultivar Norland. Norland is only moderately resistant to scab and is considered inferior to Russet Burbank for this trait (Hodgson et al. 1977; Rich 1983; Campbell et al. 1984). Hence, varietal differences alone may explain why Senanayake (1987) found a greater occurrence of common scab disease.

A second factor that may explain the absence of common scab is related to soil moisture. The scab pathogen prefers conditions of low soil moisture (Sanford 1923; Wellings and Rosser 1968; Lapwood et al. 1970, 1971, 1973; Lewis 1970; Lapwood 1972; Lapwood and Adams 1973, 1975; Davis et al. 1976; Adams and Lapwood 1978). Inhibition of scab occurs if soil is kept wet for four to six weeks, starting within three to four days of tuber initiation (Lapwood et al. 1973). Wet soils are suspected to have increased populations of antagonistic bacteria on internodes, which are the spaces between "eyes" of a tuber, which have lenticels susceptible to infection (Adams and Lapwood 1978). Internodes form successively at the apex of a growing tuber and pass through a period of susceptibility as the stomata, which they have when first formed, are converted to lenticels (Adams and Lapwood 1978). The youngest two internodes at any one time possess stomata and are resistant to infection (Lapwood and Adams 1973). However, as stomata are converted to lenticels, there is a period of susceptibility for approximately 10 days until the developing lenticels are fully suberised and resistant to infection (Adams and Lapwood 1978). Commercially, infection of the first four or five internodes to be formed is important because these expand more and therefore cause greater blemishing when scabbed. Thus, greatest potential for blemishing is in the third week after tuber initiation (Lapwood et al. 1970).

Increases in soil moisture have also been linked to liberation of manganese, particularly in acid soils (Lapwood and Adams 1975). Several studies have related the presence of manganese to decreases in scab occurrence (McGregor and Wilson 1966; Davis et al. 1976). Green manuring of fields can also cause manganese, through the action of micro-organisms, to be reduced to a soluble form which is toxic to *S. scabies* (Rogers 1969).

Tuber initiation, for Russet Burbank, occurs during the last week of June and into early July in Manitoba (M. Pritchard, pers. comm.). Mean monthly precipitation during June of 1989 and 1990 was well above normal, (Table 15), which would have raised soil moisture levels considerably during the period of tuber initiation. In addition, the rate of evaporation during this time period was likely not different from average as temperatures were below normal in 1989 and only slightly above normal in 1990 (Table 15). With high soil moisture at tuber initiation, the occurrence and severity of scab would be expected to be low. Similar weather conditions existed in 1985, which may explain why the majority of scabby tubers found by Senanayake (1987) were not severe enough to be downgraded.

Other inorganic factors may also influence the expression of common scab disease. Low soil pH's, between 5.0 and 5.3, are enough to suppress *S. scabies* altogether (Rich 1983). The levels of calcium and phosphate in tubers also affect scab levels. High levels of tuber calcium make periderm cells more susceptible to infection, but the application of phosphate, by neutralizing calcium ions, reduces scab severity (Davis et al. 1976). Suppression of calcium and increases in phosphorus levels in potato tubers are found in soils fertilized with ammonium forms of nitrogen rather than with nitrate forms (Polizotto et al. 1975). This may explain any relationships found between the form of nitrogen used to fertilize potato crops and the severity of scab (Davis et al. 1976). Although neither soil nutrients nor pH were measured in this study, it is unlikely that these had any great effect on the expression of scab, since cropping practices were not altered from earlier years. This is especially relevant with respect to the Winkler plots where scab was a recurrent problem.

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Table 13. Potato tubers with common scab in 1989 and 1990.

Year	Plot	Experimental treatment	Tuber size range (cm)[1]	Number of tubers	% Scab[2]
1989	Commercial	-	3.8 <D≤ 4.5	1	<5
1989	Commercial	-	4.5 <D≤ 4.8	2	<5
1989	Commercial	-	5.7 <D≤ 7.0	2	<5
1989	Commercial	-	4.8 <D≤ 5.1	1	<5
1989	Commercial	-	5.1 <D≤ 5.7	1	<5
1989	Commercial	-	5.7 <D≤ 7.0	1	<5
1989	Commercial	-	5.7 <D≤ 7.0	1	<5
1989	Commercial	-	5.7 <D≤ 7.0	1	<5
1990	Morden Exp.[3]	000	5.7 <D≤ 7.0	1	20
1990	Winkler Exp.[4]	000	5.7 <D≤ 7.0	1	<5
1990	Winkler Exp.	005	5.7 <D≤ 7.0	1	<1
1990	Commercial	-	5.1 <D≤ 5.7	1	40

[1] Maximum tuber diameter (D)
[2] Visual estimate of percent tuber surface covered by scab.
[3] Morden Experimental plot
[4] Winkler Experimental plot

Table 14. Results of soil core sampling for potato flea beetle immatures on 25 July, 1990. All samples were taken from the commercial field; immatures from two cores per plant are shown.

Relative infestation	Mean (± S.E.) feeding punctures per leaflet[1]	Number in two soil cores		
		Larvae	Pupae	Total
Low	3 ± 1.5	0	0	0
Low	4 ± 2.3	0	0	0
Low	9 ± 1.7	1	1	2
Low	10 ± 0.9	1	1	2
Low	10 ± 2.4	0	2	2
Moderate	11 ± 2.3	0	2	2
Moderate	12 ± 2.0	0	0	0
Moderate	15 ± 1.8	1	1	2
Moderate	19 ± 3.2	0	3	3
Moderate	20 ± 2.5	1	2	3
High	22 ± 2.2	0	1	1
High	24 ± 4.9	1	2	3
High	25 ± 1.2	0	2	2
High	30 ± 1.2	1	3	4
High	30 ± 3.2	1	4	5

[1] Lower terminal leaflets; N=3

Table 15. Climatological data for experimental locales in 1985, 1989 and 1990. (Source: Environment Canada monthly station records from Morden CDA, Winnipeg International Airport and CFB Portage la Prairie).

			Precipitation		Temperature	
Year	Month	Location	Total(mm)	% of Normal	$\overline{x}$ (°C)	Deviation from $\overline{x}$[1]
1985	April	Winnipeg	16.2	42	6.3	2.9
1985	May	Winnipeg	64.0	97	13.1	1.8
1985	June	Winnipeg	67.4	84	14.0	-2.8
1985	July	Winnipeg	34.0	45	18.8	-0.8
1985	Aug.	Winnipeg	218.0	290	16.3	-2.0
1985	Sep.	Winnipeg	28.5	53	10.0	-2.4
1989	April	Portage[2]	29.1	78	3.2	0.3
1989	May	Portage	32.7	52	13.7	2.5
1989	June	Portage	133.1	176	16.3	-0.7
1989	July	Portage	32.8	43	22.3	2.6
1989	Aug.	Portage	44.0	54	19.2	0.8
1989	Sep.	Portage	20.8	42	13.8	1.4
1989	April	Winnipeg	15.9	41	2.6	-0.8
1989	May	Winnipeg	26.0	40	13.7	2.4
1989	June	Winnipeg	150.2	188	16.5	-0.3
1989	July	Winnipeg	33.4	44	22.1	2.5
1989	Aug.	Winnipeg	76.6	102	19.5	1.2
1989	Sep.	Winnipeg	10.0	19	13.6	1.2
1990	April	Morden	46.6	113	4.2	0.2
1990	May	Morden	43.6	66	11.1	-0.8
1990	June	Morden	185.4	245	17.9	0.5
1990	July	Morden	42.4	57	19.6	-0.6
1990	Aug.	Morden	47.0	66	20.3	-0.6
1990	Sep.	Morden	17.0	33	15.1	2.0

[1] Deviations in °C from long term mean.
[2] Portage la Prairie

CHAPTER III

PART 4

Scientific Note:
Grasshopper feeding on cv. Russet Burbank potatoes

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The twostriped grasshopper, *Melanoplus bivittatus* (Say), and the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), are two of the most widespread and destructive of pests of the Canadian prairies (Smith and Holmes 1977; Hardman and Smoliak 1980). These species feed on both grassy and broadleaf plants and have one generation per year (Philip and Mengersen 1989). Although both are generalist feeders, they defoliate potato crops only during hot dry summers when numbers reach outbreak levels (Cole 1951; Hodgson et al. 1977; University of California 1986). Very few, if any, published accounts exist in which grasshoppers are described as pests of potatoes, nor do any studies relate potential yield losses caused by these insects. Therefore, a study was undertaken to determine if *M. bivittatus* and *M. sanguinipes* can successfully feed on cv. Russet Burbank potato plants, and if so, whether any relationship exists between pest density and yield.

An experiment was conducted during the summer of 1990, in a field plot 8 km west of Winkler, Manitoba. Four different levels of adult grasshoppers were tested: 0, 1, 3, and 5X field density. Field density was determined by estimating population densities of twostriped and migratory grasshoppers in field margins during the three weeks grasshoppers were placed on plants. The species composition and dates that grasshoppers were introduced to treatments are listed in Table 16. The design of the plot, types of cages used and harvesting techniques are the same as those described for the "Winkler plot" in Part 1 of this chapter.

Detailed information about the weight and grading of tubers harvested from individual plants is contained in Appendix 11. No apparent trend was discernable from the average yields of experimental treatments (Table 17), and by analysis of variance, no significant difference between treatment yields existed (F=0.7; d.f.=3,20). Grasshoppers of both species fed on plants and survived the duration of the week for which they were introduced. However, the defoliation within treatments was inconsistent and injury for even the most defoliated of plants was low. Several reasons may account for these observations. First, if late instar juveniles were misidentified as adults and introduced to treatments, differences in feeding rates between life stages could account for the variable defoliation within treatments. For example, fifth instar nymphs of *M. bivittatus* and *M. sanguinipes* are known to have greater daily feeding rates than adults (Holmberg and Hardman 1984). Also, differences in feeding rates between sexes of grasshoppers exist, as they are dependant on the egg-laying cycle of females and the mating condition of males (Holmberg and Hardman 1984).

The quality of potato foliage as food for grasshoppers may also have influenced the amount of defoliation in treatments. The concentration of glycoalkaloids in the foliage of *Solanum tuberosum* L. and wild *Solanum* spp. confers resistance to fungal diseases as well as to many insect pests (Raman et al. 1979; Casagrande 1982; Tingey 1984; Mitchell and Harrison 1985; Hare 1987). This protection from pests may be due to the inhibition of acetyl cholinesterase by these compounds (Bushway et al. 1987). Although such potato pests as *Leptinotarsa decemlineata* (Say) and *Epitrix cucumeris* (Harris) have evolved to feed on potato foliage containing glycoalkaloids, it is likely that grasshopper species which normally do not utilize Solanaceae as primary food hosts have not developed any mechanisms to sequester or metabolize these toxic substances. This notion is supported by feeding behaviour studies using *M. bivittatus*. The glycoalkaloids solanine and tomatine, both found in *S. tuberosum*, do not inhibit feeding when offered in chemically defined synthetic diets, nor do they restrict feeding under natural conditions (Harley and Thorsteinson 1967). However, both compounds cause nymphal mortality before the adult stage is reached (Harley and Thorsteinson 1967). Since these compounds interfere so greatly with nymphal development, it is unlikely that adult grasshoppers can successfully feed on plants which contain them.

In this study, feeding by *M. bivittatus* and *M. sanguinipes* appears to have been somewhat inhibited on potato foliage. Although the glycoalkaloids tomatine and solanine are known to have toxic effects in *M. bivittatus*, they are not feeding inhibitors (Harley and Thorsteinson 1967). If feeding inhibition does occur in potatoes, other glycoalkaloids or secondary plant chemicals may be causing it to occur. If this is true, the inconsistency of defoliation within treatments could be attributable to differences in the susceptibility of individuals to such plant chemicals. Although all grasshoppers survived their exposure to plants, it is unlikely that these species could survive on potato foliage for a prolonged period of time. In hot, dry summers, when grasshoppers are extremely abundant, limited feeding by transient groups of grasshoppers might occur on potato crops, but it is unlikely that these pests would remain for a prolonged period of time if feeding is inhibited. Therefore, *M. bivittatus* and *M. sanguinipes* are unlikely to be major pests of potatoes.

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Table 16. Composition and dates of grasshopper introductions to treatments, 1990.

		Treatments			
Date	Species	0X	1X	3X	5X
16 August	*M. bivittatus*	0	3	9	15
	M. sanquinipes	0	1	3	5
24 August	*M. bivittatus*	0	3	9	15
	M. sanquinipes	0	1	3	5
29 August	*M. bivittatus*	0	3	9	15
	M. sanquinipes	0	1	3	5

Table 17. Marketable yield of grasshopper treatments, 1990.

Treatment	N	Mean (± S.E.) yield (kg/plant)
0X	6	2.076 ± 0.268
1X	6	2.204 ± 0.160
3X	6	1.756 ± 0.251
5X	6	1.984 ± 0.207

Appendix 11. Numbers of tubers and their total mass (g), by size grade, for individual plants in grasshopper treatments, 1990.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
GH-1XA[1]	No.:	1	3	3	0	2	0	2	0	11
	Mass:	37.0	291.2	488.2	0	614.2	0	1300.5	0	2731.1
GH-1XB	No.:	1	0	0	0	1	4	2	0	8
	Mass:	26.4	0	0	0	301.0	1300.2	812.2	0	2439.8
GH-1XC	No.:	1	2	1	1	1	4	0	0	10
	Mass:	7.5	63.9	71.7	149.9	126.9	1556.5	0	0	1976.4
GH-1XD	No.:	2	0	1	4	0	4	0	1	12
	Mass:	64.3	0	126.1	462.6	0	1194.3	0	332.1	2179.4
GH-1XE	No.:	0	0	1	1	1	4	0	0	7
	Mass:	0	0	140.9	119.3	257.7	1121.2	0	0	1639.1
GH-1XF	No.:	1	0	0	0	1	9	0	0	11
	Mass:	4.6	0	0	0	126.7	2328.3	0	0	2459.6
GH-3XA[2]	No.:	0	2	0	0	1	4	0	0	7
	Mass:	0	137.8	0	0	203.0	1296.8	0	0	1637.6
GH-3XB	No.:	1	2	0	0	2	2	1	2	10
	Mass:	29.1	98.8	0	0	313.7	714.8	314.7	931.0	2402.1
GH-3XC	No.:	1	0	2	1	3	3	0	1	11
	Mass:	13.6	0	284.6	174.5	671.8	1109.3	0	489.0	2742.8
GH-3XD	No.:	0	0	0	0	0	1	0	2	3
	Mass:	0	0	0	0	0	438.8	0	1053.8	1492.6
GH-3XE	No.:	1	0	3	0	3	1	0	0	8
	Mass:	104.3	0	411.8	0	402.3	271.5	0	0	1189.9
GH-3XF	No.:	0	2	0	0	0	6	0	0	8
	Mass:	0	142.2	0	0	0	1456.1	0	0	1598.3
GH-5XA[3]	No.:	0	0	0	0	0	2	1	0	3
	Mass:	0	0	0	0	0	1203.7	314.0	0	1517.7
GH-5XB	No.:	1	0	0	0	2	5	1	0	9
	Mass:	58.1	0	0	0	434.3	1634.0	317.3	0	2443.7
GH-5XC	No.:	1	0	1	1	5	4	0	0	12
	Mass:	5.4	0	102.2	96.0	856.5	954.6	0	0	2014.7
GH-5XD	No.:	2	1	1	2	0	4	0	0	10
	Mass:	97.6	89.2	68.3	240.5	0	1281.6	0	0	1777.2
GH-5XE	No.:	0	1	3	1	2	3	0	0	10
	Mass:	0	60.9	360.8	137.2	301.8	827.0	0	0	1687.7

Appendix 11. Continued.

Plant		Maximum tuber diameter (D cm)								
		<3.8	3.8<D≤4.4	4.4<D≤4.8	4.8<D≤5.1	5.1<D≤5.7	5.7<D≤7.0	7.0<D≤7.6	7.6<D≤11.4	Total
GH-5XF	No.:	0	0	2	2	0	8	0	0	12
	Mass:	0	0	168.8	397.2	0	2205.9	0	0	2771.9

[1] Grasshopper 1X Treatment, Plant A
[2] Grasshopper 3X Treatment, Plant A
[3] Grasshopper 5X Treatment, Plant A

CHAPTER IV

GENERAL DISCUSSION

In these studies, economic injury levels were developed for the potato flea beetle on cv. Russet Burbank potatoes. Injury levels were determined for plants which did, and did not suffer early season defoliation by Colorado potato beetle. The levels are preliminary, but do show that defoliation by normal field densities of Colorado potato beetles increases the sensitivity of plants to late season defoliation by potato flea beetles. To better model the response of plants to both pests and examine variation among years, further trials must be undertaken which incorporate a greater range of field densities of both insects. Also needed is an examination of plant response to potato flea beetle defoliation while densities of Colorado potato beetles remain uncontrolled for the duration of the season. To ensure multiples of field densities are analogous to actual numbers of insects in Russet Burbank potato fields, further sampling of non-sprayed and sprayed fields of potatoes should also be undertaken. Finally, it would be valuable to examine whether the same response occurs in other varieties of potatoes, or is restricted to Russet Burbank.

The difference in susceptibility of plants to potato flea beetle defoliation allows the implementation of different injury levels for the periphery and centre of commercial potato fields. The lower injury level (4-19 beetles) is appropriate for field margins where Colorado potato beetle defoliation is greatest. In the centre of fields, the density of Colorado potato beetles is near zero, thereby necessitating the higher injury level (300-335 beetles), since these plants may exhibit overcompensation. Although further research is necessary, the use of two different injury levels for separate areas of potato fields is likely to reduce pesticide use against potato flea beetle, as control appears to be warranted only along field margins in Manitoba.

In Part 2 of Chapter III of this thesis, an attempt was made to model the spatial and temporal accumulation of feeding punctures per leaflet. By doing this, a relationship between accumulated potato flea beetle weeks and numbers of flea beetles per plant was determined. This provides an indirect method for calculating numbers of potato flea beetles per plant from feeding punctures per leaflet. The accumulation of feeding punctures was confirmed to be an extremely complex process; therefore, it is not surprising that other studies have found little change in yield with greatly differing numbers of holes in leaflets (Thompson 1984, 1985 1987). What is next needed is a more intensive study of how potato flea beetles cause the accumulation of feeding punctures on leaflets. In order to implement any economic injury level for potato flea beetle, an index of damage is needed for decision making. Therefore, better modelling is needed not only to provide a direct measure of potato flea beetle numbers, but to predict peak population numbers and when they will occur. The modelling done in this thesis predisposes further studies to consider the effects of plant microenvironment and population density processes.

The finding that sequential stresses on potatoes causes negative synergistic effects on yield may have implications for other potato pests. Such insects as potato leaf hopper, *Empoasca fabae* (Harris), and aphids are both late-season pests of potatoes in Manitoba (Senanayake and Holliday 1989). If, after early season Colorado potato beetle defoliation, plants are sensitive to any generalized injury, reduced densities of these insects may also cause reductions in yield. In 1989, the non-orthogonality between aphid ranking and treatments (Chapter III; Part 1) may be indicative of the sensitivity of plants, after injury by Colorado potato beetles, to late-season aphid feeding.

The development of most economic injury levels for crop pests has been based on the injury caused by one species of insect (or simulated injury thereof) to a particular plant host (Pedigo et al. 1986). Synergistic effects caused by multiple pest feeding are not well known, because few studies have attempted to examine multiple herbivore-plant interactions (Poston et al. 1983). Sequential artificial defoliation has been attempted on some crops (Thomas et al. 1978), but negative synergistic effects, such as seen in this thesis, were not evident. Plant response to multiple pest defoliation is likely dependent not only on the host crop, but on the nature of the injury as well. Although more research is needed to develop control strategies for multiple pests, the use of economic injury levels may be unsuitable for this purpose (Pedigo et al. 1986). For economic injury levels to be of use, all injuries must produce a similar host response, and all injuries must be additive and not interactive. An improved understanding of physiological responses to injury could be incorporated into economic injury levels if equivalent units were developed for guilds of species with similar types of injuries. This way a single injury level with standard units of injury could serve for pest complexes. However, if injury type varies or, as shown in these studies, significant interactive effects occur between pests, the concept of an economic injury level for multiple pests is very difficult to implement. The goals of integrated pest management will cause more modelling of multiple pest interaction to take place; however, the possible non-additive effects of multiple pest defoliation must be accounted for.

No relationship was found between the density of adult or larval potato flea beetles and the occurrence or severity of common scab disease of potato tubers, nor was it determined whether the larvae could act as vectors of the disease. This question may be of importance for the commercial growing of susceptible potato varieties. In order to answer this, laboratory studies must be undertaken in which susceptible varieties of potatoes are grown in *S. scabies* inoculated soil. Only by doing this, and specifically isolating the pathogen from the larvae, can this question be definitively answered.

The investigation of grasshopper feeding on potato plants was preliminary, but seemed to indicate that the feeding of *M. bivittatus* and *M. sanguinipes* might be inhibited by particular defences of *Solanum* spp. to herbivory. Wild *Solanum* spp. produce toxic substances, such as glycoalkaloids, which deter feeding by even well-adapted species (Hsiao 1974). The cultivated potato is the result of genetic breeding, but still possesses feeding deterrents derived from its ancestral lineage (Burton 1989). Although Colorado potato beetles, potato flea beetles, potato leafhoppers and aphids have evolved to feed on potato foliage, generalist feeders like grasshoppers seem to have been unable to utilize the potato plant as a host. The coding for such chemical defences must be retained in the genome of *S. tuberosum* when propagating new cultivars, otherwise, entire new pest complexes for potato crops have the potential for developing.

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