PEA APHID, *ACYRTHOSIPHON PISUM* (HARRIS), POPULATIONS ON CULTIVARS OF FIELD PEAS IN MANITOBA AND THEIR EFFECTS ON PEA YIELD

BY

JULIANA JUDY SOROKA

A thesis

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ABSTRACT

Pea Aphid, Acyrthosiphon pisum (Harris), Populations on Cultivars of Field Peas in Manitoba and Their Effects on Pea Yield

by

Juliana Judy Soroka

Major Advisor: Dr. Patricia A. Mackay

The research for this project was undertaken from 1984 to 1987. Natural infestations of pea aphids, Acyrthosiphon pisum (Harris), were measured throughout the summer on five (1984) or six (1985, 1986) cultivars of field peas in small field plots near Glenlea, Manitoba. Starting from equal numbers of pea aphids per cage, in 1986 pea aphid populations were also monitored in 1 m^3 field cages which contained plants of one of these six field pea cultivars. Throughout the summers of 1985 and 1986 pea aphids were also sampled in a total of nine Century, four Trapper and two Triumph commercial pea fields in several regions across the province.

In all of these tests, pea aphid population growth patterns were similar among cultivars. Aphid numbers rose from low levels during the vegetative to blooming stages of plant growth in mid-July, peaked in late July or early August as pods developed and matured, and declined rapidly by mid- to late August as pea plants senesced. However, numbers

of pea aphids at the time of population peak differed consistently and significantly with the cultivar upon which they grew. Peak numbers of pea aphids were larger on Triumph or Trapper plants than they were on Century or Tipu plants. In commercial fields, populations of pea aphids rose more rapidly on Trapper than they did on Century or Triumph plants.

In field plots seed weight was the yield component most sensitive to aphid feeding. Triumph had significantly lower seed yields in infested than in control subplots in two out of three years. Seed weight was significantly reduced in infested subplots of Tara peas in one year. Because aphid numbers were low and generally occurred later than at flowering or pod initiation in Century peas, no yield losses due to pea aphids occurred in this cultivar in any of the tests. However, linear regression of seed weight over aphid density indicated that, of the cultivars tested, Century is most susceptible to increasing aphid numbers. Trapper seed weight was least related to aphid density despite the relatively high numbers of pea aphids occurring on this cultivar.

In laboratory studies pea aphids had the greatest intrinsic rates of natural increase, r_m, on the cultivar Trapper and the smallest on the cultivars Tipu and Century. Ten days after infestation, the most antixenosis resistance was expressed by the cultivar Tipu, and the least by Triumph. After 20 days, Triumph still was most preferred by the aphid. Trapper appeared somewhat tolerant of the effects of pea aphid feeding.

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CHAPTER 1

INTRODUCTION

1.1 The Problem

With declining Canadian Wheat Board payments to producers over the last several years, prairie farmers have increased production of crops not marketed by the Board (Anonymous, 1984a). One such crop is field peas, Pisum sativum L., which has quadrupled in area of production in Manitoba in the last 10 years (Anonymous, 1985a, 1987a).

The main insect pest of field peas in Manitoba is the pea aphid, Acyrthosiphon pisum (Harris) (Anonymous, 1986). In Manitoba, economic thresholds have been established for this pest (Maiteki and Lamb, 1985a), but these were determined only for the commonly grown cultivar Century. Several new field pea cultivars have recently been released that outyield Century (Ali-Khan, 1973, 1978, 1980, 1982). Increased pea aphid densities have been reported on one of these newer cultivars (Maiteki et al., 1986), and there is speculation that aphid control is more likely to be required on cultivars sustaining high aphid populations (Lamb and Maiteki, 1985). However, no research has been conducted comparing pea aphid densities and their impact on various pea cultivars in Manitoba.

1.2 Objectives of the Study

The objectives of this research project were:

1. To determine if different field pea cultivars consistently support different densities of pea aphids in Manitoba pea fields.

2. To determine if there are any differences in cultivar reaction to pea aphid feeding.

3. To determine the bases or mechanisms of differential reactions or resistance of the cultivars.

1.3 Benefits of the Research

The occurrence of different pea aphid densities on different cultivars suggests that aphid resistance factors may be present in some pea cultivars. Host plant resistance represents one of the most cost effective means of pest control (Horber, 1972), and examination of the bases for variable aphid densities could disclose sources of resistance suitable for incorporation into the genomes of new cultivars. Many examples of garden peas with varying degrees of resistance to pea aphid have been found (Searls, 1932; Maltais, 1949; Cartier, 1963; Bintcliffe and Wratten, 1980; Bieri et al., 1983). At present pea aphid control in Manitoba is based entirely on pesticide application (Anonymous, 1986). Utilization of aphid resistant pea cultivars could result in substantial savings in production costs for prairie farmers.

1.4 Thesis Organization

This thesis is a report of the research carried out in growers' fields throughout south central Manitoba, in small field plots at the University of Manitoba's Glenlea Research Station, and in a controlled environment chamber at the University of Manitoba, Winnipeg, from May 1984 to June 1987.

Chapter 2 is a general review of the literature relevant to the research. Chapter 3 is a detailed presentation of the research project organized into four sections, each describing one aspect of the research and written in the style of manuscripts suitable for submission to scientific journals. Chapter 4 is an overall discussion of the research undertaken, and Chapter 5 summarizes the work and the conclusions drawn from it.

CHAPTER 2

LITERATURE REVIEW

2.1 Field Pea Production in Manitoba

2.1.1 Use and Importance of Field Peas

Field peas, P. sativum, are an annual pulse or edible grain legume crop. The main use of field peas in Canada is in split pea and puree soup manufacture. On the prairies, dried peas are also used to balance low-protein animal feeds (Anonymous, 1984b). To a much lesser extent, protein isolate, pea fibre and purified pea starch are also made from field peas (Nickel, 1986).

Recently, a large export market has been developed for Canadian field peas, and approximately three quarters of the Canadian crop is now exported as whole or split peas (Ali-Khan and Zimmer, 1989). Canadian field peas for human consumption are exported worldwide, reaching markets in India, Britain, Cuba, Columbia and Venezuela, among others. In 1986 the European Economic Community purchased significant quantities of Manitoba field peas for animal feed (F. Baudette, Roy Legumex Inc., St. Jean, MB, personal communication). In some years, depending on markets, premiums may be paid to producers of large-seeded peas (K. Lyons, Newfield Seeds, Nipawin, SK, personal communication).

Field pea production in Canada is centered in the three prairie provinces, with Manitoba producing about 65% of the total Canadian harvest (Anonymous, 1984a). The area sown to peas in Manitoba increased steadily from 15,400 ha in 1976, with a cash value of $4.7 million (Anonymous, 1985a), to 64,800 ha in 1986, with a cash value of $22.1

million (Anonymous, 1987a). In 1985 the crop ranked eighth in total crop value to Manitoba farmers (Anonymous, 1985a).

2.1.2 Field Pea Agronomy

Field peas are a cool season crop similar to wheat in days to maturity; therefore, the crop can be grown in most agricultural parts of the province (Anonymous, 1977). The principal production areas are located along and adjacent to the Red River Valley, but expansion of pea production to the north-west and Interlake regions of Manitoba has occurred (J. Rogalsky, Manitoba Dept. of Agriculture, Winnipeg, MB, personal communication).

Young pea seedlings are comparatively frost hardy (Anonymous, 1977) because they can regenerate from axillary buds below the soil surface. Thus early planting is advised (Anonymous, 1985b). Planting after May 25 is not recommended, because high temperatures, especially if they occur before full bloom, may decrease the number of pods, seed size, and yield (Fletcher et al., 1965; Nonnecke et al., 1971).

Seed inoculation with specific Rhizobium nodule-forming bacteria is advised (Anonymous, 1985b). Nitrogen fertilization is not recommended, for it may interfere with nitrogen-fixing Rhizobium ssp. (Salisbury and Ross, 1978), but field peas respond well to phosphorus (Gubbels et al., 1982), potassium, and sulphur fertilization (Anonymous, 1985b) where deficiencies occur.

Field peas are poor competitors with weeds, and prompt weed control is essential for maximum yields (Anonymous, 1977). Aschochyta blight caused by the fungus Mycosphaerella pinodes (Berkeley and Bloxam) Vest. is the most common disease of field peas in western

Canada (Zimmer, 1978; Martens et al., 1984). In some years bacterial blight and root rots may also damage pea plants (Martens et al., 1984). Planting peas once in a five year crop rotation and the use of pedigreed seed that has been treated with an appropriate fungicide are recommended to minimize losses from disease (Anonymous, 1977).

The pea aphid, A. pisum, is the most important insect pest in Manitoba pea fields (Lamb and Maiteki, 1985). Threshold levels of this insect in Manitoba in Century field peas are 2 to 3 aphids per 20 cm plant tip at flowering (Maiteki and Lamb, 1985a). Recommended insecticides for A. pisum control in pea fields are dimethoate at 204 g a.i./ha or malathion at 700 g a.i./ha (Smith et al., 1986).

Peas are harvested when they are mature and hard in the pod (Anonymous, 1977). Delayed harvesting may result in excessive shelling (Ali-Khan and Zimmer, 1989), and seed loss through lodging, germination, or decay in the field (Johnston and Sanderson, 1975), as well as reduced cooking quality (Gubbels et al., 1985). Green peas are susceptible to bleaching and should be harvested early, using a recommended dessicant if necessary (Anonymous, 1984b).

2.1.3 Field Pea Cultivars

Yellow-seeded cultivars are preferred for the soup industry (Anonymous, 1977). Century, Tara, and Tipu are yellow-seeded field pea cultivars recommended in Manitoba for soup production (Anonymous, 1982). Of these, the large-seeded Century, licenced in 1960, is the most popular cultivar grown in Manitoba (Anonymous, 1984b), with an average yield of 2,416 kg/ha in four years of tests in the province (Anonymous, 1986). Tara, licenced in 1978, is a medium-seeded dimpled

cultivar, with powdery mildew resistance and average yields 18% greater than those of Century (Ali-Khan, 1978). Tipu, a large-seeded cultivar licenced in 1985, is a semi-leafless pea possessing normal stipules but with leaflets reduced to tendrils. Similar in yield to Century, Tipu is superior in standing ability, has more uniform drying characteristics than Century (Ali-Khan, 1986), and the canopy has good insecticide penetration properties (Anonymous, 1987b).

Other field pea cultivars grown are Trapper, Lenca, and Triumph. Trapper, licenced in 1970, has small, yellow seeds and is commonly grown for livestock meal; it is the second most commonly grown field pea in Manitoba (Anonymous, 1984b). Lenca is a medium-sized yellow-seeded pea licenced in 1979 for the soup trade. It is not currently recommended for Manitoba production but it is well adapted to eastern Canada, where it outyielded Century by 19% in co-operative tests (Ali-Khan, 1980). Finally, Triumph is a large-seeded green pea also used in the soup industry and the only green coloured cultivar recommended in Manitoba (Anonymous, 1986). Triumph is higher yielding than Century but is more susceptible to weathering and bleaching (Anonymous, 1984b).

Although most of the more recently released field pea cultivars outyield Century, no quantitative studies have been conducted to determine comparative insect infestation levels on these cultivars or to investigate effects of the aphid on different pea cultivars.

2.2 The Pea Aphid

2.2.1 Geographical Distribution, Life Cycle, and Biology

The pea aphid, A. pisum, is cosmopolitan in distribution, occurring in every continent except Antarctica (Eastop, 1966, 1971). Of

Palaearctic origin (Blackman and Eastop, 1985), it is thought to have been introduced to North America from Europe with clover and/or peas in the second half of the nineteenth century (Folsom, 1909), and was first reported in Illinois in 1878 (Davis, 1915). Near the turn of the century the aphid was found near Ottawa, Ontario (Johnson, 1900); this is the first report of its presence in Canada. It is now widely distributed in Canada, ranging from the Atlantic to Pacific coasts in areas with a temperate climate (Mackauer, 1971). It has been collected as far north as Churchill, Manitoba (58°47′N) (Robinson, 1979).

In Canada, the pea aphid is holocyclic or sexually reproductive, overwintering as a diploid egg on leaves and stems of alfalfa, clovers, and perennial wild legumes (Harper, 1975). The fundatrix or stem-mother, which emerges from the egg in the spring, parthenogenetically and viviparously produces a generation of daughters on the overwintering host. The daughters in turn parthenogenetically and viviparously produce apterous or alate (wingless or winged) female progeny. Alatae are produced in response to the stimuli of declining host quality (Kenten, 1955; Sutherland, 1969a; Kennedy and Forsbrooke, 1972), and physical contact or crowding (Hille Ris Lambers, 1966; Sutherland, 1969b); their production is also modified by maternal age effects (Mackay and Lamb, 1979) and genetic differences among populations (Lamb and Mackay, 1979). The alate aphids migrate to other hosts, including annual legumes such as field peas, thus ensuring a wide distribution (Cooke, 1963). On the summer hosts, many generations of predominantly apterous females are parthenogenetically and viviparously produced. In the autumn reduced photoperiod and declining temperatures (Kenten, 1955; Lees, 1966; Lamb and Pointing, 1972; Ward

et al., 1984) stimulate parthenogenetic females to produce a single sexual generation composed of oviparae or sexual females and males. These sexualss mate and the oviparae lay eggs on the winter host, thus completing the life cycle (Lees, 1961).

A clone is understood to be the offspring produced through parthenogenesis by a single fundatrix and any subsequent viviparous generations (Mackauer, 1973). Thus the clonal descendents of a single fundatrix show little variability since they are genetically identical (Blackman, 1979), and, if subjected to unchanging environments, tend to remain constant over many generations. Cartier (1957) found in the laboratory that two pea aphid clones maintained stable but different mean adult weights over 44 generations. However, pea aphid fundatrices are the products of fertilized eggs, and there may be considerable genetic heterogeneity among them (Lees, 1966; Neiman, 1971). Field populations are generally composed of descendents of many fundatrices, that is, made up of many clones. The biological responses of single clones are not necessarily the same as those of the population as a whole (Lamb and Mackay, 1983; Subasinghe, 1983).

The six main pea aphid morphs -- fundatrix, apterous or alate vivipara, apterous ovipara, and apterous or alate male -- vary somewhat in appearance, notably in the presence or absence of wings and in body shape and size. The general body form in both winged and wingless morphs is elongate and fusiform. Average body dimensions of alatae are 4.5 by 1.5 mm, while apterae are about 5 mm by 1.6 mm (Folsom, 1909). In general, all morphs are light to dark green in colour. Pea aphid eyes are red and prominent, and antennae are lighter coloured than the body. Joints are darker than the rest of the long conspicuous legs

(Folsom, 1909). Davis (1915) gives a complete description of pea aphid morphs in North America.

In Europe, the pea aphid occurs as a green and a red form (Markkula, 1963). Harper et al. (1978) reported only the green form of A. pisum occurring in North America. However, the red form was collected from alfalfa in the field in Maryland in 1979 and subsequent years (Kugler and Ratcliffe, 1983). The potential of the pea aphid red form as a pest in North America may be greater than that of the green form. This type varies significantly from the green form in such biological attributes as fecundity, total number of alatae produced, searching behaviour (Lowe and Taylor, 1964), response to disturbance (Müller, 1983), and response to alfalfa cultivars (Lowe and Taylor, 1964).

The pea aphid has four nymphal instars (Folsom, 1909; Davis, 1915). Temperature is one of the principal factors affecting the duration of development from birth to adult (Kilian and Nielson, 1971; Hutchison and Hogg, 1984). Temperature thresholds for development of each instar vary with location (Campbell et al., 1974); however, Lamb et al. (1987) found that variation in developmental parameters may be greater among clones within populations than among populations collected from distant locations. Minimum and maximum developmental thresholds are about 2.4°C (Hutchison and Hogg, 1984) and 25° to 30°C (Siddiqui et al., 1973), respectively. There appear to be no deleterious effects on development of A. pisum in temperature ranges from 10° to 26°C (Campbell and Mackauer, 1975; Bieri et al., 1983).

Length of pre-reproductive period varies with degree of temperature fluctuation (Siddiqui et al., 1973), aphid clone (Frazer,

1972), alary morph (Hutchison and Hogg, 1984), and host plant (Mackauer, 1973; Bieri et al., 1983). Times from birth to adult in the laboratory at 19°-20°C vary from 6.2 days for aphids feeding on faba bean (Frazer, 1972), to 7.6 days for those feeding on alfalfa (Campbell and Mackauer, 1975), to 8.3 days for those feeding on peas (Hutchison and Hogg, 1984). Time from birth to reproduction was reported to be 8.4 days (Siddiqui et al., 1973) and 9.0 days (Cartier, 1960) for aphids feeding on pea cultivars. Harrington (1941) reported a 6.6 day period to reach adult status and a 7.4 day period to achieve reproductive ability for the pea aphid on a pea cultivar. In the field, an aphid clone from Kamloops, British Columbia, had a mean pre-reproductive period of 12.3 days feeding on alfalfa (Campbell and Mackauer, 1977). In Wisconsin, time to first reproduction of the pea aphid grown on alfalfa out of doors was 12.5 days for spring apterae and 7.5 days for apterae monitored in the summer (Hutchison and Hogg, 1984).

Fecundity also varies with temperature, with a maximum number of nymphs produced at about 15°C (Siddiqui et al., 1973; Bieri et al., 1983). Fecundity of A. pisum on a pea cultivar near Lennoxville, Quebec, was 66 nymphs at mean August temperatures of 16.5°C and 35 nymphs at mean October temperatures of 12.8°C (Sharma et al., 1974). Fecundity also varies with photoperiod (Sharma et al., 1973), morph (Mackay and Wellington, 1975), aphid clone, and host plant. Markkula and Roukka (1970) reported four pea aphid clones to have 80 to 100 progeny per female on two pea cultivars, and less than 10 per female nymphs each on red clover, while two other clones exhibited the opposite trend in fecundity. These authors also reported average numbers of descendents of one pea aphid clone varying from fewer than

five to about 50 per female on 16 different pea cultivars (Markkula and Roukka, 1971).

Under laboratory conditions reproductive rate increases rapidly to a maximum, which occurs about one third of the way through the reproductive period, and then gradually declines as adults age (Hutchison and Hogg, 1984). The post-reproductive period is extremely variable in length (Campbell and Mackauer, 1977). At a constant temperature of 19.7°C , an A. pisum clone growing on alfalfa had a mean reproductive period of 19.4 days, a post-reproductive period of 9.8 days, and a lifespan of 38.2 days (Campbell and Mackauer, 1977).

The number of generations of pea aphid in the field varies from 14 to 28 in California (Cooke, 1963); 13 generations per year were recorded in Indiana (Davis, 1915), and 6 or 7 generations in the northerly latitudes of Finland (Markkula, 1963). In Wisconsin, A. pisum produces 7 to 8 generations a year on peas in late spring and summer (Harrington, 1941).

Differences in life cycle, growth rates, fecundity and longevity on various host plants have led to the recognition of several biotypes or physiological races of A. pisum (Cartier, 1957, 1959, 1963; Neiman, 1971; Kilian and Nielson, 1971; Frazer, 1972; Mackauer, 1973; Auclair and Srivastava, 1977; Webster and Inayatullah, 1985). Neiman (1971) tested 34 parthenogenetic clones of pea aphid and assigned them to eight biotypes and two feeding complexes on the basis of feeding response. Populations from warmer U.S. regions were found to withstand higher temperatures than populations from cooler regions (Kilian and Nielson, 1971).

Eastop (1972) went so far as to suggest that A. pisum should perhaps be subdivided into many subspecies on the basis of biotype host range. However, as Frazer (1972), Mackauer (1973), and Subasinghe (1983) pointed out, in areas of holocycly biotypes are ephemeral, selected for and existing only through the summer period. Subasinghe (1983) found as great a variation in aphid response to different host plants in any single field as had been reported between clones having diverse geographic origins; further, he found no relationship between responses of clones to different host plants in one year and their responses to the same host plants in another year. There also appears to be no biochemical evidence for the existence of pea aphid biotypes. In an enzyme analysis, little electrophoretic variation was found among seven pea aphid clones, some of which had been characterized as distinct biotypes (Simon et al., 1982).

2.2.2 Host Plant Selection and Host Range

Because of the low flight speeds of alate aphids, air movement determines the direction of their flight and the distance travelled (Johnson, 1955; Dixon, 1971). Aphids are likely to be carried to high altitudes and subsequently brought to near ground level almost entirely by atmospheric circulation (Dixon, 1971). However, flight initiation is in response to reception of the short wave light radiation of the sky, while flight termination of low flying aphids is in response to longer wavelengths reflected by the ground and an optomotor reaction provoked by objects looming up along the path of the flying aphid (Kennedy et al., 1961).

Foliage colour may influence initial selection of host plants by aphids. In Wisconsin, canning pea cultivars with yellowish foliage were not as heavily infested by A. pisum as greener cultivars (Searls, 1932, 1935). Kennedy et al. (1961), on the other hand, reported that some species have a phototactic preference for the yellowest foliage. Yellow-coloured foliage was noted to influence positively the alighting response of migrant pea aphids, with migrants and colonies being least abundant on a pea cultivar with deep green foliage (Cartier, 1963).

There is no published method of distinguishing preferred from non-preferred pea plant hosts of the pea aphid on the basis of morphological characteristics of the plants (Packard, 1941). The deep green-foliaged pea cultivar described by Searls (1935) as being preferred by pea aphids is a dwarf pea with short, thick internodes and large, fleshy leaves. Markkula and Roukka (1971), however, found fewer aphids on short cultivars. At early pea growth stages, Cartier (1963) found that increased plant height has a barrier effect that favours higher initial infestation by migrants. At full growth, however, increased plant height may reduce ensuing aphid populations because taller stems, longer internodes, and less dense foliage increase exposure to inclement weather and natural enemies.

The landing of aphids on host plants appears to be based on trial and error; host selection is a matter of staying or leaving (Kennedy and Forsbrooke, 1972). If they do not like the host, aphids will leave and land indiscriminately somewhere else. The greater number on preferred hosts is not, therefore, due to more landing, but rather to fewer leaving (Muller, 1958; Kennedy et al., 1961). Non-hosts are most often rejected after a brief probe which penetrates peripheral cell

walls only and does not reach the phloem sieve tubes (Kennedy and Forsbrooke, 1972) which are the usual feeding sites (Lowe, 1967; McLean and Kinsey, 1968).

The selection of hosts by phytophagous insects is governed by the presence or absence of non-nutritional stimulatory or deterrent secondary plant compounds (Fraenkel, 1969) and by the nutritional status of the host plant (Kennedy, 1958). Although some legumes possess secondary compounds that may influence host selection by insects (Loper, 1968; Wegorek and Krzymanska, 1970; Dreyer et al., 1985, 1987), little biochemical analysis has been undertaken on the secondary compounds of peas that may act as selective cues for pea aphids. Auclair and Cartier (1960) reported an absence of toxic substances in two non-preferred pea cultivars tested.

Preferred hosts of the pea aphid are generally nutritionally superior to non-preferred plants, especially in nitrogenous compounds such as amino acid concentrations and balance (Auclair and Cartier, 1960; Auclair, 1976). A. pisum requires the usual 10 amino acids needed by insects (House, 1966), plus cysteine, along with an optimum level of sucrose, vitamins and minerals for survival and development (Auclair, 1969; Srivastava and Auclair, 1974, 1975). In multiple choice tests, pea aphids selected, fed on, and colonized diets that were nutritionally superior (Auclair, 1965, 1969). On these diets their rates of growth, reproduction, and survival were higher than on less adequate diets.

A. pisum preference for succulent foliage has been noted by Searls (1935), but another study reported reduced numbers of aphids on highly succulent garden peas produced under high moisture and reduced

light conditions (Barker and Tauber, 1954). However, this reduced number of aphids caused more injury to the succulent plants than did higher numbers of aphids on well differentiated plants produced under normal growth conditions. Observation of increased injury may have given rise to the general belief that highly succulent plants favour pea aphid colonization and growth (Barker and Tauber, 1954).

Pea aphids respond negatively to gravity; the pea aphid's most common feeding site is the plant terminal down to about the fourth internode from the plant tip (Kennedy, 1958). There is a net upward movement as plants senesce (Lowe, 1971). Apterae prefer feeding on leaf and terminal abaxial surfaces (Müller, 1984).

Patch (1938) listed 58 plant species in 23 genera as known hosts of the pea aphid world-wide and all belong to the Leguminosae. A. pisum is considered to be oligophagous and monoecious, with no regular alternation of summer and winter hosts (Eastop, 1972; Blackman and Eastop, 1985; but see also Evans and Gyrisco, 1956). Under dry conditions the aphid has been reported on the crucifer Capsella bursa-pastoris (L.) Medic. (Davis, 1915; Blackman and Eastop, 1985). In Manitoba, the pea aphid has been reported on Lathyrus odoratus L., Medicago sativa L., Melilotus alba Medic., M. officinalis (L.) Pall., P. sativum (Robinson and Bradley, 1968), and Vicia faba L. (Hanec, 1975).

In both Europe and North America, A. pisum exists as a complex of populations with several different host plant preferences (Eastop, 1966). Legumes that are the most widely distributed in an area tend to be the most favoured food (Dudley and Bronson, 1952). The primary hosts of the pea aphid in Canada are alfalfa and clover (Beirne, 1972). In

Finland, peas and red clover are the chief hosts of A. pisum (Markkula and Roukka, 1971). Peas and alfalfa are the main hosts of the aphid in the Pacific Northwest (Cooke, 1963).

2.2.3 Population Dynamics of the Pea Aphid

Perennial legumes such as alfalfa and clover species are the centers of pea aphid infestations early in the season (Russell, 1924; Cooke, 1963). As summer approaches, alatae emigrate and begin infesting annual legumes such as young field peas, usually in late May or early June in Manitoba (Lamb and Maiteki, 1985). A. pisum populations remain low in Manitoba throughout June, but increase rapidly in July when the crop is flowering and producing pods, and peak in the latter half of July or in early August when pod maturation occurs (Maiteki et al., 1986). Thereafter, populations on peas decrease rapidly as aphids die or migrate back to alfalfa. This left-skewed population curve of pea aphids in Manitoba field peas (Lamb and Maiteki, 1985) is similar to that reported for A. pisum studies on green peas in Washington state (Yencho et al., 1986).

Within individual fields, pea aphid densities may vary tremendously temporally and spatially. Incoming alatae are often more abundant in the outer rows or windward edges of crops than nearer the center (Johnson, 1955; Lewis, 1969), or in the lee of sheltering vegetation or fences (Lewis, 1965, 1966, 1969). Population increase within a field may be extremely rapid (Glasgow, 1939; Mackauer, 1971). In Manitoba, 7 to 15-fold increases in population levels occurred in pea fields in a 2 week period (Maiteki and Lamb, 1985a).

Aphid populations are susceptible to stormy weather, particularly high winds, heavy rain and hail (Bakker and Robinson, 1975; Walker et al., 1984). However, if favourable weather and host plant conditions occur after the disturbance, populations may rebound to levels similar to or greater than before (Russell, 1924).

Various factors contribute to the drastic population decline of A. pisum in mid to late summer. These include migration (Hutchison and Hogg, 1985), pathogens (Yencho et al., 1986), predators, and parasites (McDonald and Harper, 1978).

Emigration from fields has been associated with deteriorating nutritional value of the host plant (Kennedy and Forsbrooke, 1972), crowding (Lees, 1966; Sutherland, 1969b), and harvest of the crop (Cooke, 1963). However, migration from an area is much more difficult to quantify than migration to an area, since not all alatae produced in a population emigrate (e.g. Shaw, 1970), and the exact role that migration plays in most population declines is uncertain.

Diseases of fungal or bacterial origin may kill enormous numbers of aphids in a short time (Cooke, 1963). The entomophthora fungus Erynia neoaphidius Rem. and Henn. (= Entomophthora aphidis Hoff.) is one of the most important natural enemies of the pea aphid (Hutchison and Hogg, 1985). Aphid mortality due to fungal disease is increased by warm, humid weather, which promotes fungal growth and development (Rockwood, 1950; MacLeod, 1955; Cooke, 1963).

The most common insect predators of pea aphids are coccinelids, syrphids, chrysopids, and nabids (Fluke, 1925; Gyrisco, 1958; Cooke, 1963; Harper, 1972, Neuenschwander et al., 1975; Harper and Lilly, 1982). There are four native and two introduced hymenopterous parasites

of the pea aphid in Canada (Mackauer, 1971). Predators and parasites decrease pea aphid populations in certain circumstances (Neuenschwander et al., 1975; McDonald and Harper, 1978; Karner and Manglitz, 1985), but may be incapable of keeping A. pisum densities low for any length of time (Campbell, 1926; Cooke, 1963; Frazer and Gilbert, 1976).

2.2.4 Economic Importance

The pea aphid is a serious economic pest of alfalfa in the United States and causes losses estimated at $60 million in some years (Carnahan et al., 1963). In Canada, A. pisum is considered a rare pest of dryland alfalfa or red clover grown for hay (Mackauer, 1971), but may be more of a problem on irrigated alfalfa or alfalfa grown for dehydration (Harper and Lilly, 1966).

The greatest losses from this aphid in Canada arise from its attacks on canning, processing and field peas. In 1899 and 1900, A. pisum caused considerable damage to the pea crops in Quebec and the Atlantic provinces (Hewitt, 1912) and has been recorded as being injurious to peas in many localities in North America since then (Davis, 1915; Cooke, 1963). In the Annapolis Valley of Nova Scotia and in southern Quebec, pea aphid damage requires the regular application of insecticides (Mackauer, 1971). Economic thresholds were surpassed in 2 of 3 years in a survey of pea aphids in Manitoba field pea fields (Maiteki et al., 1986).

2.2.5 Plant Injury Due to Pea Aphid Feeding

Pea aphid injury to plants does not include acute stigmonose, that is, necrotic spotting of plants (Harrington et al., 1943); instead,

injury is confined to sap withdrawal from leaves, stems, blossoms and pods (Gyrisco, 1958). This sap withdrawal affects growth directly by removal of photosynthate available for plant production and indirectly by loss of potential production resulting from lost tissue (Barlow et al., 1977). In one study the pea aphid reduced the relative growth rate of new tissue by as much as 118% following a 10 day feeding period by 50 aphids per plant (Barlow and Messmer, 1982). Plants weighed less after 10 days than at the start of the experiment. In another study, the daily ingestion rate of one average adult pea aphid was about 8% of the daily net primary production of a pea seedling (Randolf et al., 1975). Pea aphid feeding reduces plant dry weight and carbohydrate and protein content of pea tissue (Barlow et al., 1977), but not the protein content of pea seeds (Maiteki and Lamb, 1985b; Yencho et al., 1986).

Pea aphid feeding may cause morphological changes in the plant. Apical meristems, upon which aphids concentrate, may become permanently shrivelled and malformed under heavy feeding pressure (Harrington, 1941). In the field, plants are stunted, wilted, and chlorotic (Harper, 1979). Plants are often covered with sticky honeydew (Gyrisco, 1958), the presence of which may promote fungal growth (Menke, 1953). At high aphid densities there is a decrease in the reducing activity of Rhizobium bacteria by as much as 86%, as well as decreased nodule weight and number (Sirur and Barlow, 1984). Direct feeding on pods may cause them to curl, shrink, and only partially fill; such peas have low market value and may not thresh out in the combine (Dudley and Bronson, 1952). Often, infested fields do not mature uniformly, as aphid-induced stress may hasten pea maturation in heavily infested areas (Yencho

et al., 1986). Seed quality may be affected, and tenderometer and sieve size readings may be altered by A. pisum feeding (Yencho et al., 1986).

As well as being local photosynthate sinks, pea aphids are the most important vectors of legume viruses (Swenson et al., 1954; Hagedorn, 1974). In 1980, tremendous losses in susceptible pea cultivars in Idaho were the result of an epidemic caused by pea leaf roll virus, not previously identified in the U.S. but transmitted by the pea aphid (Stoltz and Foster, 1984). A. pisum also transmits verticillium wilt. This virus, the most destructive disease of alfalfa in Europe, was also recently introduced into North America (Huang et al., 1983).

The ultimate amount of aphid damage to a crop varies with the number of aphids in the initial infestation, the duration and rapidity of growth of the infestation (Maltais, 1937; Barlow and Messmer, 1982), and the growth stage of the host plant (Apablaza and Robinson, 1967). Pea crops can recover from A. pisum feeding if it occurs prior to flowering (Maiteki and Lamb, 1985b), although Barlow et al. (1977) found in a laboratory study that more than 2 adult aphids or 24 first instar nymphs on a pea seedling resulted in loss of productivity greater than the compensatory ability of the plant. In Manitoba pea fields, the flowering and podding stages are very susceptible to direct feeding damage, with young pods being most susceptible (Maiteki and Lamb, 1985b). Similarly the worst damage to faba beans caused by Aphis fabae Scop. occurs at the immature pod stage (Banks and McCauley, 1967).

Earlier maturing pea cultivars generally escape pea aphid injury to a greater extent than later maturing ones (Folsom, 1909; Cooke, 1963). Temperature and other environmental factors also play an important role in the severity of A. pisum attack. Aphid damage is exacerbated by hot dry summers (Beirne, 1972); under these conditions plants are heat stressed and aphids may reproduce rapidly. Cool temperatures may inhibit aphid development (Maltais, 1937), but warm, wet conditions can encourage entomophagous fungal growth (Rockwood, 1950). Peas grown on nutrient deficient soils are injured more severely by the pea aphid than those grown on fertile soils (Barker and Tauber, 1951b).

2.2.6 Pea Aphid Control

Control in Alberta pea fields is recommended when there are more than 10 aphids per plant prior to first bloom (Harper, 1972). In Manitoba field pea crops, Maiteki and Lamb (1985a) determined the A. pisum economic threshold to be 9 to 12 aphids per sweep net sweep or 2 to 3 aphids per 20 cm of plant terminal when the crop begins to flower. Economic thresholds for pea aphids in green peas in Washington state are considerably lower than those of Maiteki and Lamb (1985a), in part because control decisions for this crop must be made well before harvest to comply with required pre-harvest intervals for pesticide application (Yencho et al., 1986).

Comparative yield alone may not be an accurate measure of the ability of the plant to withstand aphid attack (Harrington and Searls, 1940). Maiteki and Lamb (1985a) found that thousand seed weight rather than yield was a more sensitive measure of the effect of A. pisum on

peas, especially at low aphid densities. These authors found that the number of seeds per unit area was unaffected by aphid densities near the economic threshold (Maiteki and Lamb, 1985a).

Chemical control is the most common pea aphid control measure in pea crops (Mackauer, 1971; Beirne, 1972). The only cultural practice recommended for pea aphid control in Manitoba is early seeding of peas (Anonymous, 1985b); the older the plant is prior to infestation the better able it is to withstand aphid injury (Barlow and Messmer, 1982). A third method of pea aphid control is by use of host plant resistant crops. The use of resistant cultivars is the major means of A. pisum control in alfalfa crops (Jenkins, 1979), and has decreased yield losses in peas (Harvey et al., 1971).

2.3 Host Plant Resistance

2.3.1 Definitions

Resistance of plants to insect attack is composed of the heritable qualities possessed by the plant which cause it to suffer less overall loss than another plant subjected to the same level of attack (Painter, 1951; Beck, 1965). Practically, a resistant plant will outyield a susceptible one when under attack by the pest insect. Species non-specific, partial resistance is the most frequent type of insect resistance found in plants (de Ponti, 1983).

The main mechanisms of plant resistance are antibiosis, antixenosis (non-preference), and tolerance (Painter, 1951). Antibiosis results when factors exert an adverse influence on the growth and survival of the pest by preventing or hampering the insect's life

pattern (Painter, 1951). Antixenosis (Kogan and Ortman, 1978) results when host characteristics and insect responses impede the selection and use of a particular plant for food, oviposition, and/or shelter (Hedin et al., 1977). Antixenotic plants have some character that adversely affects an insect's behavioural response towards them. In both antibiosis and antixenosis, the resistance characters may be morphological, nutritional, or biochemical in nature (Russell, 1978). Tolerance does not affect insect biology; a tolerant plant can support an insect population with less loss of vigor or reduction in yield than an intolerant one (Jones et al., 1968).

2.3.2 Resistance of Plants to the Pea Aphid

One of the first published observations of resistance to pea aphids was made by Russell (1924), who noted a fifteen fold decrease in aphid numbers in Admiral as opposed to Advancers peas in the same field and in the same state of development. Since then many instances of varying A. pisum densities on different cultivars have been reported (Ridland and Berg, 1981; Cuperus and Radcliffe, 1984); several of these are cited in the extensive bibliography of Harper et al. (1978).

The basis of these different densities is most often antibiosis and/or antixenosis. Tolerance resistance is involved to a much lesser degree (Maxwell et al., 1972), although Newman and Pimentel (1974) found that in 3 of 1,250 pea races tolerance to pea aphid may be more important than their antibiotic properties.

Examples of morphological resistance mechanisms include hirsute or glandular-haired cultivars; in many crops, such cultivars possess a considerable degree of insect antibiosis (Gilbert, 1971; Lampe, 1982;

Chiang and Norris, 1982; Stipanovic, 1983). Pea aphids on glandular-haired Medicago spp. are less likely to survive, are less fecund, and have slower nymphal development rates than those developing on glabrous cultivars (Shade and Kitch, 1983).

Biochemical factors in alfalfa resistance include decreased total auxin content (Maxwell and Painter, 1962), increased intercellular pectin levels (Dreyer et al., 1987), and the presence of toxic alkaloids (Dreyer et al., 1985) and glycosides (Krzymanska et al., 1983). In peas, total and soluble nitrogen levels and amino acid concentrations are lower in resistant than susceptible cultivars (Maltais and Auclair, 1957; Markkula and Roukka, 1971; Auclair, 1976), with sugar to nitrogen ratios up to 64% higher in resistant than susceptible cultivars (Maltais and Auclair, 1957).

Criteria for evaluating resistance are based on the effect the plant has on the insect and/or the effect the insect has on the plant (Davis, 1985). Each of the three mechanisms of resistance requires different evaluation methods. Mean relative growth rate (Leather and Dixon, 1984), time to reproduction (Campbell and Mackauer, 1977), fecundity per adult (Markkula and Roukka, 1971), lifespan (Newman and Pimental, 1974), embryo number (Dewar, 1977), intrinsic rate of increase (Hutchison and Hogg, 1984), and rate of honeydew deposition (Eenink et al., 1984) have all been used to measure antibiosis reactions.

The minimum data needed to evaluate aphid response to a plant are developmental period, fecundity, and adult survival (Bournoville, 1971). Of these, time to reproduction and fecundity have the greatest impact on subsequent population growth (Lewontin, 1965). However, in

one laboratory study there was only a 3% difference in time to reproduction of pea aphids on highly resistant versus highly susceptible pea cultivars, and the differences in this parameter may be too small to be a practical measure of resistance (Harrington, 1941). Since the earliest produced progeny contribute most to a population, the number of young produced in a reproductive period equal to the pre-reproductive period has been used to determine intrinsic rates of natural increase and generation times for aphids (Wyatt and White, 1977). Measurement of adult longevity may be confounded by deteriorating host plant quality and is often considered too time consuming for use in large trials for resistance. Alfalfa resistance to the pea aphid is more apparent when expressed by fecundity than by adult survival (Isaak et al., 1963).

Evaluation of a plant's antixenotic effects on an aphid can be made by examining host selection and acceptance of cultivars by alate aphids. This may be done by recording the number of alatae colonizing a plant (Cartier and Painter, 1956). Significant differences were found between broad bean cultivars both in number of alate A. fabae settling and the number remaining when placed on the cultivars (Holt and Wratten, 1986).

Tolerance is measured by observation of plant response to high aphid densities (Dobson and Watts, 1957). Plant damage ratings have been used to assess tolerance resistance in different alfalfa (Jones et al., 1968) and pea lines (Newman and Pimentel, 1974).

Care must be taken with the methods used to evaluate host plant resistance. Often, test plants used are in the seedling stage; however, the levels of resistance in seedlings may be lower than that in mature

plants (Lowe, 1978; Bieri et al., 1983), and resistance may be underestimated. The use of excised leaves rather than whole plants may (Muller, 1958) or may not (Thomas and Sorenson, 1971) affect resistance expression. Even the size of pots in which the plants are grown affects resistance levels (Dewar, 1977).

2.3.3 Factors Affecting Expression of Resistance

Those factors that affect plant and aphid biology may also affect expression of host plant resistance. Aphid clones may vary in their ability to colonize a host (Dunn and Kempton, 1972); however they generally respond similarly to a range of levels of resistance; that is, all clones exhibit their poorest performance on the most resistant cultivars (Cartier and Painter, 1956). Temperature affects resistance and confounds its expression. Resistance of alfalfa to pea aphids is reduced as temperatures decrease (Isaak et al., 1963; Karner and Manglitz, 1985). Age, growth stage, and vigor of plants influence their resistance to insects (Auclair, 1966). Several scientists have found that rates of aphid development and reproduction vary inversely with the age of tissues on which the aphids feed (Auclair, 1966; Lowe, 1978; Bintcliffe and Wratten, 1980). Unknown physiological changes occurring in blossoming and fruiting pea plants may cause variations in aphid response to resistance (Harrington et al., 1943).

As well as significant differences in pea resistance existing between cultivars and plants of different ages, significant differences have been found between plants within cultivars (Dewar, 1977). While humidity may not directly affect resistance (Isaak et al., 1963), significant humidity by temperature, aphid clone by temperature (Isaak

et al., 1963), and cultivar by clone interactions (Markkula and Roukka, 1971) have been found in resistance expression.

2.3.4 Breeding for Host Plant Resistance

In order to incorporate resistant germplasm into a plant genome, three conditions must exist (Belloti and Byrne, 1979); there must be a genetic source of resistance to the pest, an efficient and reliable resistance evaluation scheme must be developed, and breeding methods to incorporate resistance into a commercially acceptable cultivar must exist.

Incorporating resistance characters into a plant utilizes the same breeding techniques as are used to develop any agronomic character (Dahms, 1972). The canning pea cultivar Laurier, which supported 56% fewer aphids than Perfection, was bred in six generations by single plant selection (Maltais, 1949).

In a few cases, the genetic basis of resistance has been determined. In certain alfalfa cultivars single dominant genes impart resistance to A. pisum (Glover and Stanford, 1966). Incorporating single dominant resistance genes into plant genomes imparts monogenic or vertical resistance, which tends to be highly specific and very effective against some species or populations of insects but not others (Gould, 1983).

Resistance of lettuce, Lactuca spp., accessions to leaf aphids is governed by additive genes (Eenink and Dieleman, 1982). Such additive genes can be accumulated into breeding lines to develop polygenic or horizontal resistance, which is non-specific and may be effective against a range of species (Van der Plank, 1975). At present, the

useful life of an insect pest-resistant cultivar is estimated to be about 10 years (Horber, 1972). If the combined components of resistance are based on different mechanisms and come from different backgrounds, their accumulation could increase the level and durability of a resistant cultivar (Dahms, 1972; Eenink and Dieleman, 1982).

CHAPTER 3

EXPERIMENTAL PROGRAM

Section I

Seasonal Occurrence of the Pea Aphid, Acyrthosiphon pisum (Harris) (Homoptera: Aphididae), on Cultivars of Field Peas in Manitoba and Its Effect on Pea Growth and Yield.

ABSTRACT

Pea aphid, Acyrthosiphon pisum (Harris), populations were sampled through the summer of 1984 on five cultivars and in 1985 and 1986 on six cultivars of field peas, Pisum sativum L., grown in field plots in southern Manitoba. Patterns of pea aphid population growth were generally similar among cultivars in any one year. Aphid populations on all cultivars in all years remained relatively low until mid-July, then increased rapidly, peaked at about the beginning of August, and declined sharply to low levels in late August. Consistent differences in aphid population densities were found among cultivars; the lowest densities were found on the cultivars Century and Tipu, and the highest densities on Triumph or Trapper. Pea aphid feeding was not consistently detrimental to any yield parameters except 1000 seed weight. In 1984 Triumph and Tara, and in 1985 Triumph had significantly decreased 1000 seed weights in plots in which aphid densities were not controlled. Differences in the abundance of the aphid among cultivars were not reflected in their yield responses. Over three years the regression line of Century seed weight and aphid densities was significantly steeper than those of Trapper, Lenca, or Tara. Trapper was least affected by aphid feeding.

1. Introduction

The pea aphid, Acyrthosiphon pisum (Harris), is a pest of legumes across North America. There have been numerous studies of pea aphid abundance in and damage to alfalfa, Medicago sativa L. (Hobbs et al., 1961; Cooke, 1963; Harper and Lilly, 1966; Cuperus et al., 1982; Cuperus and Radcliffe, 1984). Fewer studies have investigated A. pisum on peas Pisum sativum L. (Barker and Tauber, 1951b; Cooke, 1963; Barlow et al., 1977; Maiteki and Lamb, 1985a, 1985b; Yencho et al., 1986), even though pea aphid control requires the regular application of insecticides in peas grown for processing and canning (Mackauer, 1971). A. pisum numbers surpassed the economic threshold in most commercial Manitoba field pea crops surveyed over a three year period (Maiteki et al., 1986).

Manitoba is the second largest producer of field peas in Canada, with a total of 74,000 ha seeded to field peas in this province in 1987 (Ali-Khan and Zimmer, 1989). Although economic thresholds have been established for the pea aphid in Manitoba (Maiteki and Lamb, 1985a), these thresholds are based on the activities of A. pisum on the cultivar Century only. Several cultivars have recently been registered which outyield Century (Ali-Khan, 1973, 1978, 1980, 1982). However, pea aphid densities greater than those occurring on Century occur on at least one of these newer registered cultivars, Trapper (Maiteki et al., 1986). Speculation has arisen that pea aphid control is more likely to be required in fields of Trapper than those of Century (Lamb and Maiteki, 1985), but no comparative studies have yet been undertaken to determine pea aphid densities on different field pea cultivars in Manitoba.

The objectives of this investigation were to determine if different field pea cultivars consistently support different densities of pea aphids in Manitoba and to determine the effects of natural infestations of A. pisum on the yield components of pea cultivars in the field.

2. Materials and Methods

The study was conducted during the summers of 1984, 1985 and 1986 at the University of Manitoba Glenlea Research Station (97°08′W, 49°38′N) on a Red River-Osborne clay soil type. Prior to seeding, field peas were inoculated with peat-based Rhizobium leguminosarum strain C1 (Nitragin Co., Milwaukee, WIS) in a 20% (wt/vol) sucrose slurry solution. Inoculated seeds were planted into cereal stubble with two passes of a single cone four row seeder with rows spaced 0.3 m apart. Other field procedures are summarized in Table 1. On June 10, 1985, when the peas had two or three leaf pairs, all plots were sprayed with permethrin at 150 g a.i./ha to eliminate potential cutworm damage.

With the exception of Lenca, all cultivars sown are recommended for field pea production in Manitoba. Lenca, which is suitable for growth in Central and Atlantic Canada, was included to increase the scope of the experiment.

The experimental plan was a split plot field design with five replicates. Main plots were peas sprayed or not sprayed with malathion to control pea aphid populations. The different cultivars constituted the subplots. Malathion 500 EC (750 g a.i./ha) was applied with a bicycle sprayer in 1984 and a backpack sprayer in 1985 and 1986; all cultivars in one half of each replicate were sprayed when aphids

Table 1. Experimental conditions, Glenlea 1984-1986.

Factor	Year 1984	1985	1986
Cultivars seeded	Century, Lenca, Tara, Trapper, Triumph	Century, Lenca, Tara, Trapper, Triumph, Tipu	Century, Lenca, Tara, Trapper, Triumph, Tipu
Subplot Size	1.3 x 6.1 m	1.3 x 4.9 m	1.3 x 4.9 m
Planting Date	May 30	May 16	May 21
Emergence Date	Jun 16	Jun 3	May 29
Malathion Spray Dates	Jul 23 Aug 2	Jul 16 Aug 6	Jul 22 Aug 2
Aphid Sampling Dates	Jul 13,20,27 Aug 3,10,16	Jul 3,10,16,22,29 Aug 6,15,22	Jul 3,15,22 Aug 1,8,14,20
Harvest Period	Aug 27-31	Aug 22-Sep 10	Aug 11-Sep 18

appeared, at about the time of 80% first bloom in 1984 and 1986, and at the beginning of pod formation in 1985. Malathion was reapplied to the spray subplots when aphid numbers became so high that there was concern aphid injury might affect pea growth.

Each sprayed and unsprayed subplot was divided into two halves of 4 rows each, and one half, randomly chosen, was sampled. A plant approximately 1.0 m from the end of the subplot was selected as the first sampling unit; nine other plants, each 0.3 m from the preceding one, were then sampled. The same half of the subplot was sampled on each sample date. When plants were small the entire plant was examined and the number of aphids per plant was counted. As plants grew taller the terminal 20 cm of a plant was bent over a white enamel pan, the aphids gently tapped off, and the numbers of nymphs and apterous and alate adults were recorded. The plant terminal was then examined for any remaining aphids. Ten plants per replicate of each subplot were examined at every sample date until harvest. The growth stage of randomly selected plants in each subplot was determined according to the classifications of Gane et al. (1984) and Maiteki (1985), which are combined in Appendix 1.

For determination of yield components only the half of each subplot which had not been sampled was harvested, to ensure that possible damage to plants which may have occurred during sampling did not affect yields. In all years, a 1 m length sample of the two middle rows was randomly selected from each half subplot. From this sample, the number of plants and the weight of seeds per m row were averaged over the two rows. As well, the mean number of pods per plant of all (1984) or ten (1985, 1986) plants per row and the mean number of peas per pod of 100 (1984)

or 30 (1985, 1986) pods per plant were determined. These values in turn were averaged over the two rows. Because the two inner rows often did not have enough seeds, weight of 1000 seeds was determined from pods sampled from all four rows. In 1984, the number of seeds per m row averaged over the two rows and seed yield from the entire half subplot minus the 1 m sample were recorded. In 1985 and 1986, the mean number of aborted pods per plant, that is, missing or unfilled pods, of ten plants and the average plant height at harvest of five plants per m sample of subplot were also recorded, but the number of seeds per row and the total subplot yield were not.

Weather records during the study period were obtained from a climatological station at the Glenlea site.

Analysis was conducted on aphid numbers (alatae, apterae and nymphs, as well as total aphid number) recorded on the first sampling date after initial spraying, when most plants were in the late bloom and early pod initiation stages, and at the time of peak aphid abundance. Differences in aphid abundance on the various cultivars and spray regimes, as well as differences among cultivar yield components, were assessed by analysis of variance using SAS (SAS Institute, 1985). Variation was attributed to spray regime, cultivars, and their interactions, with spray regime by replicate being the main plot error term. The numbers of aphids per plant were transformed by $\sqrt{x + 0.05}$; the Wilk-Shapiro test statistic W (Shapiro and Wilk, 1965) indicated that such transformed data fit a normal distribution pattern. The stability of variances was checked by means of a Bartlett's test of homogeneity of variance (1937; in Steele and Torrie, 1980). Means were

compared by Duncan's multiple range test (1955; in Steele and Torrie, 1980) at the 5% level of probability unless otherwise stated.

Pearson product-moment correlations measured the amount of association between yield per area and the other harvest components measured (SAS Institute, 1985).

Linear regression was used to analyze relationships between aphid densities (x), at both the time of flowering-pod initiation and at peak aphid abundance, and yield components of peas (y). Each harvest component was considered as a separate experiment; the analyses of aphid densities on the cultivars at the two dates meant that there were 10 (1984) or 12 (1985, 1986) possible individual regressions for a single harvest component. With the addition of each individual comparison, α_C, the overall probability of committing one or more Type 1 errors accumulates to an experiment-wise error rate of α_E (Jones, 1984). Jones (1984) uses the term "statistically valid" in its mathematical sense. However, analysis may be mathematically correct, yet biologically irrelevant (Perry, 1986). In experiments in which emphasis is on the individual α_C level at which each comparison is made, the researcher should select the desired α_C and allow α_E to float up to its value for the entire experiment (Jones, 1984). Because I was primarily interested in the effects of individual cultivars on aphid numbers, and the effects of aphids on yields of individual cultivars, α_C values of 0.05 and 0.01 were selected. This resulted in α_E values of 0.4596 in 1984 and 0.4012 in 1985 and 1986 for α_C=0.05, while the α_E values at α_C=0.01 were 0.10 in 1984 and 0.11 in 1985 and 1986. Floatation of the experiment-wise error rate exposed patterns and meaning in the results which may have otherwise been obscured (Perry, 1986).

3. Results

3.1 Aphid Populations

3.1.1 1984

The cool, wet spring of 1984 was followed by a warm and dry summer (Appendix 2) so that while pea emergence was patchy and slow, the crop developed rapidly. Plant growth stages of the five cultivars over the summer are summarized in Table 2. There was little variation in plant development between spray regimes.

When growing in the field Tara, Lenca, Century, and Trapper plants were similar in appearance. Triumph plants were easily distinguishable from the others because of their shorter internodes. Average vine length of Triumph plants was about half of plants of Century, the tallest cultivar grown. The colour of Triumph foliage appeared slightly darker green than that of other cultivars.

Heavy June rains resulted in all cultivars in replicate 1 sprayed and unsprayed plots as well as replicate 2 Lenca sprayed and Triumph unsprayed plots being flooded. These subplots were not sampled for aphids, nor were they harvested.

One alate pea aphid was found on the ground near the plots on June 27. Six apterae were found on a total of five plants on July 5. Populations increased rapidly from July 13 to peak on all cultivars except Tara on August 3; the number of aphids on Tara plants was greatest on August 10 (Figure 1). The most rapid period of aphid population increase occurred at the R_2-R_3 or late bloom-early pod formation period of plant growth.

Table 2. Growth stages of cultivars of field pea Pisum sativum (L.) grown in the field near Glenlea, Manitoba, in 1984 (R_1 = bud stage; R_2 = flower; R_3 = pod formation and enlargement; R_4 = pod swelling and filling; R_5 = pod maturity).

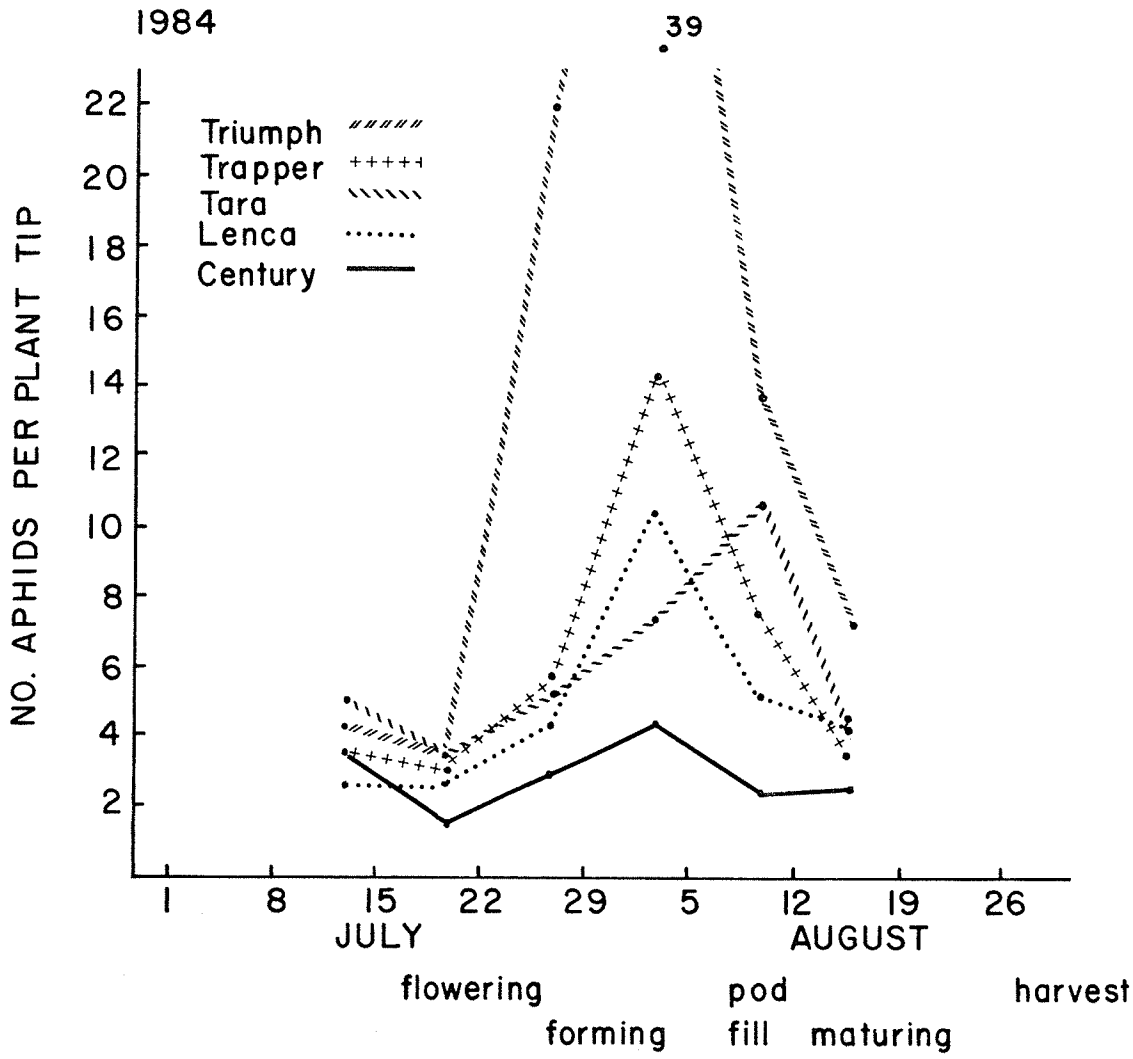
a) Unsprayed Plots (n = 20)

	Growth Stage					
	Sample Date:Days Post Emergence					
Cultivar	Jul 13:27	Jul 20:34	Jul 27:41	Aug 3:48	Aug 10:55	Aug 16:61
Century	Vegetative	Veg-R_1	R_2-R_3	R_3	R_4	R_4-R_5
Lenca	Vegetative	R_2	R_2-R_4	R_3	R_3-R_4	R_4-R_5
Tara	Vegetative	R_1-R_2	R_2-R_3	R_3-R_4	R_4	R_5
Trapper	Vegetative	Veg-R_2	R_2	R_3	R_4	R_5
Triumph	Vegetative	Veg-R_1	R_1-R_3	R_3	R_4	R_4-R_5

b) Sprayed Plots (n = 20)

	Growth Stage					
	Sample Date:Days Post Emergence					
Cultivar	Jul 13:27	Jul 20:34	Jul 27:41	Aug 3:48	Aug 10:55	Aug 16:61
Century	Vegetative	Veg-R_1	R_1-R_2	R_2-R_3	R_4	R_4-R_5
Lenca	Vegetative	Veg-R_1	R_2	R_3	R_4	R_4-R_5
Tara	Vegetative	R_1	R_2-R_3	R_3-R_4	R_4	R_5
Trapper	Vegetative	R_1-R_2	R_2-R_3	R_3-R_4	R_4-R_5	R_5
Triumph	Vegetative	Vegetative	R_3	R_3	R_4	R_4-R_5

Figure 1. Mean number of pea aphids per plant tip on unsprayed subplots of five cultivars of field peas, Glenlea, 1984 (n=40).


1984
39
NO. APHIDS PER PLANT TIP
22
20
18
16
14
12
10
8
6
4
2
Triumph
Trapper
Tara
Lenca
Century
1
8
15
22
29
5
12
19
26
JULY
AUGUST
flowering
forming
pod
fill
maturing
harvest

Because the total number of aphids found on the plants through most of the season was composed chiefly of one growth stage, nymphs only the results of analyses of total aphid numbers are included in the text. Data pertaining to alatae, apterae and nymphs are presented in Appendices 3 and 4.

On July 27, four days after applying malathion to the sprayed plots, significantly lower numbers of aphids were found in these plots than in the unsprayed plots ($F=11.32$, $P\leq0.05$) (Table 3). On August 3, one day after respraying, differences in aphid populations between the two spray treatments were greater (Appendix 3) and had a lower P value ($F=116.09$, $P\leq0.001$). Over both spray regimes, significantly different numbers of aphids were found among cultivars as early in the season as late flowering ($F=4.20$, $P\leq0.01$) (Table 3). The disparities in aphid populations among cultivars were even more significant at the peak of aphid abundance on August 3 ($F=21.10$, $P\leq0.001$). On both sampling dates, spray regime by cultivar interactions were significant ($F=5.20$, $P\leq0.01$ on July 27, $F=9.37$, $P\leq0.001$ on August 3) (Table 3); that is, the ranking of aphid numbers among cultivars differed between the spray regimes. On July 27 Lenca had the highest number of aphids of any cultivar in the sprayed plots; this value was higher than the number of aphids found in the unsprayed plots of Lenca on that date.

A comparison of aphid population means on the cultivars was made in each spray regime using Duncan's Multiple Range Test ($P\leq0.05$). In the sprayed plots, populations of A. pisum were similar among cultivars at flowering (Table 4), attesting to the efficacy of spraying. At the later sampling date, plants of Century had significantly fewer aphids on them than those of Triumph, despite the fact that spraying had occurred the

Table 3. Analysis of variance mean square values for spray regime and cultivar effects on the mean number of aphids per pea plant tip at flowering-pod initiation and at aphid population peaks, Glenlea, 1984-1986.

Source of Variation	Mean Square Values[1]								
	1984			1985[2]				1986	
	d.f.[3]	Jul 27	Aug 3	d.f.	Jul 22	Aug 6	Aug 15	d.f.	Aug 1	Aug 14
Spray Regime	1	5.69*[4]	45.63**	1	0.65	22.51	249.27**	1	10.86**	37.46*
Replicate	3	1.00	1.00	4	0.16	2.40	5.00	4	4.07*	1.36
Spray*Rep[5]	3	0.50	0.39	4	0.19	3.17	4.69	4	0.39	2.56
Cultivar	4	2.65**	7.29**	5	0.08	18.45**	6.01**	5	1.59**	0.83
Cult*Spray[6]	4	3.28**	3.23**	5	0.07	1.15	2.32	5	0.29	0.73
Error[7]	24	0.63	0.35	40	0.07	1.66	0.96	40	0.30	1.10
	39			59				59		
r^2		0.691	0.917		0.509	0.683	0.895		0.763	0.785
C.V.		36.75	23.03		48.26	18.59	18.85		53.80	40.27
Pooled S.E.		0.40	0.29		0.12	0.58	0.44		0.24	0.52

1 Analysis of variance and standard error based on $\sqrt{x + 0.05}$ transformed data.

2 Aug 6 - peak aphid populations on unsprayed Century, Tara and Trapper subplots;
Aug 15 - peak aphid populations on unsprayed subplots of Lenca, Tipu and Triumph.

3 degrees of freedom

4 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).

5 Spray regime * replicate, experimental error applicable to main plot comparisons.

6 Cultivar * spray regime interaction.

7 Experimental error applicable to subplot comparisons.

Table 4. Mean pea aphid populations (± S.E.M.) per field pea plant tip on sprayed subplots at the time of late flowering - early pod initiation and at peak aphid abundance at Glenlea (n=40, 50 and 50 in 1984, 1985 and 1986, respectively).

a) Flowering - Pod Initiation

	Mean No. Aphids/Plant Tip[1]		
Cultivar	Jul 27, 1984	Jul 22, 1985	Aug 1, 1986
Tipu	--	0.08 ±0.04 a	0.12 ±0.07 a
Century	2.75 ±1.06 a[2]	0.22 ±0.05 a	0.18 ±0.09 ab
Lenca	5.98 ±0.46 a	0.14 ±0.07 a	0.50 ±0.29 ab
Tara	3.35 ±1.64 a	0.16 ±0.09 a	1.42 ±0.73 ab
Trapper	2.90 ±1.16 a	0.16 ±0.05 a	0.54 ±0.49 ab
Triumph	2.98 ±1.12 a	0.20 ±0.10 a	1.66 ±0.81 b

b) Peak Aphid Abundance

	Mean No. Aphids/Plant Tip[1]			
		1985[3]		
Cultivar	Aug 3, 1984	Aug 6	Aug 15	Aug 14, 1986
Tipu	--	18.14 ± 2.28 a	4.64 ±1.14 a	2.40 ±0.65 a
Century	0.98 ±0.40 a	41.72 ± 6.70 b	12.12 ±4.58 ab	1.85 ±1.01 a
Lenca	4.18 ±2.20 ab	37.30 ± 2.69 b	11.10 ±1.45 ab	0.67 ±0.34 a
Tara	2.05 ±0.73 ab	49.80 ±14.02 b	13.90 ±3.13 b	1.35 ±0.90 a
Trapper	1.78 ±0.57 ab	66.06 ±16.93 b	10.78 ±4.46 ab	3.32 ±2.24 a
Triumph	4.38 ±1.27 b	44.42 ±10.05 b	15.28 ±6.29 b	1.76 ±0.80 a

[1] Analysis of variance based on $\sqrt{x + 0.05}$ transformed data.

[2] Means followed by the same letter(s) within each column are not significantly different ($P \leq 0.05$; Duncan's Multiple Range Test).

[3] Aug 6 - peak aphid populations on unsprayed subplots of Century, Tara and Trapper; Aug 15 - peak aphid populations on unsprayed subplots of Tipu, Lenca, Triumph peas.

day before. In the unsprayed subplots, Triumph plants supported a significantly greater aphid population than plants of the other cultivars (Table 5), both at flowering and at the aphid population peak. This difference in aphid densities between Triumph and the other cultivars continued throughout the season (Figure 1). On August 3, Trapper had significantly higher aphid numbers per plant tip than Tara or Century peas; the Trapper figure was higher than the peak abundance on Tara, which occurred a week later. Pea aphid numbers in unsprayed Century plots remained relatively low throughout the summer (Figure 1; Table 5).

3.1.2 1985

In 1985 the newly released cultivar Tipu was added to the experiment. Tipu, a semi-leafless cultivar, has its leaflets reduced to tendrils, and was easily distinguished from the other cultivars on the basis of foliage appearance.

Cool August temperatures and above average rainfall (Appendix 2) slowed pea crop development and extended the harvest period in 1985. Some sprayed Tipu subplots tended to mature faster than subplots which were not sprayed. The other cultivars developed at similar rates in both spray regimes (Table 6).

The first record of aphids in the field plots was on July 3, when four alatae and 13 nymphs were found in a survey of 600 plants. Populations of pea aphids built up slowly until the first week in August, when very large numbers of aphids were counted. This corresponded to the R_4 or pod swelling and filling stage of pea growth (Figure 2). Aphid numbers peaked on the unsprayed subplots of Century,

Table 5. Mean pea aphid populations (± S.E.M.) per field pea plant tip on unsprayed subplots at the time of late flowering - early pod initiation and at peak aphid abundance at Glenlea (n=40, 50 and 50 in 1984, 1985 and 1986, respectively).

a) Flowering - Pod Initiation

	Mean No. Aphids/Plant Tip[1]		
Cultivar	Jul 27, 1984	Jul 22, 1985	Aug 1, 1986
Tipu	--	0.58 ±0.53 a	1.94 ±0.79 ab
Century	3.00 ±1.01 a[2]	0.20 ±0.07 a	0.52 ±0.20 a
Lenca	4.60 ±1.90 a	0.28 ±0.21 a	2.40 ±0.69 b
Tara	5.18 ±1.99 a	0.52 ±0.22 a	3.14 ±0.94 b
Trapper	5.80 ±1.24 a	0.52 ±0.16 a	4.10 ±1.86 b
Triumph	22.05 ±6.76 b	0.88 ±0.31 a	5.72 ±2.23 b

b) Peak Aphid Abundance

	Mean No. Aphids/Plant Tip[1]			
		1985[3]		
Cultivar	Aug 3, 1984	Aug 6	Aug 15	Aug 14, 1986
Tipu	--	30.30 ± 3.22 a	35.70 ± 6.42 a	14.10 ±5.86 a
Century	4.70 ±0.72 a	48.34 ± 5.60 ab	32.64 ± 3.95 a	12.28 ±4.18 a
Lenca	10.60 ±1.28 bc	57.76 ± 2.21 b	68.32 ±13.93 b	18.48 ±3.88 a
Tara	7.42 ±1.14 ab	69.00 ±11.57 b	61.00 ±11.43 b	21.12 ±4.64 a
Trapper	14.30 ±1.63 c	104.62 ±11.34 c	69.94 ± 9.38 b	18.20 ±5.65 a
Triumph	39.25 ±6.25 d	49.88 ±10.17 ab	63.32 ± 8.86 b	19.62 ±4.51 a

[1] Analysis of variance based on $\sqrt{x + 0.05}$ transformed data.

[2] Means followed by the same letter(s) within each column are not significantly different ($P \leq 0.05$; Duncan's Multiple Range Test).

[3] Aug 6 - peak aphid populations on unsprayed subplots of Century, Tara and Trapper; Aug 15 - peak aphid populations on unsprayed subplots of Tipu, Lenca, Triumph peas.

Table 6. Growth stages of cultivars of field pea Pisum sativum (L.) grown in the field near Glenlea, Manitoba, in 1985 (V_n=vegetative stage, nth node; R_1=bud stage; R_2=flower; R_3=pod formation and enlargement; R_4=pod swelling and filling; R_5=pod maturity; R_6=pod drying).

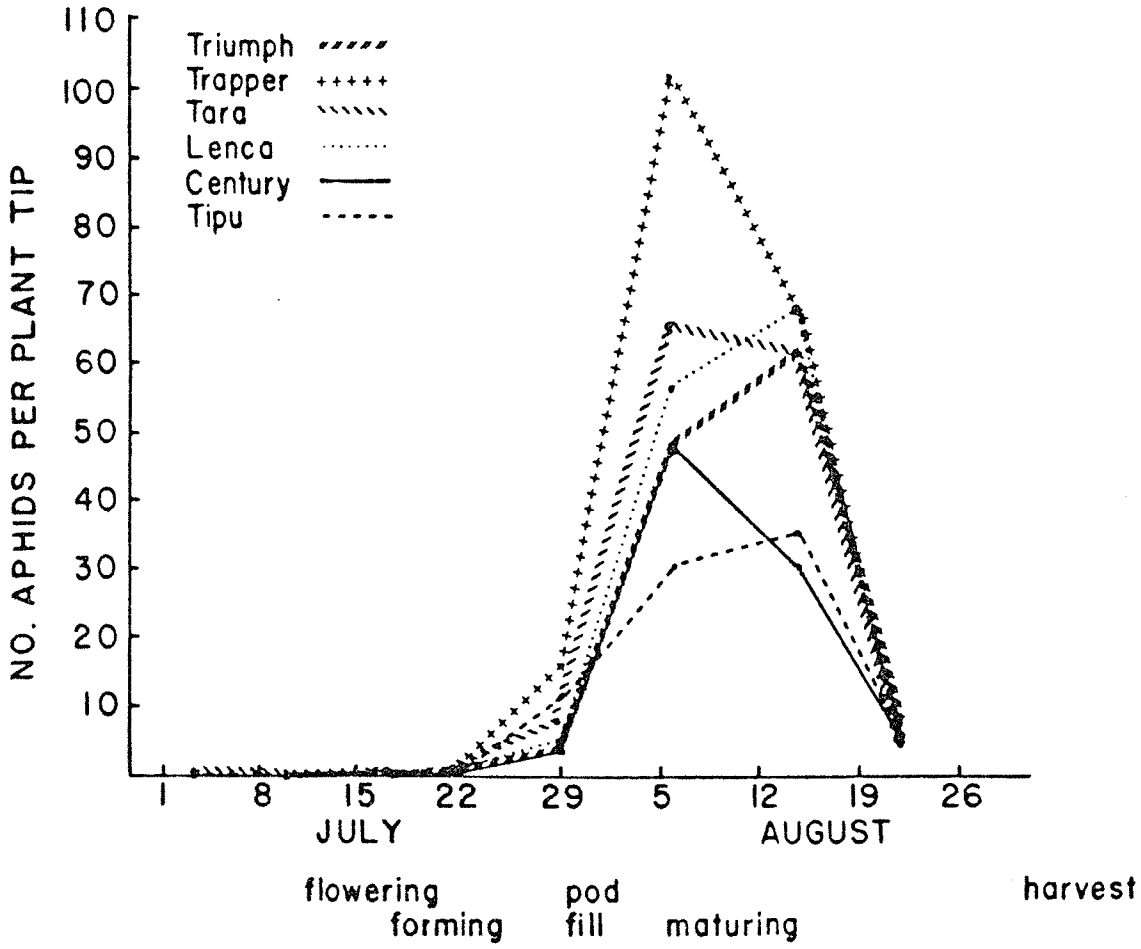
a) Unsprayed Plots (n = 5)

	Growth Stage							
	Sample Date:Days Post Emergence							
Cultivar	Jul 3:30	Jul 10:37	Jul 16:43	Jul 22:49	Jul 29:56	Aug 6:64	Aug 15:73	Aug 22:80
Century	$V_{9.8}$	V_{12}-R_1	R_2	R_2-R_3	R_2-R_4	R_4-R_5	R_4-R_5	R_4-R_5
Lenca	$V_{9.6}$	R_1-R_2	R_2-R_4	R_2-R_3	R_3-R_5	R_4-R_5	R_5	R_5-R_6
Tara	$V_{10.8}$	R_1	R_2	R_2-R_3	R_4	R_4-R_5	R_5	R_5
Trapper	$V_{10.0}$	R_1	R_2	R_2-R_3	R_3-R_4	R_4-R_5	R_5-R_6	R_5-R_6
Triumph	$V_{9.4}$	V_{12}-R_1	V_{12}-R_2	R_2-R_3	R_3-R_4	R_5	R_5	R_5
Tipu	$V_{9.8}$	R_1	R_2	R_2-R_3	R_4	R_4-R_5	R_4-R_5	R_5-R_6

b) Sprayed Plots (n = 5)

	Growth Stage							
	Sample Date:Days Post Emergence							
Cultivar	Jul 3:30	Jul 10:37	Jul 16:43	Jul 22:49	Jul 29:56	Aug 6:64	Aug 15:73	Aug 22:80
Century	$V_{9.6}$	V_{12}-R_1	R_2	R_2-R_3	R_3-R_4	R_4	R_5	R_5
Lenca	$V_{9.8}$	R_1	R_2	R_2-R_3	R_3-R_4	R_4-R_5	R_5	R_5-R_6
Tara	$V_{10.2}$	V_{11}-R_1	R_2	R_2-R_3	R_3-R_4	R_4-R_5	R_5	R_5
Trapper	$V_{10.2}$	V_{13}-R_1	R_2	R_2-R_3	R_4	R_4-R_5	R_4-R_5	R_5-R_6
Triumph	$V_{9.4}$	V_{12}-R_1	V_{13}-R_2	R_2-R_3	R_3-R_4	R_4-R_5	R_4-R_5	R_5
Tipu	$V_{11.4}$	R_1	R_2-R_3	R_2-R_3	R_3-R_5	R_5	R_5	R_6

Figure 2. Mean number of pea aphids per plant tip on unsprayed subplots of six cultivars of field peas, Glenlea, 1985 (n=50).


NO. APHIDS PER PLANT TIP
110
100
90
80
70
60
50
40
30
20
10
Triumph
Trapper
Tara
Lenca
Century
Tipu
1
8
15
22
29
5
12
19
26
JULY
AUGUST
flowering
forming
pod
fill
maturing
harvest

Tara and Trapper on August 6, while the greatest number of aphids on Tipu, Triumph and Lenca occurred on August 15. Populations decreased rapidly from August 15 to 22. On the latter date many diseased aphid bodies were found.

Aphid numbers in both spray treatments were very low on July 22 (Tables 4 and 5), so that there were no significant differences in aphid densities between spray treatments or among cultivars at late flowering (Table 3). Nor were there significant differences in aphid numbers between the spray regimes on August 6 ($P=0.06$); this is probably because spraying occurred after sampling on this date and the length of time between this and the previous spray application allowed populations in both spray treatments to rise considerably. The effect of the spray treatment applied on August 6 continued to be apparent on August 15, so that significantly fewer aphids ($F=53.11$, $P\leq0.01$) were found in sprayed plots than in unsprayed plots on this date.

Significant differences in aphid densities among cultivars were found on both August 6 ($F=11.12$, $P\leq0.001$) and August 15 ($F=6.24$, $P\leq0.001$) (Table 3), with unsprayed plots of Tipu and Century supporting the lowest aphid densities and Trapper the highest on both dates (Table 5). The spray regime by cultivar interaction was not significant on any of the three sampling dates in 1985; that is, the ranking of aphid populations among cultivars was similar in both spray regimes.

3.1.3 1986

The very wet spring of 1986 (Appendix 2) delayed and decreased pea emergence in some subplots of replicates 1 and 2. Subsequent plant growth in these replicates tended to be non-uniform, with low-lying

subplots having shorter plants in sparser densities which matured faster than those on higher ground. Harvest data from eight subplots in these two replicates were deleted from analysis because of abnormal growth due to flooding.

Rain fell on eight of the ten days following initial spraying of the flowering peas on July 22. The rain did not arrest pea development, so that by the time post-spraying sampling could be done on August 1 the majority of peas had completed flowering and were in the pod filling stage.

In a comparison of plant growth stages between spray regimes there were some differences in maturation rates (Table 7). Plants in sprayed Tipu subplots, especially, tended to mature faster and over a shorter period of time than their unsprayed counterparts, as they did in 1985. Days from emergence to harvest in unsprayed Tipu plots averaged 95.0 $\pm$9.6 days, while the average value in sprayed plots was 83.0 $\pm$2.7 days. However, in an analysis of variance, the wide range in values within treatments resulted in differences in days from emergence to harvest between treatments being nonsignificant.

The first pea aphids were found in the pea plots on July 3; on this date, six nymphs were discovered on one Triumph plant out of a total of 600 plants examined. Aphid populations were low throughout most of July but built up rapidly toward the end of the month (Figure 3). By this time peas were in the R_3-R_4 or pod formation to filling stage. The number of aphids on all cultivars peaked on August 14. A. pisum population levels were similar to those recorded in 1984 and were much lower than in 1985 (Appendix 3).

Table 7. Growth stages of cultivars of field pea Pisum sativum (L.) grown in the field near Glenlea, Manitoba, in 1986 (V_n=vegetative stage, nth node; R_1=bud stage; R_2=flower; R_3=pod formation and enlargement; R_4=pod swelling and filling; R_5=pod maturity; R_6=pod drying).

a) Unsprayed Plots (n = 5)

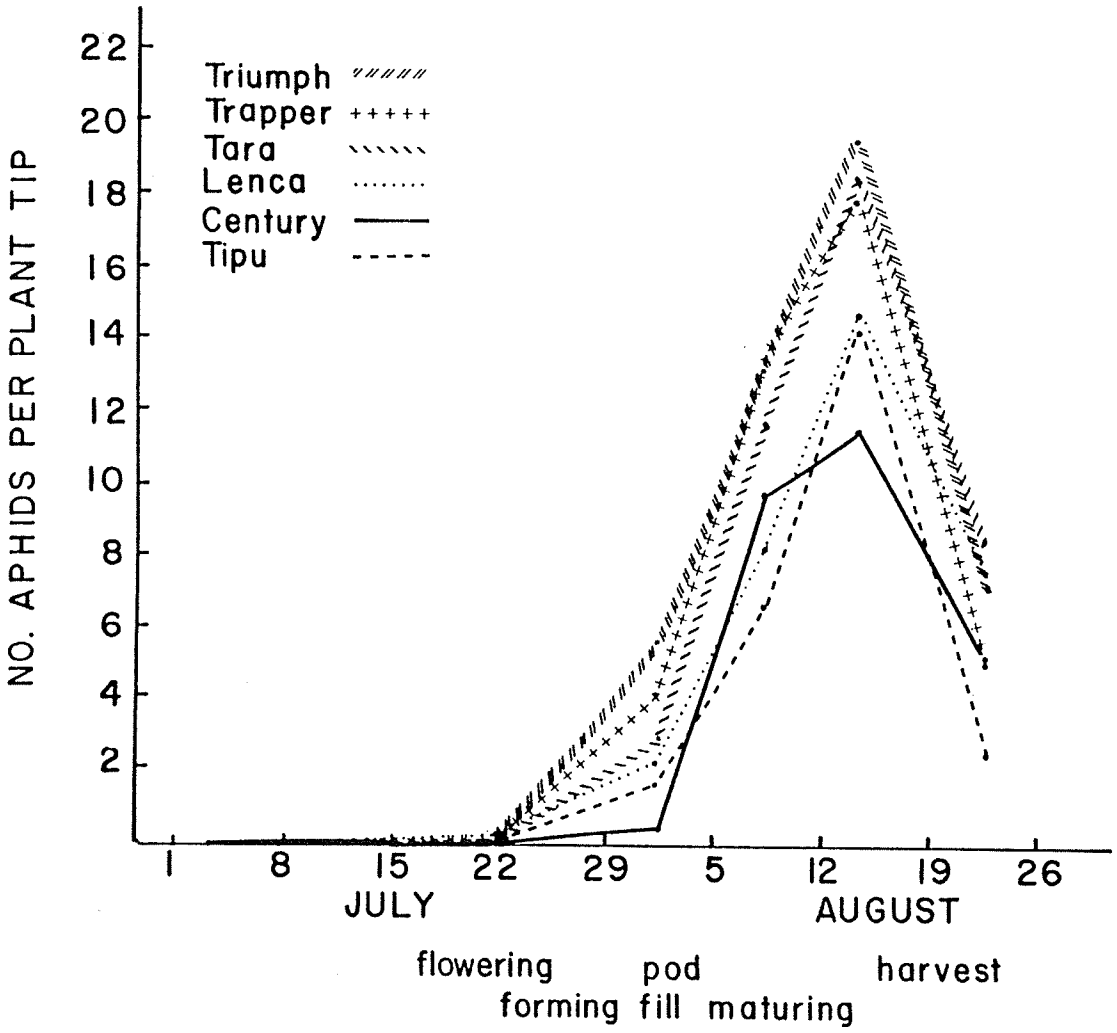
	Growth Stage					
	Sample Date:Days Post Emergence					
Cultivar	Jul 3:35	Jul 15:47	Jul 22:54	Aug 1:64	Aug 8:71	Aug 20:83
Century	$V_{9.4}$	V_{13}-R_3	R_2-R_4	R_4-R_5	R_4-R_6	R_5-R_6
Lenca	$V_{9.4}$	$V_{9.2}$	R_3	R_4-R_5	R_5-R_6	R_5-R_6
Tara	$V_{9.6}$	V_{15}-R_1	R_2	R_4-R_5	R_5-R_6	R_5-R_6
Trapper	$V_{9.6}$	R_1-R_2	R_2	R_3-R_4	R_5	R_6-Harv[1]
Triumph	$V_{10.0}$	V_9-R_1	R_1-R_2	R_3-R_4	R_4-R_5	R_5-R_6
Tipu	$V_{9.8}$	V_{10}-R_2	R_1-R_2	R_3-R_4	R_5	R_6

b) Sprayed Plots (n = 5)

	Growth Stage					
	Sample Date:Days Post Emergence					
Cultivar	Jul 3:35	Jul 15:47	Jul 22:54	Aug 1:64	Aug 8:71	Aug 20:83
Century	$V_{10.0}$	V_{13}-R_1	R_2-R_4	R_4-R_5	R_5-R_6	R_5-R_6
Lenca	$V_{9.0}$	V_{13}-R_1	R_2-R_3	R_4-R_5	R_5-R_6	R_5-R_6
Tara	$V_{10.6}$	V_{14}-R_1	R_2	R_4-R_5	R_5-R_6	R_5-R_6
Trapper	$V_{10.2}$	V_{14}-R_1	R_2	R_4-R_5	R_6	R_6-Harv
Triumph	$V_{9.8}$	V_{15}-R_2	R_1-R_2	R_4	R_5	R_5-R_6
Tipu	$V_{9.0}$	V_{14}-R_2	R_2	R_4-R_5	R_5-R_6	R_6-Harv

[1] Harv = some replicates harvested.

Figure 3. Mean number of pea aphids per plant tip on unsprayed subplots of six cultivars of field peas, Glenlea, 1986 (n=50).


NO. APHIDS PER PLANT TIP
22
20
18
16
14
12
10
8
6
4
2
Triumph
Trapper
Tara
Lenca
Century
Tipu
1
8
15
22
29
5
12
19
26
JULY
AUGUST
flowering
pod forming
fill
maturing
harvest

As on most dates in previous years, spraying was effective in significantly reducing pea aphid numbers in sprayed as opposed to unsprayed plots on both August 1 ($F=27.84$, $P\leq0.01$) and August 14 ($F=14.61$, $P\leq0.05$) (Table 3). Interactions between aphid densities and cultivars were not significant. While aphid numbers varied significantly among cultivars at pod fill on August 1 ($F=5.38$, $P\leq0.001$), the large standard errors of the means of A. pisum densities on the cultivars on August 14 precluded differences among them being statistically significant. On August 1 the fewest aphids were found on Century and Tipu plants, while Triumph plants had the highest numbers of aphids in both spray treatments (Tables 4 and 5).

From Figures 1, 2, and 3 and Tables 4 and 5 it is evident that pea aphid populations surpassed the published economic threshold of two to three aphids per plant tip (Maiteki and Lamb, 1985a) on all cultivars in all three years. However, only in 1984 was the threshold surpassed during flowering and pod formation, plant growth stages most sensitive to feeding damage (Auclair, 1976, Maiteki and Lamb, 1985b). In 1985 populations peaked at R_4 or pod filling; however, aphid numbers were so high on most of the cultivars that feeding damage might be expected because of sheer aphid volume. The relatively small aphid population growth on the different cultivars in 1986 came late in the summer, so that yield depression of any of the cultivars was not expected.

3.2 Harvest Results

3.2.1 1984

In an analysis of variance of the harvest data presented in Table 8, variation was partitioned into that due to spray regime,

Table 8. Means (± S.E.M.), coefficient of variation values, and pooled standard error of yield components averaged over two rows, 1 m in length, of various field pea cultivars at Glenlea in 1984 (n = 4).

Cultivar	No. Plants /Row	No. Pods /Plant	No. Peas /Pod	No. Seeds /Row	Weight/ Row (g)	Weight/ 1000 Seeds(g)	Weight/ Subplot(g)[1]
a) Sprayed plots							
Century	11.1 ±2.4	6.4 ±1.2	3.8 ±0.3	207.4 ±32.8	42.4 ± 7.7	208.8 ±2.1	1317.3 ± 89.7
Lenca	15.1 ±1.5	6.7 ±0.9	4.8 ±0.2	394.2 ±14.5	69.2 ± 3.6	170.3 ±2.3	1526.4 ±182.9
Tara	7.4 ±1.5	9.1 ±1.2	5.0 ±0.2	296.0 ±49.1	54.2 ± 7.8	175.0 ±2.4	1685.8 ± 17.1
Trapper	13.4 ±1.3	8.5 ±1.2	4.3 ±0.2	447.1 ±56.0	52.0 ± 7.4	113.6 ±0.8	1402.4 ± 43.9
Triumph	8.9 ±1.6	7.5 ±1.7	3.7 ±0.2	230.0 ±55.1	63.8 ±15.7	258.4 ±2.3	1721.7 ±233.5
b) Unsprayed Plots							
Century	15.0 ±1.6	5.2 ±0.3	3.6 ±0.1	266.5 ±11.4	57.6 ± 4.1	208.8 ±2.6	1516.6 ± 65.5
Lenca	15.0 ±2.9	4.9 ±0.7	5.3 ±0.1	340.1 ± 9.9	59.0 ± 2.8	172.5 ±1.5	1609.3 ± 29.8
Tara	8.6 ±1.6	9.0 ±1.7	5.1 ±0.1	361.6 ±64.5	60.7 ±12.9	163.8 ±2.5	1651.1 ±161.1
Trapper	14.0 ±0.6	7.5 ±1.0	4.6 ±0.1	493.8 ± 9.5	60.0 ± 9.5	114.4 ±3.5	1465.4 ±169.5
Triumph	9.5 ±1.4	6.9 ±0.8	3.9 ±0.1	253.8 ±36.5	60.9 ± 7.3	242.0 ±2.7	1418.8 ± 59.8
C.V.	24.38	38.20	7.12	29.10	31.01	2.54	15.74
Pooled S.E.	1.4	1.3	0.2	47.9	9.0	2.3	120.6

[1] Excluding half of subplot sampled for aphids.

replicate, cultivar, and spray regime by cultivar interaction. Mean 1000 seed weights in sprayed plots were significantly larger than mean seed weights in unsprayed plots ($F=30.12$, $P\leq0.01$) (Tables 8 and 9). Spraying did not significantly affect any other yield component measured. The spray regime by cultivar interaction was significant for 1000 seed weight ($F=5.09$, $P\leq0.01$) because of the non-uniform trend among cultivars. Sprayed Triumph and Tara plants had heavier seeds than their unsprayed counterparts. According to t-tests, the differences in mean seed weights of these two cultivars were significant between the two spray regimes, while the other cultivars had similar seed weights in the two treatments (Table 10).

There were significant differences among cultivars in number of plants per row ($F=8.92$, $P\leq0.01$), number of peas per pod ($F=34.40$, $P\leq0.001$), number of seeds per row ($F=3.19$, $P\leq0.001$), and weight of 1000 seeds ($F=909.76$, $P\leq0.001$) (Tables 8 and 9). These differences in most part reflected the disparities in agronomic qualities of the cultivars themselves; thus, large-seeded cultivars had fewer plants per row and heavier seeds than smaller-seeded cultivars. There were no significant differences among cultivars in number of pods per plant, weight of seeds per m row, or total yield per plot.

Linear regressions indicated that the weight of 1000 seeds was negatively related to peak aphid densities in all cultivars. This weight-density relationship was significant for Triumph sampled on August 3 and Tara on August 10 (Table 11). There were no significant linear regressions of any other harvest component in 1984.

Table 9. Analysis of variance mean square values for spray regime and cultivar effects and their interaction on harvest components of various cultivars of field peas, Glenlea, 1984 to 1986.

Source of Variation	Degrees of Freedom	No.Plants /Row	No.Pods /Plant	No.Seeds /Row	No.Peas /Pod	Weight /Subplot(g)	Weight /Row(g)	Weight /1000 Seeds(g)
a) 1984								
Spray Regime	1	15.88	8.94	7,952.40	0.32	22.80	109.96	246.05**[1]
Replicate	3	4.02	1.29	3,005.42	0.19	142,507.45	79.17	38.93
Rep*SprayReg[2]	3	51.73	11.16	15,123.75	0.39	38,910.37	415.14	8.17
Cultivar	4	73.84**	16.05	75,058.29**	3.44**	88,432.75	247.13	18,685.05**
SprayReg*Cult[3]	4	4.73	0.79	4,746.84	0.18	71,760.66	196.65	107.51**
Error[4]	24	8.28	6.35	9,166.50	0.10	58,156.72	323.32	21.12
r^2		0.72	0.43	0.63	0.87	0.46	0.30	0.99

1 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).

2 Replicate by spray regime interaction used as error term for main effect comparisons.

3 Spray regime by cultivar interaction.

4 Experimental error applicable to subplot comparisons.

Table 9. (Cont'd) Analysis of variance mean square values for spray regime and cultivar effects and their interaction on harvest components of various cultivars of field peas, Glenlea, 1984 to 1986.

Source of Variation	Degrees of Freedom	No.Plants /Row	No.Pods /Plant	No.Aborted Pods/Plant	No.Peas /Pod	Height (cm)	Weight /Row(g)	Weight /1000 Seeds(g)
b) 1985								
Spray Regime	1	3.75	0.15	0.14	0.09	83.23	138.62	1,617.20*
Replicate	4	4.10	3.13*	0.26	0.04	57.55	702.67	191.40
Rep*SprayReg[2]	4	5.92	0.20	0.06	0.02	18.66	257.86	103.44
Cultivar	5	83.26**	7.35**	0.47**	3.14**	5,257.48**	1,632.52**	38,592.42**
SprayReg*Cult[3]	5	8.27	1.12	0.09	0.18	8.56	167.66	53.08
Error[4]	40	26.39	1.11	0.10	0.89	50.01	345.77	97.19
r^2		0.68	0.56	0.52	0.82	0.93	0.48	0.98
c) 1986								
Spray Regime	1	11.07	5.35	2.76	0.18	105.73	68.82	18.76
Replicate	4	3.23	2.90	2.51	0.25	1,306.76	1,325.82	1,087.36*
Rep*SprayReg[2]	4	6.26	1.50	0.71	0.46	301.13	301.27	156.07
Cultivar	5	164.23**	3.32*	6.71**	2.26**	4,411.39**	1,578.70**	28,173.61**
SprayReg*Cult[3]	5	40.24**	4.26*	1.71*	0.13	414.15	541.82	128.29
Error[4]	32[5]	9.72	1.18	0.59	0.13	318.69	310.45	235.38
r^2		0.79	0.60	0.76	0.79	0.75	0.65	0.95

1 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).
2 Replicate by spray regime interaction used as error term for main effect comparisons.
3 Spray regime by cultivar interaction.
4 Experimental error applicable to subplot comparisons.
5 Data from eight subplots deleted due to flooding.

Table 10. Differences in weight of 1000 seeds between sprayed and unsprayed subplots of six cultivars of field peas, Glenlea, 1984 to 1986.

	1984		1985		1986	
Cultivar	Trt[1] Diffs(g)	t Value	Trt Diffs(g)	t Value	Trt Diffs(g)	t Value
Century	-0.02[2]	0.008	5.74	0.920	4.58	0.472
Lenca	-2.20	0.675	10.10	1.618	-7.46	0.769
Tara	11.15**	3.431	9.88	1.583	-4.78	0.492
Trapper	0.78	0.238	6.54	1.048	3.50	0.360
Triumph	16.39***	5.044	18.72**	3.000	8.69	0.900
Tipu	---	---	11.38	1.824	-5.66	0.584

[1] Treatment differences - yield from sprayed minus unsprayed subplots.

[2] Within each column treatment differences vary significantly from zero at 0.01(**), or 0.001(***) level of probability, two-tailed t test.

Table 11. Linear regressions of 1000 seed weight (Y) upon mean numbers of aphids per plant tip (x) at the time of peak aphid populations on cultivars of field peas at Glenlea, 1984 to 1986.

Cultivar	n	Year	Aphid Sample Date	Regression Eq.	Significance Level (P=)	r^2
Century	7	1984	Aug 3	Y=209.97-0.376x	0.659	0.042
	10	1985	Aug 6	Y=260.86-0.901x	0.016	0.536
	8	1986	Aug 14	Y=208.63-0.249x	0.556	0.061
Lenca	7	1984	Aug 3	Y=172.41-0.105x	0.739	0.024
	10	1985	Aug 15	Y=201.67-0.159x	0.145	0.245
	7	1986	Aug 14	Y=184.52-0.525x	0.149	0.368
Tara	8	1984	Aug 10	Y=176.16-1.047x	0.012	0.680
	10	1985	Aug 15	Y=197.42-0.263x	0.008	0.606
	8	1986	Aug 14	Y=164.11+0.243x	0.449	0.099
Trapper	8	1984	Aug 3	Y=114.39-0.053x	0.851	0.006
	10	1985	Aug 6	Y=123.13-0.065x	0.345	0.112
	9	1986	Aug 14	Y=101.60-0.041x	0.909	0.002
Triumph	7	1984	Aug 3	Y=259.55-0.424x	0.006	0.803
	10	1985	Aug 15	Y=320.02-0.268x	0.020	0.510
	9	1986	Aug 14	Y=279.62-0.150x	0.881	0.003
Tipu	10	1985	Aug 15	Y=211.98-0.354x	0.003	0.695
	8	1986	Aug 14	Y=185.98+0.528x	0.319	0.164

3.2.2 1985

Cultivars matured at different rates in 1985, with all Tipu plots harvested on August 22, those of Trapper on August 29, and the remaining cultivars harvested between September 6 and 10.

In the analysis of variance of the harvest components presented in Table 12, only 1000 seed weight varied significantly between spray regimes ($F=15.63$, $P\leq0.05$) (Table 9), as in 1984. All cultivars had heavier seeds in sprayed subplots, with the difference between treatments in Triumph subplots being significant ($t=3.00$, $P\leq0.01$) (Table 10). There were significant differences among cultivars in all harvest components ($P\leq0.001$), but there were no significant cultivar by spray regime interactions (Table 9).

Linear regressions indicated that a negative relationship existed between 1000 seed weights and aphid numbers in all cultivars at the time of maximum aphid densities. This relationship was significant for Century, Tipu, Tara and Triumph peas (Table 11). As in 1984, none of the other harvest components of any cultivar had significant regression relationships with aphid numbers.

3.2.3 1986

Harvest began on August 11 and ended on September 18, with low lying replicates maturing more quickly than others.

In 1986 there were no significant differences between sprayed and unsprayed plots in any of the harvest components presented in Table 13 and analyzed in Tables 9 and 10. All components except number of pods per plant were significantly different among cultivars at the $P\leq0.01$ level of probability (Table 9). Because spray regime by cultivar

Table 12. Means (± S.E.M.), coefficient of variation values, and pooled standard error of yield components averaged over two rows, 1 m in length, of various field pea cultivars at Glenlea in 1985 (n=5).

Cultivar	No. Plants /Row	No. Pods /Plant	No. Aborted Pods/Plant	No. Peas /Pod	Height (cm)	Weight/ Row(g)	Weight/ 1000 Seeds(g)
a) Sprayed plots							
Century	13.4 ±0.5	6.1 ±0.6	1.3 ±0.2	3.8 ±0.2	106.3 ±3.4	69.1 ±10.4	223.8 ±10.0
Lenca	15.2 ±0.5	4.9 ±0.4	1.4 ±0.2	4.8 ±0.1	98.6 ±4.4	71.4 ± 7.7	199.6 ± 2.5
Tara	14.2 ±0.7	6.9 ±0.4	1.5 ±0.2	4.7 ±0.7	89.2 ±1.4	85.9 ±10.6	192.1 ± 1.9
Trapper	19.8 ±1.9	7.0 ±0.7	1.4 ±0.2	4.5 ±0.2	---	56.3 ± 7.3	120.5 ± 2.6
Triumph	14.6 ±1.1	5.3 ±0.4	1.0 ±0.1	3.5 ±0.1	53.3 ±2.4	91.9 ± 5.2	318.8 ± 3.0
Tipu	19.2 ±1.3	4.8 ±0.2	1.2 ±0.1	5.0 ±0.2	---	87.0 ± 5.4	210.5 ± 2.3
b) Unsprayed Plots							
Century	14.2 ±0.5	5.9 ±0.3	0.9 ±0.1	4.2 ±0.2	103.5 ±3.0	69.2 ±10.4	218.1 ± 5.3
Lenca	16.8 ±0.7	4.9 ±0.3	1.2 ±0.1	5.0 ±0.2	95.9 ±4.2	75.9 ± 7.0	189.5 ± 5.8
Tara	14.0 ±1.0	7.3 ±0.6	1.5 ±0.2	5.1 ±0.1	83.9 ±2.6	92.0 ±11.9	182.3 ± 6.2
Trapper	22.8 ±1.8	5.7 ±0.6	1.5 ±0.6	4.3 ±0.1	---	51.5 ± 7.8	114.0 ± 3.0
Triumph	14.8 ±0.9	5.0 ±0.5	0.8 ±0.1	3.6 ±0.1	52.5 ±1.9	76.7 ± 8.5	300.2 ± 2.2
Tipu	16.8 ±0.8	5.4 ±0.5	1.4 ±0.1	4.8 ±0.1	---	78.1 ± 7.6	199.1 ± 2.9
C.V.	15.00	18.26	25.12	6.95	8.47	24.65	4.79
Pooled S.E.	1.1	0.5	0.1	0.1	3.2	8.3	4.4

Table 13. Means (± S.E.M.), coefficient of variation values, and pooled standard error values of yield components averaged over two rows, 1 m in length, of various field pea cultivars at Glenlea in 1986 (n=5).

Cultivar	No. Plants /Row	No. Pods /Plant	No. Aborted Pods/Plant	No. Peas /Pod	Height (cm)	Weight/ Row(g)	Weight/ 1000 Seeds(g)
a) Sprayed plots							
Century	16.0 ±1.2	5.8 ±0.3	2.6 ±0.3	3.5 ±0.1	142.8 ± 6.6	66.8 ± 9.9	209.2 ± 6.6
Lenca	20.0 ±1.4	3.2 ±0.3	2.4 ±0.3	4.3 ±0.1	123.8 ±12.2	40.3 ± 9.5	168.5 ±12.2
Tara	19.2 ±1.4	5.8 ±0.3	2.8 ±0.3	4.5 ±0.3	151.6 ± 6.9	74.5 ± 5.2	164.2 ± 3.7
Trapper	21.2 ±1.8	5.0 ±1.0	3.7 ±0.7	3.1 ±0.2	122.5 ±14.2	32.2 ± 5.0	103.1 ± 6.0
Triumph	11.4 ±1.2	6.3 ±0.5	5.3 ±0.6	3.8 ±0.1	86.9 ± 4.2	75.5 ± 7.7	282.0 ±13.9
Tipu	31.0 ±0.4	3.7 ±0.5	1.8 ±0.3	3.3 ±0.2	125.0 ± 9.8	60.2 ±10.9	182.4 ± 7.0
b) Unsprayed Plots							
Century	19.0 ±2.6	4.3 ±0.4	2.0 ±0.2	3.5 ±0.3	147.0 ±13.4	58.8 ±17.4	204.7 ± 1.5
Lenca	21.2 ±1.4	4.8 ±0.3	3.1 ±0.2	4.8 ±0.2	154.9 ± 3.6	74.9 ± 3.3	176.0 ± 5.3
Tara	18.5 ±1.0	4.7 ±0.4	2.9 ±0.2	4.5 ±0.1	146.1 ± 8.2	60.8 ± 8.4	168.9 ± 8.2
Trapper	23.2 ±1.8	5.0 ±0.7	3.2 ±0.5	3.6 ±0.3	136.2 ± 8.7	38.9 ± 9.0	99.6 ± 4.9
Triumph	16.5 ±1.0	4.6 ±0.7	3.5 ±0.8	3.9 ±0.3	84.8 ± 8.0	80.2 ± 9.1	273.4 ±14.0
Tipu	23.8 ±0.9	4.1 ±0.6	1.9 ±0.3	3.4 ±0.2	124.1 ±11.6	66.5 ±12.2	188.0 ±10.5
C.V.	15.54	22.83	25.97	9.43	13.95	29.21	8.29
Pooled S.E.	1.4	0.5	0.3	0.2	8.0	7.9	6.9

interactions were significant for number of plants per row ($F=4.14$, $P \leq 0.01$), an analysis of covariance was conducted with plants per row as a covariate term. Results of the analysis were similar to those of the ANOVA (Table 9) with the following exceptions. Cultivars ceased to be a significant source of variation in the number of pods per plant; the spray regime by cultivar interaction was not significant for the number of aborted pods per plant but became so for weight of seeds per row (d.f.=31, $F=3.69$, $P \leq 0.01$). This was due mainly to the fact that in sprayed subplots Lenca plants had an inexplicably large decrease in weight of seeds per row over their unsprayed counterparts (Table 13).

Unlike data from previous years, there were several significant positive relationships between harvest components and aphid numbers in 1986. In subplots of Lenca on August 1, the first sample date after initial spraying, the number of pods per plant (Y) were related to aphid density (x) by $Y = 3.06 + 0.59x$, $P \leq 0.01$, $r^2=0.600$, $n=10$; the number of aborted pods per Lenca plant (Y) was related to aphid density (x) by $Y = 2.15 + 0.33x$, $P \leq 0.05$, $r^2=0.520$, $n=10$; and the weight of Lenca peas per m row (Y) was related to aphid numbers (x) by $Y = 31.57 + 14.11x$, $P \leq 0.01$, $r^2=0.672$, $n=10$. Tara and Tipu had positive relationships between number of aborted pods per plant (Y) and aphid densities ($Y = 2.06 + 0.24x$, $P \leq 0.05$, $r^2=0.532$, $n=10$ and $Y = 1.61 + 0.23x$, $P \leq 0.05$, $r^2=0.431$, $n=10$, respectively). Seed weight per row (Y) of Trapper peas increased with increased aphid number (x) by the relationship $Y = 24.35 + 3.51x$, $P \leq 0.05$, $r^2=0.422$, $n=10$. There were no other significant linear regressions of harvest components on aphid densities on this date or at the peak aphid density two weeks later. Two of the cultivars,

Tara and Tipu, had positive relationships between 1000 seed weight and aphid densities on August 14 (Table 11).

3.2.4 Harvest Component Correlations

In an attempt to determine the yield component most important to overall yield, correlation coefficients were calculated for the correlation of yield from each subplot in 1984 with individual yield components. No consistent significant correlations were found (Appendix 5). Correlations of seed yield per row with other harvest components were examined for each cultivar and year, with the results presented in Appendix 6. In 1984 only number of seeds per row, measured in this year only, were consistently correlated with yield per row. In the next two years, several cultivars had high linear correlations between yield and weight of 250 seeds, which were sampled from the two inner rows, and weight of 1000 seeds, which were randomly selected from all four rows of the 1 m sample. Correlations between yield per row and number of pods per plant, and in 1986 between yield and peas per pod, were also high for several cultivars (Appendix 6).

3.2.5 Analysis of Covariance and Seed Weight Regressions

Analysis of covariance of 1000 seed weight was conducted with mean maximum aphid numbers per plant tip as the covariate term. The least squares model used was:

$$Y = \mu + T + R + C + bA + b_T A_T + b_C A_C + b_{TC} A_{TC} + e$$

where Y was 1000 seed weight;
μ was the overall least squares mean;
T was the effect of year;
R was the effect of replicate;

C was the effect of cultivar;
b was the partial regression coefficient for the overall effect of aphid numbers, A, on Y;
b_T was the deviation from b due to year;
b_C was the deviation from b due to cultivar;
b_{TC} was the deviation from b due to the year x cultivar interaction; and
e was the error term.

Aphids, years, replicates within years, cultivars, and the year times cultivar interaction all significantly affected 1000 seed weight (d.f.=101, P for all factors $\leq$0.001; F=24.40, 58.14, 4.32, 316.12 and 3.36, respectively). F values for b_T, b_C and b_{TC} were not significant, indicating homogeneity of the slopes of the regression lines among cultivars and years. However, while the ANCOVA indicated overall homogeneity of the slopes, results presented in Table 11 suggested that not all regression lines were similar in slope.

Analysis of covariance was conducted on 1000 seed weight among cultivars within each of the three years. In 1984 aphid numbers were significantly associated with reduced seed weights (d.f.=27, F=27.59, P$\leq$0.001), but slopes of the regression lines did not significantly differ among cultivars. In 1985 aphid numbers were again significantly and negatively associated with seed weight (d.f.=48, F=29.10, P$\leq$0.001). However, slopes were not homogeneous among cultivars (d.f.=48, F=3.27, P$\leq$0.05). Comparison of the slopes by means of t-tests indicated that the slope of Century differed significantly (d.f.=48, t=-2.78, P$\leq$0.01) from the slopes of the other cultivars, which were homogenous. In 1986 aphid numbers were negatively associated with seed weight, but not significantly so, and slopes of the regression lines did not differ among cultivars. The estimates of the slopes of the regression lines for the three years are listed in Table 14.

Table 14. Regression coefficients of 1000 seed weight (Y) on mean numbers of aphids per plant tip at the time of peak aphid populations combined over cultivars at Glenlea, 1984 to 1986.

Year	n	Regression Coefficient
1984	38	-0.424 ***[1]
1985	60	-0.268 *
1986	50	-0.150 n.s.

[1] Regression coefficients within the column vary significantly from zero at the 0.05 (*) or 0.001 (***) level of probability, ANCOVA; n.s.=not significant.

Covariance analysis was conducted for each cultivar to determine the effect of aphids and to check for homogeneity of the slopes of the regression lines among years. The 1000 seed weight significantly varied with aphid numbers in the cultivars Century ($d.f.=9$, $F=7.92$, $P\leq0.05$), Tara ($d.f.=10$, $F=7.06$, $P\leq0.05$), and Triumph ($d.f.=9$, $F=9.95$, $P\leq0.01$). A significant departure from homogeneity of regression slopes among years was found for the cultivar Tara ($d.f.=10$, $F=4.55$, $P\leq0.05$). For this cultivar the slope of the regression line for 1984 differed significantly from the slopes of data from 1985 ($d.f.=14$, $t=2.60$, $P\leq0.05$) and 1986 ($d.f.=12$, $t=3.08$, $P\leq0.05$) which, despite being opposite in sign (Table 11), were not significantly different from each other. The slopes of the Tipu regressions were also different in sign (Table 11), although borderline in significance ($d.f.=14$, $t=2.08$, $P\leq0.08$).

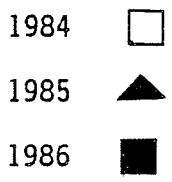
As well as being negatively related to aphid populations, 1000 seed weights were also greatly influenced by year. The seed weights of all cultivars were greater in 1985, in which there was a very early, warm spring, than in the other two years. The relationship between 1000 seed weight and aphid density for each cultivar is illustrated in Figure 4, with separate line segments for each year. All cultivars except Tara and Tipu were graphed with similar regression slopes for the three years.

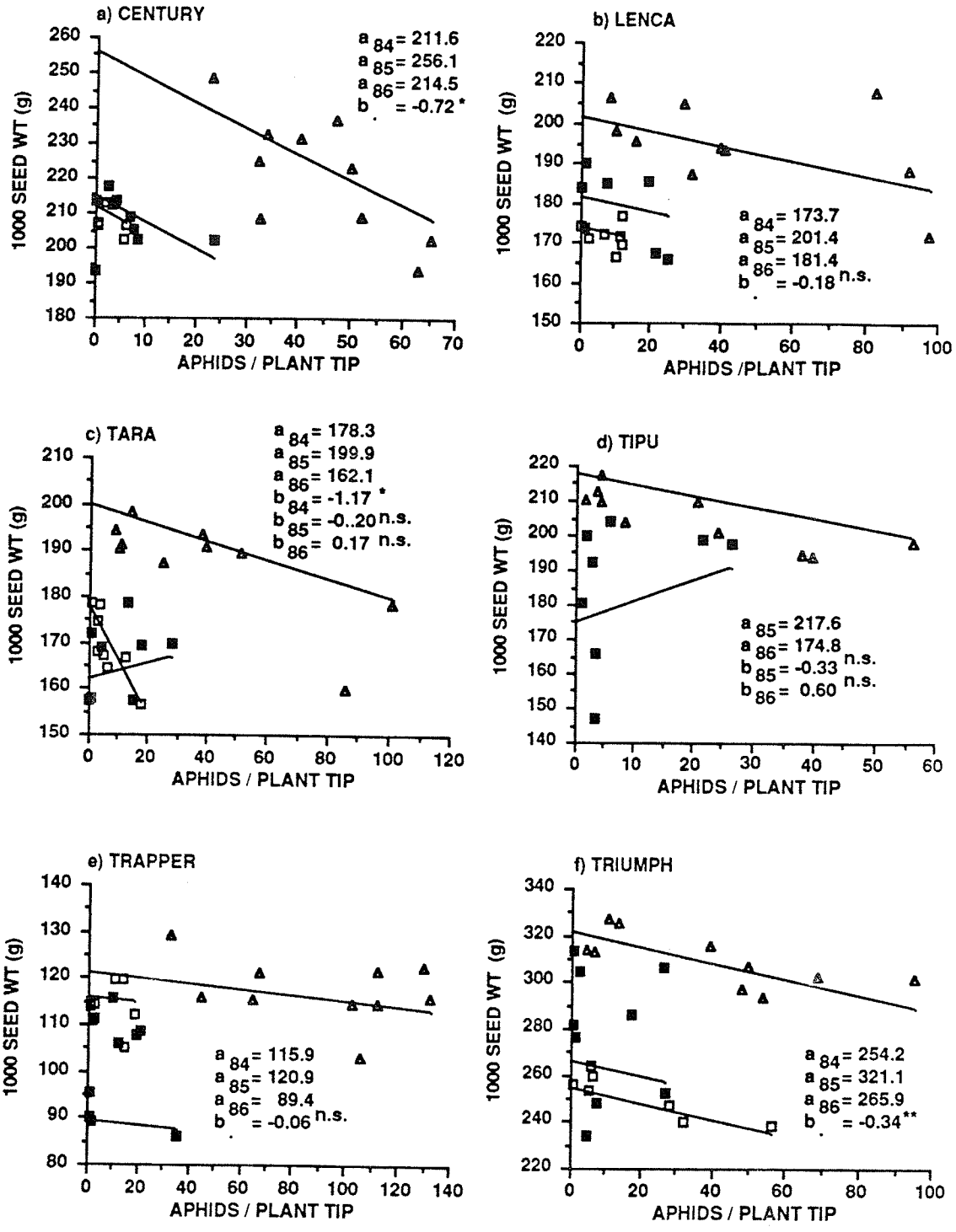
4. Discussion

4.1 Pea Aphid Populations

In all three years aphid populations on the various cultivars had generally similar patterns, building up slowly, peaking during the first

Figure 4. Relationship between 1,000 seed weight and number of aphids per plant tip on 6 cultivars of field peas naturally infested with pea aphids at Glenlea, 1984-1986.




a) CENTURY
a 84= 211.6
a 85= 256.1
a 86= 214.5
b . = -0.72 *
1000 SEED WT (g)
APHIDS / PLANT TIP
b) LENCA
a 84= 173.7
a 85= 201.4
a 86= 181.4
b . = -0.18 n.s.
1000 SEED WT (g)
APHIDS /PLANT TIP
c) TARA
a 84= 178.3
a 85= 199.9
a 86= 162.1
b 84= -1.17 *
b 85= -0..20 n.s.
b 86= 0.17 n.s.
1000 SEED WT (g)
APHIDS / PLANT TIP
d) TIPU
a 85= 217.6
a 86= 174.8
b 85= -0.33 n.s.
b 86= 0.60 n.s.
1000 SEED WT (g)
APHIDS / PLANT TIP
e) TRAPPER
a 84= 115.9
a 85= 120.9
a 86= 89.4
b . = -0.06 n.s.
1000 SEED WT (g)
APHIDS / PLANT TIP
f) TRIUMPH
a 84= 254.2
a 85= 321.1
a 86= 265.9
b . = -0.34 **
1000 SEED WT (g)
APHIDS / PLANT TIP

part of August, and declining rapidly to low levels by late August. These patterns resulted in left-skewed population curves similar in form to aphid patterns found by Maiteki et al. (1986) in Century fields in Manitoba and by Yencho et al. (1986) in green pea fields in Washington. There were considerable differences in aphid numbers in different years, with 1985 densities up to five times greater on some cultivars than in 1984 or 1986. Maiteki et al. (1986) reported significant differences in peak aphid densities in 3 years of observations.

Although spraying decreased pea aphid numbers in all cultivars, the effect of spraying varied with year. In 1985, after the plots were initially sprayed at flowering, aphid populations reached a considerable size in both sprayed and unsprayed plots by the time of pod formation and fill. This may have decreased potential disparities in yield components between the two treatments. Resurgence of pea aphid populations after chemical application is not uncommon, and was observed by Maiteki and Lamb (1985a) in some Century plots.

The population curves (Figures 1 to 3) clearly demonstrate that pea aphid populations differ among some cultivars of field peas grown in Manitoba. In all three seasons there were significant differences in aphid numbers among cultivars at times of peak aphid populations, with populations on Century, and Tipu in 1985 and 1986, being generally low and populations on Trapper and Triumph being relatively high. Although Maiteki et al. (1986) observed much lower peak aphid densities on Century peas than on the cultivar Trapper, the observations were based on only one Trapper field in one year and, as such, were little more than anecdotal.

Pea aphid abundance may be influenced by the morphology of the various cultivars on which the aphids feed. The preferred feeding sites of the pea aphid are the stem terminal and the abaxial surfaces of leaflets (Lowe, 1971; Müller, 1984). Therefore, Tipu may support fewer aphids than other cultivars because the reduction of its leaflets to tendrils allows for less preferred space for aphid population development. Although aphids, especially small nymphs, were occasionally observed on leaf tendrils of Tipu, the majority of A. pisum on Tipu were located on the plant terminal, stems and pods. The reduced foliage of Tipu may also expose the pea aphid to increased predation or adverse weather conditions. However, predator populations, chiefly coccinellids, were low in all three years of this study and further experiments would have to be conducted to test this postulation.

Triumph vines are much shorter than those of the other cultivars tested; it has short internodes and dark green medium-sized leaves (Ali-Khan, 1973). Cartier (1963) proposed that pea plant height has two opposing effects on pea aphid populations. Higher initial infestations are found on taller plants because these act as a barrier to aphid flight. However, ensuing aphid populations increase more rapidly on short as compared to tall plants because the former have shorter internodes and more clumped leaves, which offer more protection from predators and the environment. In this study, pea aphid populations on Triumph peas early in the season were lower than on several of the other cultivars and height may possibly have been a factor in colonization.

Triumph foliage tends to remain green and succulent later in the season than that of other cultivars; its compact growth may require desiccation before harvest (Anonymous, 1984b). This increased succulence

of Triumph plants relative to that of other cultivars may have contributed to high pea aphid populations on Triumph plants in two of the three years studied. Aphids in general may thrive better on plants with high water content of tissues (Shaposhnikov, 1959). And although a study by Barker and Tauber (1954) reported decreased numbers of pea aphids on cultivars of highly succulent garden peas as opposed to other peas, in an early investigation Searls (1935) noted that A. pisum preferred a deep green dwarf pea cultivar which had short, thick internodes and large fleshy leaves.

Pea morphology may be only part of the reason for varying aphid densities on the cultivars, for Century, with relatively low aphid populations, and Trapper, with relatively high ones, appear to the human eye to be very similar in form and colour. The nutritional status of a cultivar, particularly the amino acid levels and balance, plays a major role in pea aphid development and fecundity (Maltais and Auclair, 1957; Auclair 1969). A negative correlation exists between A. pisum reproductive rate and the sugars/amino acid ratio of its host plant (Febvay et al., 1988). While Auclair and Cartier (1960) reported an absence of toxic substances in two cultivars of peas on which pea aphid growth was suboptimal, the use of improved biochemical techniques may result in the discovery of antibiotic and antixenotic factors in pea cultivars as have been recently found in other legumes (Dreyer et al. 1985, 1987). No biochemical analysis of the constituents of the pea cultivars used in this study has been undertaken.

4.2 Cultivar Yields

Maiteki and Lamb (1985a) estimated the economic threshold for pea aphids on the field pea cultivar Century to be two to three aphids per plant tip at the time when 50% to 75% of the plants are flowering. In a consideration of the effects of pea aphid feeding on pea yield components, they found that at aphid densities near the economic threshold, 1000 seed weight rather than comparative yield more accurately reflects pea response to aphid stress. At these aphid densities, the number of Century seeds per area is not affected by aphid feeding. Similarly, Bouchery (1977) found that A. pisum reduces seed weight of Vicia faba L., but not the number of seeds per pod. In the present study, the varying sizes of pea populations in the three years and the different plant growth stages at which the rapid expansion of aphid populations occurred led to different degrees of plant injury by the aphids. However, the only yield component to be consistently affected by pea aphid feeding was 1000 seed weight (Tables 8, 9, 12, 13), an indication of the sensitivity of this variable to the presence of aphids.

The question arises of the validity of using seed weight as a predictor of economic damage, as done by Maiteki and Lamb (1985a, 1985b). On a large scale, reduced seed size results in fewer kilograms per hectare of harvested crop. On the small scale used in the present study, pea yield per area was less precisely determined than 1000 seed weight, as evidenced by the standard errors for these values in Tables 8, 12 and 13. Real differences among yield means from small plots, although they may be present, are much harder to detect than differences among 1000 seed weights.

The size of peas may directly affect the price a farmer receives for his crop. In some years, for sales to certain markets such as India, a premium is paid to growers of exceptionally large seed (F. Rempel, Newfield Seeds, Nipawin, SK, personal communication). Further, one of the factors in the determination of grade of field peas is the percentage of shrivelled or undersized peas in the sample (Canadian Grain Commission, 1988). Irregularly-sized or undersized seeds are of particular concern because they must be removed before marketing, decreasing the value of the crop (Wilkins, 1988; N. Arbuckle, The B.C. Pea Growers Ltd., Portage la Prairie, MB, personal communication).

Even without the confounding effects of pea aphid feeding, pea yield per area is not consistently correlated with peas per pod, pods per plant, and plants per unit area (Gritton and Eastin, 1968). The only correlation between individual yield components and yield per m row which was consistent and significant among cultivars in this study was number of seeds per m row, measured in 1984 (Appendix 6). Yet this variable was not significantly correlated with aphid densities, nor was number of seeds per pod, as Maiteki and Lamb (1985a) also discovered. Therefore, while the effect of seed weight on yield per unit area may not be more important than the combination of the other individually insignificant components, it was the most important single factor measured in the three years. Furthermore, it provides the most precise single measure of pea aphid damage to the crop.

Despite the variation in the size and the timing of the A. pisum population increase relative to the growth stages of the peas, the responses of most of the individual cultivars to aphid feeding in terms of seed weight were relatively uniform over the three years (Tables 10,

11, 14). Trapper seed weight appeared to be little influenced by aphid infestation levels in the range found in the field, as evidenced by the small treatment differences in Table 10 and the very shallow slopes of the regression lines for this cultivar (Table 11 and Figure 4). Although sprayed Trapper plants had high numbers of aphids on them in August of 1985, unsprayed subplots had nearly twice these levels throughout most of the summer (Tables 4 and 5, Appendix 3). The very high numbers of aphids found on unsprayed Trapper plants from pod formation to drying in this year had no significant effects on any yield components, a strong indication that Trapper is comparatively tolerant to aphid feeding. Newman and Pimentel (1974) found some garden pea lines with higher levels of tolerance to A. pisum feeding than other lines.

When the regression data were combined over years, the slope of the relationship between Lenca seed weight and aphid densities did not differ significantly from zero (Figure 4). Thus this cultivar, like Trapper, was minimally affected by pea aphids. The fact that Lenca had the most yield components positively related to the low aphid numbers of 1986 suggests that the response of this cultivar to low levels of herbivory may be somewhat different than that of the other peas.

There were no significant decreases in any yield components in 1986, despite Lenca, Tara and Tipu having a significantly increased number of aborted pods per plant with increasing aphid numbers. The significant positive relationships between aphid feeding and yield components of the cultivars in this year may be due to plant compensation for herbivory. The first stage of plant loss due to injury is a plateau at optimum yield because of plant compensation for the injury (Tammes, 1961). Developing fruiting structures compete for

available assimilates, reducing their final size and number, so that some degree of compensation for injury to reproductive structures is not unusual (McNaughton, 1983). Pruning flowers from peas may result in better fruit setting in other flowers and larger seeds over the entire plant (Tammes, 1961). A decrease in the number of pea pods per plant with aphid feeding, as seen in 1986, may be a reflection of this compensatory reaction towards nutrient loss.

Several yield components other than aborted peas per pod in the cultivars Lenca and Trapper had significant positive relationships with aphid densities in 1986. Another explanation for a positive relationship between yield and aphid number is that aphids may accumulate on the most vigorous plants. Rapidly growing plants may have high levels of amino acids and other nitrogenous compounds which ameliorate aphid growth. Thus, as long as aphid numbers do not reach injurious levels, healthy plants may yield more in spite of rather than because of increased numbers of aphids feeding upon them as opposed to lower yields from less vigorous plants. This lends credence to the suggestion that Trapper and Lenca were the cultivars least affected by aphid feeding.

The slope of the linear regression of Tipu seed weight on aphid densities combined over years did not differ significantly from zero. However, the Tipu relationship is based only on two years' data, and the regression line for 1986 accounts for a relatively small proportion of the variation in seed weight (Table 11). Aphid populations on Tipu plants were very low and occurred very late in 1986 (Figure 3). Data from 1985 (Table 11) and from cage studies (Section II) indicate that the response by Tipu to aphid feeding may be greater than the slope of this cultivar in Figure 4 denotes.

The observation of delayed maturity in unsprayed Tipu subplots was unexpected, for pea-aphid induced stress has been found to increase the rate of green pea maturation (Yencho et al., 1986). However, insect feeding damage has been found to cause delayed and uneven maturity in other crops (Bardner, 1968; Bardner and Fletcher, 1974). Tipu's reduced leaf area in comparison with other cultivars may make it more susceptible to withdrawal of photosynthates by aphids and more variable in maturation.

Tara and Triumph appeared generally susceptible to pea aphid feeding. Over the first two years of the experiment, aphid densities were most closely related to seed weight in these cultivars (Table 11). In 1984, Tara had the steepest slope of the seed weight regression line of those calculated in any one year. Since the amount of damage to a crop by an aphid population varies with the duration of infestation as well as the total aphid number (Maiteki and Lamb, 1985a), the fact that Tara had the largest aphid populations of any cultivar until midflowering in 1984 (Figure 1) may account for the steep slope of the regression in this year. The positive slope of the regression line of Tara seed weight in 1986, although not significant, was unexpected given the similarity of aphid population growth patterns on the cultivars in this year (Figure 3) and the general trend of decreasing seed weight with increasing aphid densities prevalent in the investigation. Although the positive slope may have been due to plant compensation for herbivory or mere chance, it had the effect of decreasing this cultivar's combined regression value, as happened with the slope of Tipu. Therefore, the general response of Tara peas to pea aphid infestation, like those of Tipu, may be greater than indicated in Figure 4.

Triumph's susceptibility to injury by aphids is indicated by the fact that it had the greatest difference in seed weights between spray treatments in all three years (Table 10) and the second largest combined slope of the seed weight-aphid density regression (Figure 4). Given large aphid populations, Triumph may be susceptible to aphid damage later in the season than the other cultivars. In 1985, aphid levels in Triumph subplots were below four per plant tip until pod fill; aphid levels in both sprayed and unsprayed subplots rose sharply after this until the second application of malathion on August 6, as pods were maturing (Figure 2, Tables 4 and 5, Appendix 3). Despite the maturity of the plants and the brevity of the time interval in which aphids were lower in sprayed versus unsprayed subplots of Triumph, the difference in seed weight between treatments was significant for this cultivar, as was the linear regression. Results from cage studies (Section II) and farmers' fields (Section III) also indicate that Triumph yield may be more strongly affected by aphid feeding late in the summer than the other cultivars.

The fact that pea aphid numbers varied significantly with seed weight in the cultivar Century was surprising, given the generally low aphid numbers on this cultivar and the small differences in Century seed weights between spray treatments (Table 10). However, the small seed weight differences were a reflection of the generally small differences in aphid populations between sprayed and unsprayed subplots of this cultivar over the three years (Tables 4 and 5, Appendix 3). The significance of the Century regression lines in Figure 4 is due mainly to the cultivar's response to the high aphid densities at pod fill in 1985 (Figure 4a), since the Century regression lines in 1984 and 1986

were not significant (Table 11). Although young pods are the Century plant growth stage most susceptible to direct aphid feeding damage (Maiteki and Lamb, 1985b), feeding by large numbers of aphids later in plant phenology, as appeared in 1985, can also affect Century yield. The potential of pea aphids to cause yield losses has been noted in the past (Lamb and Maiteki, 1985). Maiteki et al. (1986) found the economic threshold of pea aphids was exceeded in most plots and commercial Century fields in Manitoba sampled over a three year period.

The differences in ranking of aphid densities on the individual cultivars of this study were not reflected in yield responses. The cultivars fell into three groups in terms of aphid population development on them. Trapper and Triumph supported high aphid populations, Lenca and Tara had aphid populations in the middle of the range, and Century and Tipu supported generally low A. pisum populations. Yet, Trapper and Lenca appeared relatively tolerant of aphid feeding while Century, Tara and Triumph appeared susceptible. The response of Tipu was variable but tended toward the susceptible end of the spectrum. In an open field experiment such as this study, a comparison of cultivar yield responses is confounded by varying and inconsistent aphid populations. To clarify some of the results of this study, a closer look is necessary at the mechanisms behind the degrees of resistance expressed by the cultivars.

Section II

Growth of Pea Aphid, Acyrthosiphon pisum (Harris), Populations on Caged Plants of Six Cultivars of Field Peas, and the Effects of Pea Aphids on Harvest Components of Caged Field Peas.

ABSTRACT

A known number of pea aphids, Acyrthosiphon pisum (Harris), were placed in 1 m^3 field cages, each containing one of six field pea cultivars, with an equal number of control cages remaining uninfested. The cages were monitored to determine if aphid population development differed among cultivars and if values of harvest components differed between infested and control cages. The largest population of aphids was found on the cultivar Trapper and the smallest on the cultivar Century, with differences between these cultivars being significant at the plant maturation stage of growth. Infested plants of Trapper had a significantly lower number of pods per plant, and infested plants of all cultivars had decreased seed weights, both per m row and per 250 seeds, when compared with control plants. In all cultivars except Trapper, the most severely affected yield component was weight of 250 seeds.

1. Introduction

The pea aphid, Acyrthosiphon pisum (Harris), is the insect most damaging to world legume production (Duke, 1981). In Manitoba, control of this insect on the field pea cultivar Century has been reported to be economically justifiable if aphid densities are greater than 2 to 3 per 20 cm plant tip at flowering (Maiteki and Lamb, 1985a). It has been noted that A. pisum densities are greater on Trapper and Triumph peas than on Century in the same year (Section I); yet it is not known if pea aphids affect the productivity of cultivars other than Century in the same way.

Reliance on natural infestations of the pea aphid on peas in open field studies may be an unsatisfactory method of assessment of potential damage because of unpredictable and sometimes low infestation rates. Pea aphid densities fluctuate greatly between years (Maiteki, 1985; Section I), and may not reach outbreak levels during short-term studies. Artificial infestation of pea aphids on plants in field cages eliminates the confounding effects of parasites and predators without eliminating major weather changes which may affect plant quality and insect growth. Artificial infestation also ensures that maximum effects of pea aphid herbivory are observed on plants.

The purpose of this experiment was to determine how different field pea cultivars influence the population growth of a known initial population of pea aphids, and to determine the extent to which high pea aphid densities damage different field pea cultivars.

2. Materials and Methods

A preliminary experiment was conducted in the summer of 1985 in field plots near Glenlea, Manitoba. Because of various problems encountered during the summer, chiefly contamination of control cages by natural infestations of aphids, the data obtained were not reliable. The experimental methods were modified to overcome this problem in 1986. The experimental design was a split plot with field pea cultivars as main effects and presence or absence of field-collected or laboratory-reared pea aphids as sub-plots. Six cultivars of field peas -- Century, Lenca, Tara, Tipu, Trapper and Triumph -- were planted in each of two blocks. Plots consisted of each cultivar, grown in 8 rows of peas 0.3 m apart and 4.3 m in length. Four 1 m^3 plastic-screened cages were placed on each plot, with two randomly selected cages infested with aphids and two cages remaining uninfested. Each cage covered 4 rows of peas, one of which was an outside row of the plot. Cages were placed on the plants on June 18, at which time plants were in the 3 to 5 node vegetative stage and were 6 to 12 cm tall. When the cages were examined just prior to infestation, all 48 were found to be free of insects. Aphids were placed in the cages on July 7 and 8, when plants were starting to bloom. One hundred mostly apterous adult and fourth instar plus one hundred earlier instar aphids were placed in each of 24 cages, corresponding to a density of approximately three aphids per plant.

Sweeping of a nearby alfalfa field did not supply a sufficient number of aphids in the correct morph ratios to infest all the aphid-present cages. Therefore, A. pisum collected from the alfalfa were placed in a random selection of half the cages to be infested, while in

the other 12 cages were placed aphids which had been reared in growth chambers on their respective pea cultivars. Rearing conditions in the growth chambers were 20°C and 16 h photoperiod. The original source of these laboratory-reared aphids was a single virginoparous aphid collected on June 1, 1983, from the same alfalfa field as was swept to obtain the field-caught aphids in the other cages.

Entry to the cages was gained by means of a 70 cm zipper in the middle of one side of each cage. Plant growth stage (Appendix 1) and the number of aphids on the terminal 20 cm of 5 pea plants per cage were recorded at approximately weekly intervals throughout the season.

Two inner rows per cage were hand harvested when the majority of plants were mature and dry and the following data were recorded and averaged over the two rows: the number of plants per m row, the mean number of pods and aborted or missing pods per plant from 10 randomly selected plants, the mean number of peas per pod from 30 pods, the weight of seeds per m row, and the weight of 250 seeds. As well, the heights of 5 plants randomly selected from the two rows were recorded. The weight of 250 seeds rather than 1000 seeds was measured because of an insufficient number of seeds for the latter statistic.

Aphid numbers were transformed by $\sqrt{x + 0.05}$ to stabilize variances before data analysis. Data analysis consisted of analysis of variance of aphid numbers in infested cages among cultivars and analysis of variance of harvest components of infested and control subplots (SAS Institute, 1985). To detect real differences t-tests were used to compare infested and control means of each harvest component for each cultivar in turn. Harvest components were also regressed upon aphid numbers and t-tests were used to compare slopes of the regression equations.

3. Results

Caged plants were taller, more succulent, and had more brittle stems than plants outside the cages. Two weeks after the introduction of aphids into the cages, many of the plants of all cultivars except Triumph had reached the top of the cage. This resulted in considerable curling and distortion of plant tips. Triumph plants appeared least affected by the caging, although late in the season considerable amounts of powdery mildew, Erysiphe polygani DC. ex Mérat appeared on them.

Plant development proceeded at similar rates in aphid infested and non-infested cages of most cultivars; local variation in microclimate influenced plant maturation more than aphid infestation did. All four cages, infested and non-infested alike, of Lenca in one block and of Trapper in the other block senesced rapidly and were harvested 6 days before general harvest began. These cages were in low spots in the field and the sites were often water-logged. The only instances where cultivars did not mature at equal rates over treatments were the Trapper and Triumph cages of one block, in which the infested cages were harvested 12 days earlier than their non-infested counterparts.

The non-infested cages of all cultivars remained virtually aphid-free throughout the season except for both cages of one block of Trapper peas. A mean of 16.0 ±10.5 aphids per plant tip was found in one non-infested Trapper cage on August 1. This cage was subsequently sprayed with insecticide but on August 14 A. pisum populations had rebounded to a mean of 88.0 ±30.6 aphids per plant tip. On August 8 pea aphid populations in the second non-infested cage had reached a mean of 7.1 ±6.5 aphids per plant tip from zero a week previously. All aphids found

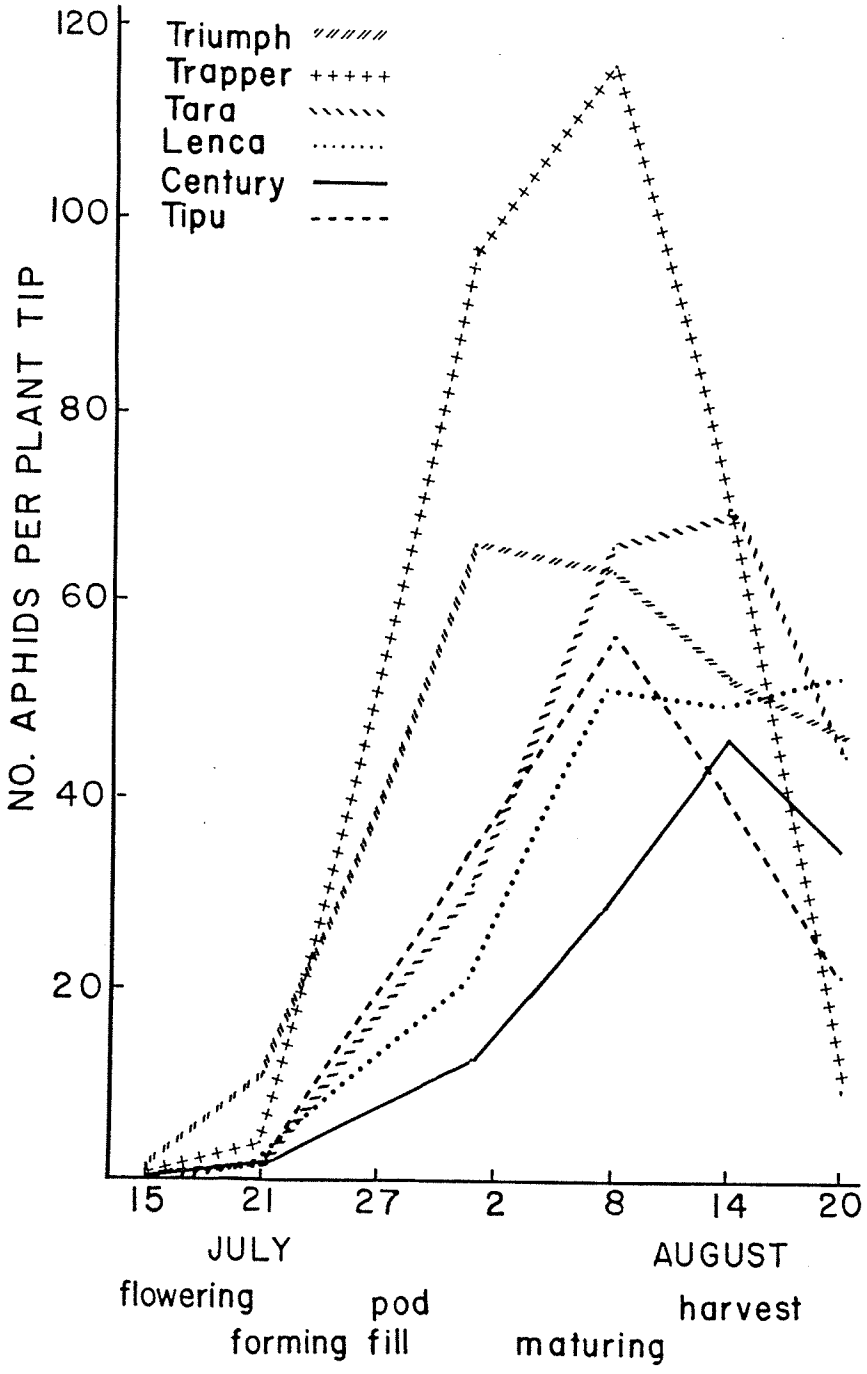
were hand-killed but August 14 populations of A. pisum in this cage were 11.6 ±4.7 per plant tip. These were also hand-killed and on August 20 no aphids were found in this cage.

There was tremendous variation in aphid numbers among infested cages on the same cultivar. This was not attributable to block; nor were there significant differences in aphid numbers between cages initially infested with aphids which were laboratory reared or field caught, with one exception. On August 8, cages with laboratory reared aphids had 407.9 ±59.4 aphids per plant tip, significantly higher than cages with field caught aphids, which averaged 235.9 ±188.9 aphids per plant tip (ANOVA, d.f.=6, $F=14.79$, $P \leq 0.05$).

Aphid populations in infested cages of all cultivars exhibited typical pea aphid growth curves, rising to peak at about the second week in August, then generally falling rapidly as plants matured (Figure 5). Aphids on Triumph plants reached the economic threshold of 2 to 3 per plant tip at flowering, while aphid numbers on all cultivars reached this level by the middle of pod formation, a growth stage which is still susceptible to damage by the pea aphid (Maiteki and Lamb, 1985a). Pea aphid populations peaked on the cultivars over a 3 week period (Figure 5).

An analysis of variance conducted on mean aphid numbers per cultivar in infested cages on July 22, when plants were in the late flowering to early pod initiation stages of development, found no significant differences in aphid populations among cultivars. On August 1, as pea aphid populations rose on all cultivars and peaked on Triumph, there were significant differences in numbers of aphids found on Trapper and Triumph as compared to numbers on Century (d.f.=6,

Figure 5. Pea aphid populations on plant tips of caged field pea cultivars infested with aphids at Glenlea, 1986 (n = 20 except Trapper and Lenca on August 20, where n = 10).


Triumph
Trapper
Tara
Lenca
Century
Tipu
NO. APHIDS PER PLANT TIP
120
100
80
60
40
20
15
21
27
2
8
14
20
JULY
AUGUST
flowering
pod forming
fill
maturing
harvest

F=7.11, P≤0.05) (Figure 5, Table 15). By August 8, A. pisum populations had peaked in Trapper and Tipu cages, as well as in all four cages of Lenca plants. As in the previous week, mean aphid numbers per plant tip on Trapper plants were significantly higher than those on other cultivars, while populations on Tara were significantly higher than those on Century (d.f.=6, F=8.44, P≤0.05) (Table 15). As aphid populations declined, no further significant differences were found in their numbers among cultivars.

Because two of the Trapper control cages at times contained a considerable number of aphids, analysis of variance and linear regressions of harvest components were conducted including and omitting data from these cages. There were only slight differences between the results of analyses with and without the Trapper data, none of which affected the significance of the components in the F tests. Therefore, the following results include data from all the cages.

Analysis of variance indicated that there were no significant differences in yield component data recorded from cages infested with aphids which had been laboratory reared or field caught. Therefore, these data were combined for comparison with data from control cages. Analysis of variance further indicated that plant stand differed significantly between aphid infested and control cages. Because no plant deaths were observed in the cages over the summer, disparity in plant density between treatments was not attributable to aphid feeding. Analysis of covariance was conducted on harvest components with number of plants per row as covariate to remove the effect of varying plant density on other yield components.

Table 15. Mean number of pea aphids per plant tip on field pea cultivars in cages infested with aphids (n=20).

Cultivar	No. Aphids/Plant Tip[1] August 1	August 8
Trapper	96.30 a[2]	116.70 a
Triumph	66.10 ab	63.65 bc
Tipu	34.50 bc	56.40 bc
Tara	31.15 bc	66.25 b
Lenca	20.85 bc	51.05 bc
Century	11.95 c	32.15 c
Pooled Standard Error	2.60	2.38

[1] Analysis of variance and standard error based on $\sqrt{x + 0.05}$ transformed data; standard error for each column was calculated from the error mean square of an analysis of variance.

[2] Means followed by the same letter(s) within a column are not significantly different (Duncan's multiple range test, $P \leq 0.05$).

Of the yield components summarized in Table 16, number of pods per plant, weight per row and weight of 250 seeds were significantly reduced in infested compared to control cages (ANCOVA, d.f.=23; F=11.40, P≤0.05; F=20.21, P≤0.01; F=18.12, P≤0.01, respectively). Over all cultivars, plants in infested cages averaged 4.11 ±0.46 pods per plant while their control counterparts averaged 5.11 ±0.23 pods; infested cages averaged 50.27 ±7.46 g of seed per row while aphid-free cages averaged 76.72 ±5.84 g; and 250 seed weight in infested cages was 41.51 ±5.43 g and 49.96 ±6.08 g in control cages. Differences in number of aborted pods per plant, number of peas per pod, and height of plants between control and infested cages were not significant.

The cultivar by aphid level interaction term was significant for the number of pods per plant (d.f.=23, F=4.58, P≤0.05), indicating that not all cultivars responded similarly to aphid infestation. A two-tailed t-test to compare individual cultivar means of this variable between infested and control cages revealed that the number of pods per Trapper plant in infested ($\bar{x}$=2.21 ±0.46) and in control cages ($\bar{x}$=5.53 ±0.29) were significantly different (t=4.67, P≤0.01). Tara plants also had fewer pods when fed upon by aphids ($\bar{x}$=4.14 ±0.77) than when aphids were excluded from cages ($\bar{x}$=5.57 ±0.44), although the difference between means was borderline in significance (t=2.05, P=0.06). There were no significant differences in the number of pods per plant between aphid treatments in the other four cultivars.

All cultivars had both lower yield per row and decreased 250 seed weight in infested cages. Individual cultivar t-tests indicated that differences in weight of seed per m row between infested and control cages of Tara, Lenca and Trapper plots were significant, as were

Table 16. Means (± S.E.M.), coefficients of variation values, and pooled standard error for yield components averaged over two rows, 1 m in length, of field pea cultivars in cages infested and not infested with pea aphids, 1986 (n = 4).

Cultivar	No. Plants /Row	No. Pods /Plant	No. Aborted Pods/Plant	No. Peas /Pod	Height (cm)	Weight/ Row(g)	Weight/ 250 Seeds(g)
a) Control Cages							
Century	16.0 ±0.9	5.08 ±0.39	1.55 ±0.12	4.52 ±0.10	155.1 ± 2.1	79.5 ± 7.0	55.5 ±0.5
Lenca	20.1 ±1.9	4.96 ±0.65	2.40 ±0.24	5.16 ±0.19	166.6 ± 6.2	83.8 ±21.4	45.4 ±1.2
Tara	16.9 ±1.0	5.57 ±0.44	2.50 ±0.35	5.02 ±0.09	178.3 ± 8.1	91.0 ±14.5	47.4 ±1.6
Trapper	21.1 ±1.6	5.53 ±0.24	2.36 ±0.28	4.20 ±0.21	149.2 ± 6.2	49.6 ± 5.0	28.1 ±1.1
Triumph	13.1 ±0.8	5.34 ±0.37	3.62 ±0.27	3.49 ±0.27	104.1 ± 2.0	74.8 ± 6.3	73.6 ±2.5
Tipu	24.9 ±0.4	4.21 ±0.50	1.34 ±0.13	4.54 ±0.14	136.4 ± 3.3	81.6 ± 8.4	49.9 ±0.7
b) Infested Cages							
Century	14.8 ±0.7	5.43 ±0.53	1.60 ±0.13	4.66 ±0.26	159.8 ± 4.5	70.5 ± 5.4	52.3 ±1.4
Lenca	18.9 ±2.3	3.73 ±0.44	1.92 ±0.07	5.01 ±0.09	168.7 ±14.1	48.9 ± 8.0	35.1 ±1.2
Tara	17.1 ±1.4	4.14 ±0.77	2.19 ±0.24	4.68 ±0.07	174.2 ± 7.0	54.6 ±16.0	37.2 ±2.9
Trapper	19.8 ±1.2	2.20 ±0.46	1.80 ±0.76	4.48 ±0.28	152.0 ±11.6	17.0 ± 3.4	22.2 ±3.2
Triumph	12.2 ±0.4	5.04 ±0.56	3.02 ±0.46	3.39 ±0.26	101.9 ± 6.8	49.3 ± 4.4	59.2 ±3.5
Tipu	20.4 ±0.1	4.12 ±0.14	1.34 ±0.03	4.42 ±0.01	138.7 ± 0.4	61.4 ± 2.3	43.3 ±0.4
C.V.	--[1]	21.41	23.68	6.13	6.88	28.50	7.25
Pooled S.E.	--	0.49	0.25	0.14	5.1	9.0	1.7

[1] Analysis of covariance with no. of plants/row as covariate.

differences in 250 seed weight between treatments of all cultivars except Century (Table 17). Similar trends among cultivars resulted in nonsignificant cultivar by aphid level interactions for the two yield variables.

Treatment differences were greater for seed weight than for yield per row in all cultivars except Trapper (Table 17). It should be noted that Trapper was the only small-seeded cultivar used in the experiment.

Linear regressions were conducted on number of pods per plant, weight per row and weight of 250 seeds; these variables were regressed over mean number of aphids per plant tip at the time of the aphid population peak of the particular cultivar. For the cultivar Lenca, this date was selected as August 8 rather than August 20 (Figure 4) since half of the Lenca plots had been harvested by the latter date. The number of pods per Trapper and Tara plant decreased significantly in the presence of aphids (d.f.=1,5, F=50.03, $P \leq 0.001$ and d.f.=1,6, F=12.91, $P \leq 0.05$, respectively) (Table 18). None of the other cultivars had a significant relationship between number of pods per plant and aphids per plant tip.

The regression equation for Trapper was significant for the weight of seeds per m row variable (d.f.=1,5, F=30.96, $P \leq 0.01$), as were those of Tara and Tipu (d.f.=1,6, F=6.48, $P \leq 0.05$ and d.f.=1,6, F=6.56, $P \leq 0.05$, respectively). However, the differences between slopes were not significant for any cultivar comparisons.

Tipu, Tara and Lenca had significant negative relationships between weight of 250 seeds and density of pea aphids (d.f.=1,6, F=22.98, $P \leq 0.01$; d.f.=1,6, F=10.56, $P \leq 0.05$; and d.f.=1,6, F=7.62, $P \leq 0.05$, respectively) (Table 18). At peak aphid densities, the range in

Table 17. Differences in weight per m row and weight of 250 seeds between plants in pea aphid infested and control cages on six cultivars of field peas, Glenlea, 1986 (n=4).

Cultivar	Weight/row Treatment[1] Differences(g)	Weight/row t Value	Weight of 250 seeds Treatment Differences(g)	Weight of 250 seeds t Value
Trapper	32.6 *[2]	2.548	5.9 *	2.515
Triumph	25.5	1.993	14.4 ***	6.140
Tara	35.4 *	2.767	10.2 **	4.349
Lenca	34.9 *	2.727	10.3 **	4.392
Tipu	20.2	1.579	6.6 **	2.814
Century	9.0	0.703	3.2	1.364

[1] Control (not infested) minus aphid infested cages.

[2] Within each column, treatment differences vary significantly from zero at 0.05 (*), 0.01 (**), or 0.001 (***) level of probability, t-test.

Table 18. Linear regressions of various harvest components (Y) on maximum pea aphid densities per plant tip (x) of six caged field pea cultivars at Glenlea (n=8).

Cultivar	Sample Date	Regression Equation	Significance Level (P=)	S.E.$_b$[1]	r^2
a) Number of Pods per Plant:					
Century	Aug 14	Y= 5.144+0.005*x*	0.740	0.014	0.020
Lenca	Aug 8	Y= 4.331+0.000*x*	0.966	0.011	0.000
Tara	Aug 14	Y= 5.752-0.026*x*	0.012	0.007	0.683
Tipu	Aug 8	Y= 4.462-0.010*x*	0.440	0.012	0.102
Trapper	Aug 8	Y= 5.604-0.029*x*	0.001	0.004	0.909
Triumph	Aug 1	Y= 5.484-0.009*x*	0.127	0.005	0.343
b) Weight of Seeds per m row (g):					
Century	Aug 14	Y=79.602-0.200*x*	0.332	0.190	0.156
Lenca	Aug 8	Y=69.477-0.122*x*	0.708	0.311	0.025
Tara	Aug 14	Y=92.087-0.558*x*	0.044	0.219	0.519
Tipu	Aug 8	Y=84.246-0.449*x*	0.043	0.175	0.522
Trapper	Aug 8	Y=51.720-0.295*x*	0.003	0.053	0.861
Triumph	Aug 1	Y=68.307-0.189*x*	0.075	0.088	0.436
c) Weight of 250 Seeds (g):					
Century	Aug 14	Y=55.099-0.061*x*	0.143	0.036	0.322
Lenca	Aug 8	Y=42.724-0.097*x*	0.033	0.035	0.559
Tara	Aug 14	Y=46.665-0.127*x*	0.018	0.039	0.638
Tipu	Aug 8	Y=49.870-0.115*x*	0.003	0.024	0.793
Trapper	Aug 8	Y=27.765-0.043*x*	0.281	0.036	0.226
Triumph	Aug 1	Y=68.305-0.058*x*	0.381	0.061	0.130

[1] S.E.$_b$ = Standard error of the regression coefficient $_b$.

magnitude of slopes, from the steepest slope of Tara to the shallowest slope of Trapper, was not large and t-tests revealed no significant differences among cultivars in the slopes of the regression lines of 250 seed weight. However, the 250 seed weight of Triumph peas was most closely related to aphid density two weeks after the aphid population peaked on this cultivar, as plants reached the pod maturing to drying stages. The regression equation for weight of 250 Triumph seeds upon aphid densities on August 14, $Y=73.34-0.264x$, differed significantly from zero ($d.f.=1,6$, $F=13.00$, $P \leq 0.01$) and had an r^2 value of 0.684. A comparison of the slope of this line with those of the other cultivars at the time of their aphid population peaks revealed no significant differences between its slope and those of the Lenca, Tara or Tipu regression lines.

The most consistent relationship between the harvest components and aphid density was found in the cultivar Tara. This cultivar had the steepest or next-to-steepest slope of the regression lines for all three of the harvest components considered (Table 18).

4. Discussion

Pea aphid populations in infested cages grew more slowly and had their lowest numbers on Century plants while they grew more rapidly and reached their greatest numbers on those of Trapper. These population patterns parallel measurements of A. pisum populations on pea cultivars in open field experiments (Section I) and agree with observations of Maiteki et al. (1986) in commercial fields.

Since the patterns of aphid abundance in this experiment were in general similar to those of the field experiment in Section I, varying levels of predation and parasitism of the aphids in the field can be ruled out as the main cause of differences in aphid abundance among the cultivars. The greater development of A. pisum populations on some cultivars as opposed to others may be due to closer to optimal levels of nitrogenous and other nutritional components in susceptible than in resistant plants (Auclair et al., 1957; Auclair, 1976), although the role of pectins and certain secondary plant compounds in host plant resistance to the pea aphid cannot be discounted (Dreyer et al, 1985, 1987). The relatively low numbers of pea aphids on the cultivar Century (Figure 5, Table 15) may be due to levels of amino acids and other plant nutrients which are lower or in less suitable proportions than levels of such substances in Trapper plants. However, it is difficult to distinguish between dietary deficiencies and sublethal toxic factors in aphid host plants based on their effects on aphid biology. In the present study, while the exact nature of the antibiosis expression was not determined, Century plants clearly demonstrated antibiosis effects on pea aphids.

Tipu supported relatively high numbers of pea aphids in the cage study compared to its position in open field experiments, where it ranked lowest or second to lowest in terms of aphid populations (Section I). Since the rankings of aphid populations on the other pea cultivars were approximately the same on open field and caged plants, altered physiology of caged plants is unlikely to be the primary reason for the change in aphid population ranking on caged as opposed to uncaged Tipu plants. It may be that predators and parasites play a more

important role in pea aphid population regulation on Tipu than on other cultivars; this theory was not tested in the present experiment. Alternatively, Tipu plants, which have leaflets reduced to tendrils, may exert an antixenotic effect on pea aphids, which prefer to feed on plant terminals and leaflets (Lowe, 1971). This antixenotic effect would be inhibited in the cage experiment since aphid migration was suppressed because of the caging.

Aphid species vary in their dependence on phloem pressure in feeding (van Emden and Wearing, 1965); congruently, decreased phloem and turgor pressure in plants may adversely affect an aphid's biology (Risebrow and Dixon, 1987). In this study caged plants of all cultivars became more succulent than uncaged ones; however, Triumph plants appeared least affected by the caging. Had this physiological effect not occurred, Triumph plants, which were normally relatively succulent, may have supported greater numbers of aphids than other cultivars because of the greater difference in succulence between them. In two of three years in the open field experiment, the largest populations of pea aphids occurred on Triumph plants (Section I).

Aphid-induced stress may increase the rate of maturation of peas (Maiteki and Lamb, 1985b; Yencho et al., 1986). In this study Trapper and Triumph plants in infested cages of one block matured and senesced much faster than plants in uninfested cages. A decline in Trapper plant quality preceded the rapid and early pea aphid population decline on this as compared to other cultivars (Figure 5). Plant age significantly affects pea aphid biology (Auclair, 1966; Bintcliffe and Wratten, 1980). In cages, where migration is not an option, density dependent feed-back mechanisms may operate between plants and aphids (Raworth et al., 1984).

Maiteki and Lamb (1985b) reported that pea aphids reached such high numbers in cages of Century plants that plants died prematurely, after which all the aphids died.

Even though there was considerable variation in densities of aphid populations among the cultivars, yield responses of the cultivars to aphid feeding were generally similar, with weight of 250 seeds being the most sensitive measure of aphid feeding in most cultivars. Maiteki and Lamb (1985b), using initial infestation rates of one aphid per caged Century plant at flowering, found significant decreases in total yield and 1000 seed weight but not pods per plant of treatment versus control plants. In an open field experiment, these authors (1985a) found that weight of 1000 Century seeds proved a more precise measure of aphid damage than weight of seeds per unit area. The fact that only three of the six cultivars in the present study had significantly reduced yields per row in infested cages attests to the difficulty in quantifying the effects of aphids on pea plants in small plots.

The results of this study allowed inferences to be drawn about the nature of cultivar yield responses to aphid presence. The decline in 250 seed weight of caged Trapper plants, which had approximately twice the population of aphids on August 8 as Tara, Triumph, Tipu and Lenca plants, was considerably smaller than the decline in seed weight of the latter cultivars (Table 17). This is an indication that Trapper seed weight is not as sensitive to aphid feeding as is this yield component in the other cultivars. Of all the cultivars, the slope of the regression equation of 250 seed weight over aphid densities was shallowest for Trapper in this study (Table 18), as it was in three years of open field experiments (Section I). It should be noted that,

while Trapper may exhibit more tolerance to aphid feeding than the other cultivars in terms of seed weight, it was the only small-seeded cultivar in the experiment. Physiological constraints of small seed size may have been a factor in this differential response to aphid feeding.

It is doubtful that the decline in number of Trapper pods with increasing aphid densities is a unique response of this cultivar; given aphid infestations of a similar magnitude, other cultivars may respond similarly. Tara's significant decrease in number of pods per plant with a medium-sized infestation suggests a heightened response of this cultivar to aphid feeding over that of Tipu, Triumph or Lenca. Maiteki and Lamb (1985b) found that there was no decrease in pods per Century plant when cages were infested with pea aphid densities of up to one per plant at flowering, although a similar infestation during the vegetative stage reduced pod number by 75% or more.

In the present study, the infestation level of pea aphids on caged Century plants at flowering was near the economic threshold of Maiteki and Lamb (1985b), but the subsequent population rise was relatively small and protracted, peaking at pod drying (Figure 5). This delayed infestation may be the reason for the absence of significant yield losses, both per m row and per 250 seed weight, in this as opposed to the other cultivars (Table 17). Had aphid populations on Century reached the same level as quickly as on the other cultivars, yield losses may have been as great as or greater than those of the other cultivars. In 1985 in an open field test pea aphid numbers on subplots of Century rose more rapidly and reached greater levels than in the present caged experiment, and significantly decreased 1000 seed weight was found when infested plots were compared with control plots (Section I). Pea aphid

populations are correlated with reductions in various yield parameters of Century plants, most notably seed weight (Maiteki and Lamb, 1985a, 1985b).

Although they had similar aphid numbers per plant tip in infested cages, there were indications of differences in the responses of Tara, Tipu, Triumph and Lenca under heavy aphid feeding. Unlike those of the other cultivars, seed weights of Triumph were most closely related to aphid densities later in the season than at the time of the aphid population peak. Aphid densities on a plant at any one time are correlated with densities preceding and following that time. The variability in slope of the regression lines of 250 seed weight of Triumph on August 14 as opposed to that of August 1 may indicate that Triumph plants respond to the cumulative effect of aphid feeding over a long period of time; it may be an indication that Triumph pods are more susceptible to aphid feeding than earlier stages of fruiting. The fact that the slope of 250 seed weight of Triumph on the later date was significantly different from that of Trapper at the time of the aphid population peak on this cultivar indicates a greater potential for reduction in seed weight with aphid feeding in Triumph plants. And even though the 250 seed weight of Tipu was most closely related to aphid densities, when considering all yield components, Tara was most consistently influenced by aphid feeding (Table 18).

Thus, this cage study clearly demonstrated differential pea aphid population growth patterns on various field pea cultivars similar to those found in open field studies (Section I). It also indicated that the responses of the cultivars to aphid feeding were in general similar, with reduction in seed yield and seed weight being common to all

cultivars tested. Subtle differences in cultivar response did occur, however. Trapper was not as affected as the other cultivars in terms of seed weight. Triumph was affected later in the season than the other cultivars. The yield components of Tara were the most consistently depressed in the presence of aphids, while the aphid populations on Century did not reach high enough levels early enough in the season to render significant damage to plants of this cultivar.

Section III

Population Growth of the Pea Aphid, Acyrthosiphon pisum (Harris) (Homoptera: Aphididae) and Plant Response to Aphid Numbers in Three Cultivars of Commercially Grown Field Peas in Manitoba.

ABSTRACT

Densities of pea aphids, Acyrthosiphon pisum (Harris), were sampled weekly or biweekly in a survey of commercial plantings of field peas in several regions of Manitoba. In two years a total of nine fields of Century, four fields of Trapper and two fields of Triumph peas were surveyed. Pea aphid populations on the cultivar Trapper tended to rise faster and higher, and decline more sharply than did densities on the other two cultivars. All four Trapper fields were aerially sprayed with insecticides; at the time of spraying, plants in the Trapper fields had greater numbers of aphids on them than plants of the other two cultivars. These differences, estimated by sweep net sampling, were significant in one year. A. pisum numbers per plant tip surpassed the published economic threshold in all fields sampled; however, in Century fields, aphid population increases generally occurred after the most susceptible plant stages of bloom and pod initiation. In both years, plants of Triumph remained green longer than plants of the other two cultivars; in one year pea aphid numbers on this cultivar were highest on the last sampling date. Yield

components were measured in sprayed and unsprayed plots within the commercial fields. When yield results were averaged over cultivars, number of pods per plant increased and number of peas per pod decreased significantly in Century plots which had been sprayed for aphid control. There were no significant yield differences between aphid infested and aphid controlled plots when yields were averaged over Trapper or Triumph fields. On an individual field basis, the field which had the greatest infestation of aphids, a Trapper field in which aphid densities peaked at 48.5 $\pm$9.2 per plant tip during pod formation and filling, had significantly reduced numbers of pods per plant, yield per m^2, and weight of 1000 seeds in unsprayed plots. Significant yield losses occurred in unsprayed plots of a Triumph field which had aphid populations of 4.8 $\pm$1.6 per plant stem at pod maturation. Indications are that the economic threshold of pea aphids on Trapper peas is higher than the economic threshold on Century peas, while Triumph peas are susceptible to pea aphid damage later in the season than plants of the other two cultivars.

1. Introduction

The pea aphid, Acyrthosiphon pisum (Harris), is the most important pest of field and other peas (Duke, 1981). Variations in A. pisum densities have been reported on different cultivars of green peas in Canada (Maltais, 1949; Cartier, 1963). In Manitoba, greater densities of pea aphid were found in one field of Trapper fields peas than in fields of the cultivar Century (Maiteki et al., 1986). The economic threshold of the pea aphid has been estimated on Century crops grown in Manitoba (Maiteki and Lamb, 1985a). It is not known whether other field pea cultivars grown in this province respond to aphid feeding as do plants of Century.

In a survey of 22 Century and 4 Trapper pea fields in Manitoba, pea aphids were found to be chemically controlled in only one Century field (Maiteki et al., 1986). However, some farmers, especially those growing the cultivar Trapper, chemically control pea aphids in two out of three years (A. Dueck, Morris, MB; A. Loewen, Plum Coulee, MB; personal communication). The decision to control pea aphids chemically may be based on such scant information as shaking one pea plant and counting how many pea aphids land in the palm of a hand (R. Ritz, St. Jean, MB, personal communication.) The purpose of this experiment was to determine if pea aphid densities vary in commercial plantings of different field pea cultivars and if pea aphid feeding affects the growth and yield of these cultivars to the same degree.

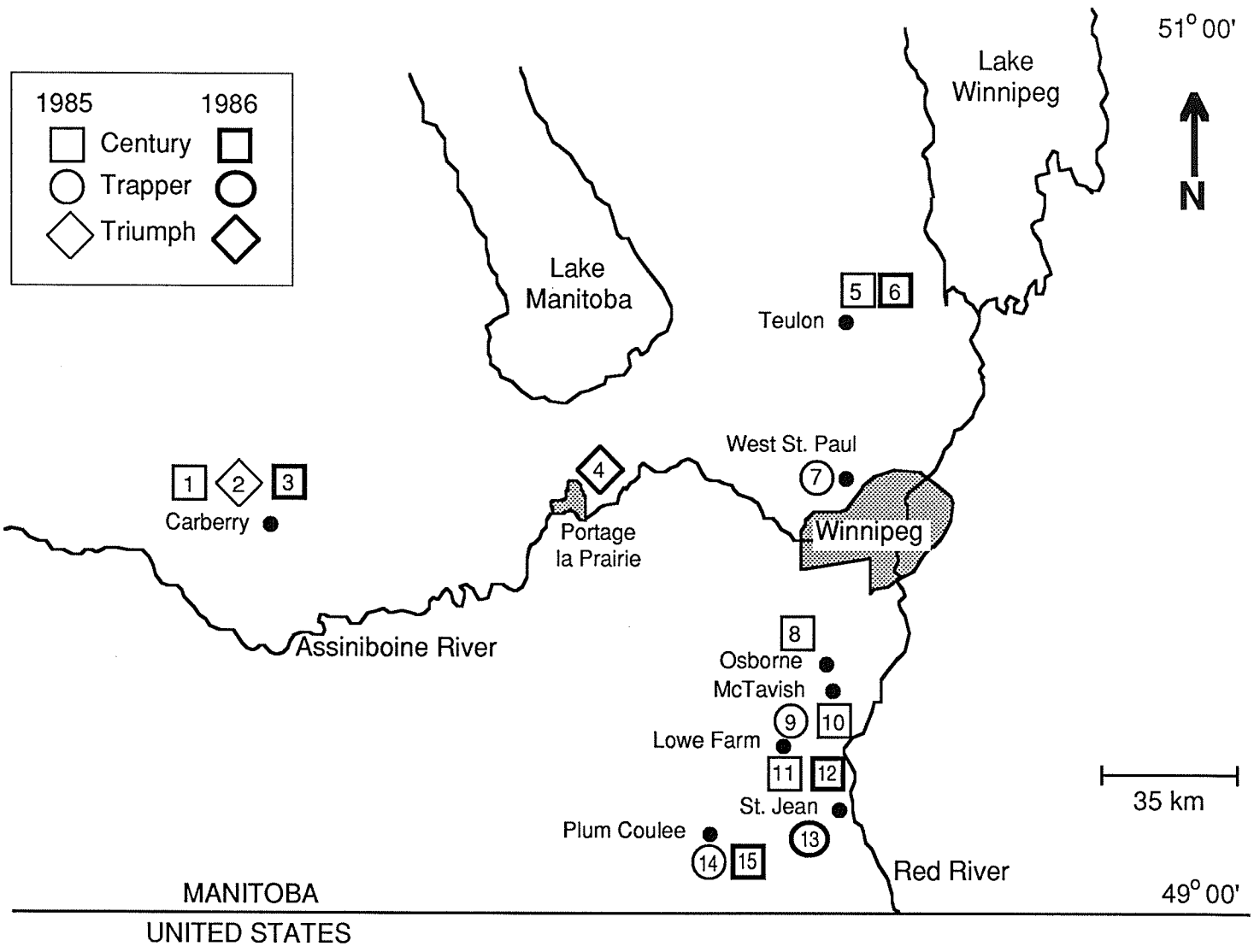
2. Materials and Methods

In 1985 and 1986 sampling for pea aphids in farmer's fields was carried out every 6 to 16 days from the end of June until harvest. In

1985 four fields of Century, three fields of Trapper and one field of Triumph peas were sampled in eight sampling periods; in 1986 five fields of Century, one field of Trapper and one field of Triumph were sampled in seven sampling periods. Pea fields varied from 6 to 105 ha in size and averaged 36.8 ha. Fields were located in the Red River Valley, which is the traditional field pea growing area of Manitoba, in the Interlake Region, where the hectarage of peas is increasing, and in west central Manitoba. Field locations, sizes and cultivars are diagrammed in Figure 6. Fields were sampled in a zig-zag pattern starting 35, 70 or 140 m diagonally from a corner of the field, depending on field size. Twenty sites in each field, 25 or 50 m apart, were sampled at each date. Sweep net and plant tip sampling methods were used. At each site in the field 20 sweeps through an arc of 180° were taken with a 38 cm diameter insect net and the number of pea aphids was counted and recorded. If more than approximately 200 aphids were in the net, its contents were emptied into a plastic bag and sprayed with a synergized pyrethrin insecticide (Raid$^{(R)}$, S.C. Johnson and Sons, Ltd.). The bag was later returned to the laboratory and the number of aphids was determined. Also at each sample site, behind and to the side of each sweep sample, five randomly selected pea plants were examined and the number of aphids in the top 20 cm of the five plant tips was counted. One plant was removed at each of the 20 sites per field per date and the plant height and growth stage was noted.

In each field, when the peas began flowering, two 5x5 m areas, adjacent to but separated from each other by about 10 m, were staked. One of these two plots was randomly selected and sprayed with

Figure 6. Locations and cultivars of field pea fields sampled for pea aphids throughout the summers of 1985 and 1986. Field areas were: 1 - 33 ha; 2 - 11 ha; 3 - 16 ha; 4 - 22 ha; 5 - 33 ha; 6 - 61 ha; 7 - 6 ha; 8 - 67 ha; 9 - 105 ha; 10 - 57 ha; 11 - 57 ha; 12 - 28 ha; 13 - 22 ha; 14 - 10 ha; 15 - 33 ha.


1985
1986
Century
Trapper
Triumph
Lake Manitoba
Lake Winnipeg
51° 00'
N
Teulon
5
6
West St. Paul
7
1
2
3
4
Carberry
Portage la Prairie
Winnipeg
Assiniboine River
8
Osborne
McTavish
9
10
Lowe Farm
11
12
St. Jean
13
Plum Coulee
14
15
35 km
Red River
MANITOBA
UNITED STATES
49° 00'

malathion 500 EC at 750 g a.i./ha using a backpack sprayer to control pea aphid numbers. On subsequent sample dates the 20 cm tips of ten plants from each staked plot were examined and the number of aphids per single plant tip was recorded. Staked plots were located near field edges and/or windbreaks to maximize aphid densities in them and to minimize the impact of aerial spraying if the farmer chose to spray for aphid control.

All four of the Trapper fields surveyed in the two years were aerially sprayed with dimethoate when pea aphid populations started to climb; sampling was discontinued in three of these fields after this time. In 1985 one 2 ha section of the field located near West St. Paul was not sprayed because of its proximity to hydroelectric lines and dwellings. When surveying this field, we initially sampled ten sites in the main part of the field and ten in the sheltered area. After aerial spraying, sampling of the main part of the field was discontinued but sampling of the sheltered area continued until harvest. The staked plots were also located in this area and aphid populations in them appeared minimally affected by the aerial spraying. In two of the other three fields of Trapper peas surveyed, one located near Plum Coulee in 1985 and the other near St. Jean in 1986, the staked plots which had not been hand-sprayed were covered with tarpaulins prior to aerial spraying so that they remained insecticide-free. Aphids in both the sprayed and unsprayed staked plots in the Trapper field near McTavish in 1985 were killed by the aerial spray.

At harvest the number of plants from five randomly selected 1 m^2 samples in 1985 and from ten 1 m^2 samples in 1986 in each of the sprayed and unsprayed staked plots in each field were counted and

clipped at soil level. The height of one plant from each m^2 sample was measured and the entire sample was bagged and returned to the laboratory. After the samples were dried, an average number of pods and aborted pods per stem of 30 (1985) or 10 (1986) stems, an average number of peas per pod of 30 pods, the total weight of peas and the weight of 1000 peas were recorded from each m^2 sample in each sprayed or unsprayed plot.

For each year's data the densities of aphids on each cultivar in the sample period just prior to aerial spraying of Trapper fields were compared by analysis of variance using the general linear model of SAS (SAS, 1985). Sweep net and plant tip counts were transformed by $\sqrt{x + 0.05}$ to stabilize variances. The means of harvest data were normally distributed and these data were not transformed. One way analyses of variance were conducted on means of harvest data from individual fields; two way ANOVA's were conducted on means combined over cultivars, using spray treatments and fields as the classes. Analyses of covariance were used to adjust means when significant differences were found in number of plants per treatment. Linear regression (y=a+bx) of yield parameters (y) against aphid numbers at the time of maximum numbers of aphids per plant tip in unsprayed plots was conducted for each pea cultivar.

3. Results

3.1 Aphid Numbers

3.1.1 Aphid Populations in Entire Fields

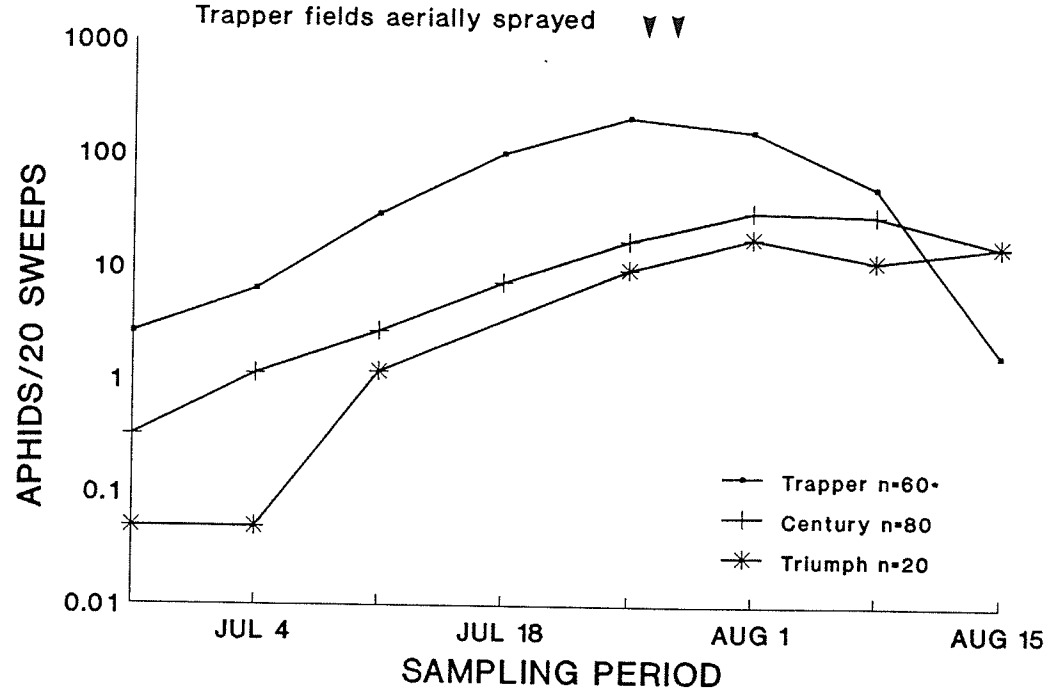
In 1985 pea aphid numbers were of greater magnitude and rose and declined more quickly in fields of the cultivar Trapper than in fields of the other two cultivars (Figure 7a and b). Aphid numbers over the three Trapper fields peaked at 220.7 ±29.0 per 20 sweeps by July 25, when plants were in the late flowering to early pod developing stages and, in the field not completely aerially sprayed, declined to very low levels by August 20. Numbers of aphids on Trapper plant tips surpassed the published threshold of 2 to 3 aphids per plant tip (Maiteki and Lamb, 1985a) (10 to 15 aphids per 5 plant tips) at about July 18; by July 25, shortly before the fields were aerially sprayed, aphid numbers had reached 68.4 ±10.1 per 5 plant tips.

A. pisum numbers peaked around August 1 at 31.3 ±4.5 aphids per 20 sweeps of Century plants. The maximum number of 24.2 ±2.6 aphids per 5 Century plant tips was reached on August 8, when plants were in the pod maturing stage. Aphid numbers on Triumph plants reached their maximum of 15.8 ±1.7 aphids per 20 sweeps or 14.2 ±2.7 aphids per 5 plant tips on August 15, at which time pods were maturing.

In 1986 differences in aphid population densities among the cultivars were not as clear as in 1985 (Figure 8a and b). On July 27 only 1 site, rather than 20, was sampled in the Trapper field near St. Jean prior to aerial spraying; however, indications were that A. pisum populations in this field were the highest of any field

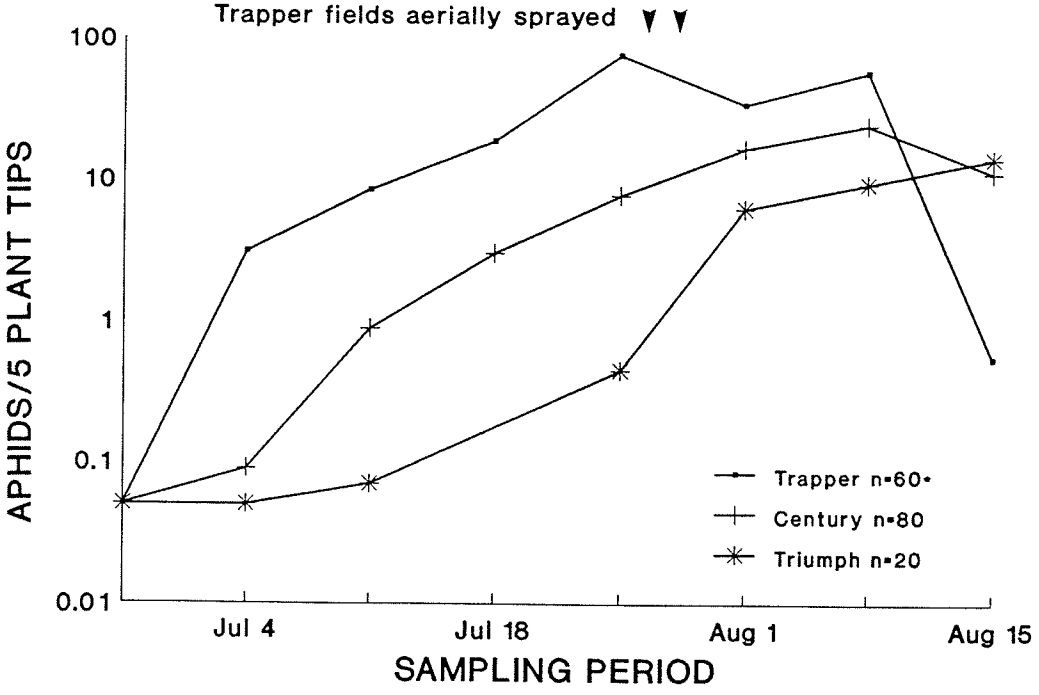
Figure 7. Mean numbers of pea aphids per a) 20 sweeps and per b) 5 plant tips of three cultivars of field peas from eight locations in Manitoba sampled in the same four day period over the summer of 1985. Coefficients of variation were 23 to 115 and 20 to 154 for sweep and plant tip sampling, respectively.

a) SWEEP SAMPLING



* after aerial spraying n=10

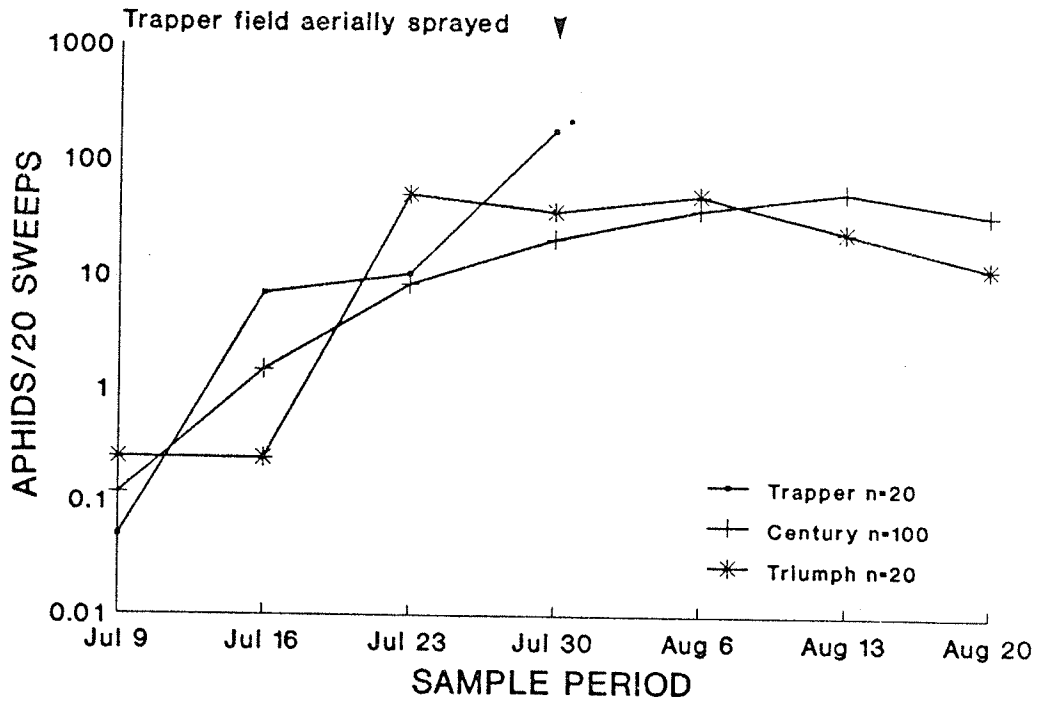
b) PLANT TIP SAMPLING



* after aerial spraying n=10

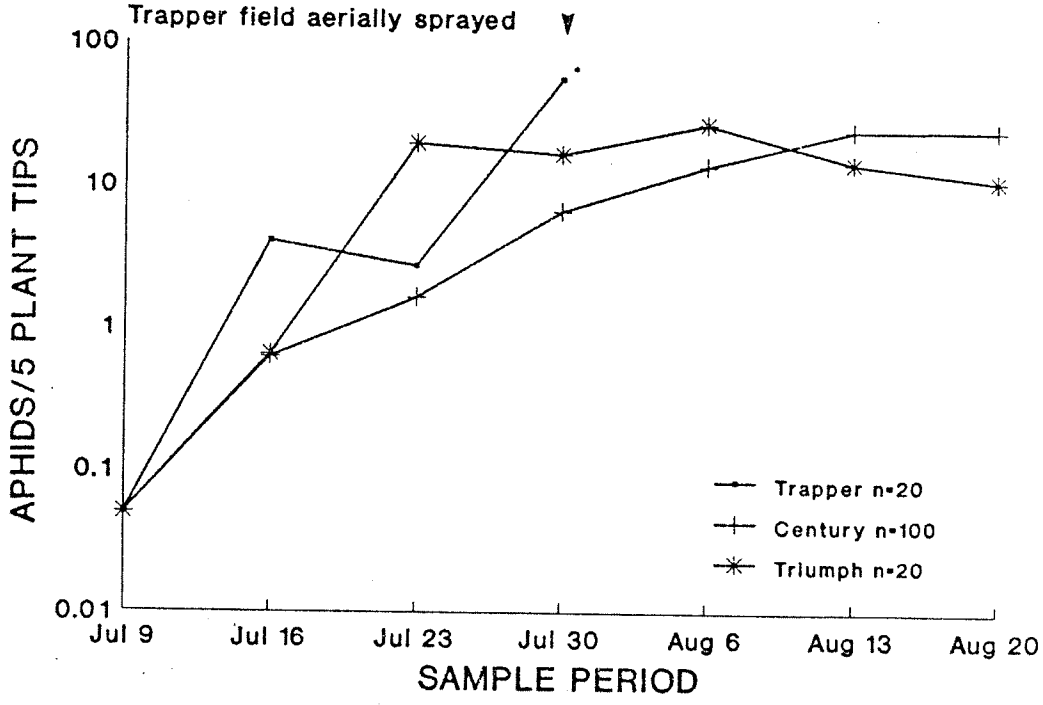
Figure 8. Mean numbers of pea aphids per a) 20 sweeps and per b) 5 plant tips of three cultivars of field peas from seven locations in Manitoba sampled in the same four day period over the summer of 1986. Coefficients of variation were 33 to 165 and 62 to 199 for sweep and plant tip samples, respectively.

a) SWEEP SAMPLING



• one sample only

b) PLANT TIP SAMPLING



• one sample only

sampled in this period. This Trapper field experienced two germination flushes, so that when the one sample, 184 aphids per 20 sweeps or 56 aphids per 5 plant tips, was taken, plants varied from late vegetative to mature pod development. In 1986 pea aphid numbers on plants of Triumph peas were similar to but somewhat greater than the numbers on Century plants for much of the season. The maximum aphid density on Century plants, 54.3 $\pm$9.1 aphids per 20 sweeps or 24.7 $\pm$4.7 aphids per 5 plant tips, occurred at the August 13 sampling period, when most plants were in the mature pod stage. Maximum aphid numbers in the Triumph field, 50.8 $\pm$7.2 per 20 sweeps or 27.6 $\pm$7.2 per 5 plant tips, occurred on August 6, when plants were in the pod elongating to filling stages. On this sampling date a local concentration of diseased, dead aphids was found. On the subsequent sampling date, August 13, the aphid population was in decline, with 13.2% of the total number of aphids in the nonsprayed staked plot found dead, apparently from disease. This disease level was the highest recorded in any of the fields in the two years.

In an analysis of variance of pea aphid populations among cultivars in the sample period preceding aerial spraying of Trapper fields, variation was attributed to cultivar and field, with fields within cultivars as the error term. In 1985 there were significantly more aphids in sweep net samples of the three Trapper fields than in the four Century fields or one Triumph field (d.f.=152, F=8.74, $P \leq 0.05$) (Table 19). There were also considerable but not significant differences among cultivars in numbers of aphids on plant tips.

In 1986 aerial spraying of the Trapper field on July 25 coincided with sampling and prevented its completion, so that the aphid

Table 19. Mean number (± S.E.M.) of pea aphids on plants of three cultivars of field peas in Manitoba sampled just prior to aerial spraying of Trapper fields (n per field = 20).

Year	Cultivar	No. of Fields	Mean No. of Aphids Per 20 Sweeps	Mean No. of Aphids Per 5 Plant Tips
1985	Trapper	3	220.7 ±29.0 a[1]	68.4 ±10.1 a
	Century	4	20.4 ± 2.4 b	7.4 ± 1.5 a
	Triumph	1	9.6 ± 2.4 b	0.4 ± 0.4 a
1986	Trapper	1[2]	10.2 ± 4.6 b	2.7 ± 1.6 b
	Century	5	8.3 ± 2.9 b	1.6 ± 0.5 b
	Triumph	1	50.7 ±12.2 a	19.8 ± 5.8 a

[1] Means within the same section followed by the same letter are not significantly different ($P \leq 0.05$; Duncan's multiple range test).

[2] Sampled one week prior to aerial spraying.

population data from Trapper plants used in the analysis were the low figures from the previous week's sample (Figure 8). Both sampling methods revealed significant differences in aphid populations among cultivars in 1986, with the Triumph field supporting a larger population of pea aphids than the Trapper or Century fields (d.f.=133, sweep sampling $F=13.33$, $P\leq0.05$, plant tip sampling $F=44.23$, $P\leq0.01$).

3.1.2 Aphid Populations in Staked Plots

Plants in the unsprayed staked plots had pea aphid numbers which surpassed the published economic thresholds of 2 to 3 aphids per plant tip at all 15 locations surveyed (Table 20). All four of the Trapper fields had plants in the susceptible bloom to pod initiation stages of growth when pea aphid populations surpassed 2 to 3 per plant tip. On the other hand, most of the Century fields had the majority of plants beyond these stages when pea aphid populations surpassed the economic threshold. This level of aphid infestation was reached about one week later in most Century fields than in most Trapper fields. In 1985, the Triumph field near Carberry had plants in the pod maturation stage when the numbers surpassed 2 to 3 per plant tip on August 9. In 1986, Triumph plants near Portage la Prairie were mainly flowering when these numbers were reached on July 31 (Table 20).

Aphid control in the adjoining sprayed plots was generally good, with eight of the 15 plots never reaching densities greater than three per plant tip, and five plots surpassing this level at plant maturation or later. In 1985 the sprayed site in the Century field near Lowe Farm had a maximum of 8.5 ± 3.9 aphids per plant tip on August 7, when pods were filling to maturing; plants in the sprayed site in the Century

Table 20. Maximum densities (± S.E.M.) of pea aphids per plant tip in unsprayed staked plots in fields of three different field pea cultivars and the date and plant stage at which densities surpassed 2 - 3 aphids per plant tip.

Field	Cultivar	Maximum[1] Density	Densities > 2 to 3 Per Plant Tip: Date	Plant Stage[2]
a) 1985				
Carberry	Century	13.0 ±3.5	Aug 1	R_3 - R_4
Lowe Farm	Century	5.8 ±1.8	Aug 7	R_4 - R_5
Osborne	Century	6.0 ±2.0	Aug 8	R_3 - R_4
Teulon[3]	Century	6.9 ±3.3	Jul 30	R_2 - R_3
Plum Coulee	Trapper	48.5 ±9.2	Jul 18	R_2 - R_3
McTavish[4]	Trapper	12.0 ±3.1	Jul 25	R_2 - R_3
West St. Paul	Trapper	9.4 ±3.5	Jul 24	R_2
Carberry	Triumph	4.8 ±1.6	Aug 9	R_5
b) 1986				
Carberry	Century	18.9 ±4.4	Aug 7	R_5
Lowe Farm	Century	13.3 ±4.1	Aug 5	R_4 - R_5
McTavish	Century	6.6 ±1.7	Jul 30	R_4
Plum Coulee	Century	28.6 ±12.1	Aug 5	R_6
Teulon	Century	5.6 ±5.6	Aug 6	R_5
St. Jean	Trapper	7.4 ±2.0	Aug 1	Veg/R_5[5]
Portage La Prairie	Triumph	15.9 ±5.2	Jul 31	R_2

1 No. aphids/plant tip.

2 Veg = vegetative; R_2 = flowering; R_3 = pod formation and enlargement; R_4 = pod swelling and filling; R_5 = pod maturing; R_6 = pod drying.

3 Field not harvested.

4 Prior to aerial spraying.

5 Two germination flushes about 3 weeks apart.

field near Osborne in 1985 had a maximum of 3.3 ±2.3 A. pisum per plant tip on July 31, as pods were developing to filling.

Trends in aphid numbers among cultivars were similar in staked unsprayed plots as they were in whole fields. In 1985, maximum A. pisum numbers were highest in the unsprayed Trapper plots, at 23.3 ±4.7 (n=30) aphids per plant stem at about flowering to pod formation. Maximum numbers of aphids on Century plant tips in unsprayed plots averaged 7.9 ±1.4 (n=40) at pod fill to maturity, while aphids on Triumph numbered 4.8 ±1.6 (n=10) at pod maturation. In 1986, the mean maximum aphid numbers per Trapper plant tip were 7.5 ±2.0 (n=10) at blooming to pod maturity, 14.6 ±3.1 (n=50) per Century plant tip at pod fill to maturity, and 15.9 ±5.2 (n=10) per Triumph plant tip at blooming to pod development. None of these differences, however, were statistically significant. Although the unsprayed plots in three of the four Trapper fields were in some way protected when the fields were aerially sprayed, pea aphid populations in these plots may have been detrimentally affected by the spraying procedure or the subsequent decimation of the surrounding aphid population.

3.2 Harvest Results

In 1985 the Century pea field near Teulon was ploughed as a green manure crop and no samples were harvested from it. In both years, plants and pods of Triumph stayed green longer than those of the other two cultivars; in 1985 the Triumph field near Carberry was aerially sprayed with a desiccant on August 13 to hasten pod drying.

Metre square samples from the staked plots of the most southerly located fields, those near Plum Coulee, were harvested earliest, on

August 12, 1985, and on August 16, 1986. Wet weather prolonged completion of harvest operations of other fields to September 25, 1985, while the drier autumn of 1986 facilitated harvest, undertaken, apart from the Plum Coulee location, from September 2 to 15.

When harvest data were compared on an individual field basis, analysis of variance indicated that there were significant differences in plant stand densities between treatments at fields near Lowe Farm and West St. Paul in 1985 (Table 21). Causes of differences in stand densities between treatments at these two sites were not apparent. Analyses of covariance were performed on data from these locations, with plant stand density as the covariate term. Stand density did not significantly covary with other harvest parameters at either location.

The yield component most consistently affected by spray treatment was number of pods per plant, which significantly increased in five sprayed plots of Century and one Trapper over their unsprayed counterparts, and decreased in the sprayed Trapper plot near St. Jean (Table 21). Under the extremely heavy feeding pressure of pea aphids in the Trapper field near Plum Coulee in 1985 (Table 20), weight of peas per m^2 and weight of 1000 peas were also significantly higher in the sprayed plots; this was so even though peas had reached the pod development to fill stages when the economic threshold was reached.

At the Plum Coulee site in 1986, sprayed samples had significantly greater numbers of pods and aborted pods per plant, fewer peas per pod, heavier seeds and taller plants than their unsprayed counterparts (Table 21). Although the maximum aphid density in the unsprayed plot was ten times the published economic threshold, this maximum occurred as pods were mature and starting to dry, with aphid numbers being very

Table 21. Means (± S.E.M.) of harvest components of individual pea fields in which plots were sprayed (treatment SP) or were not sprayed (treatment NS).

Location	Cultivar	Trt	No. Plants/m^2	No. Pods/Plant	No. Abpods /Plant[1]	No. Peas/Pod	Weight/m^2 (g)	Weight/ 1000 seeds(g)	Height (cm)	n
a) 1985										
Carberry	Century	NS	65.6±7.3	*4.64±0.17[2]	1.02±0.05	3.89±0.15	386.0±32.5	233.7±2.5	133.3± 4.5	5
		SP	59.8±4.0	*5.56±0.28	0.36±0.08	4.24±0.11	370.7±17.2	231.0±3.7	143.3± 4.2	5
Lowe Farm	Century	NS	**106.6±9.3	*3.80±0.29	0.68±0.05	4.21±0.15	333.6±15.1	200.1±4.9	127.7± 5.1	5
		SP	** 81.8±5.1	*5.58±0.34	0.82±0.07	4.12±0.21	410.9±46.9	199.2±4.2	136.6± 4.6	5
Osborne	Century	NS	52.0±1.3	4.92±0.21	1.30±0.13	4.76±0.09	316.1±10.3	187.9±3.5	138.3± 8.2	5
		SP	52.4±2.3	5.10±0.48	1.34±0.17	4.51±0.19	361.4±35.5	190.1±3.2	126.3± 4.3	5
Plum Coulee	Trapper	NS	91.0±3.1	*4.82±0.19	1.74±0.09	3.70±0.13	**264.3± 4.8	**102.9±1.2	119.9± 5.0	5
		SP	85.2±6.6	*5.62±0.15	1.70±0.10	3.81±0.14	**331.9±18.7	**114.1±1.0	126.0± 2.6	5
McTavish	Trapper	NS	84.8±7.2	5.24±0.36	1.64±0.39	3.94±0.11	327.5±24.5	105.8±0.7	122.0± 6.6	5
		SP	78.4±7.6	5.24±0.26	2.32±0.34	3.73±0.14	287.8±42.3	108.3±1.8	126.4±11.1	5
West St. Paul	Trapper	NS	*68.6±5.2	4.66±0.12	1.46±0.19	4.46±0.39	278.0±21.0	120.0±2.9	102.9±12.0	5
		SP	*98.0±4.4	4.56±0.26	1.00±0.18	3.63±0.12	226.7±29.6	108.6±3.7	84.1± 9.8	5
Carberry	Triumph	NS	52.2±2.1	3.30±0.10	0.72±0.04	3.66±0.07	*258.2±16.2	241.7±3.1	73.0± 1.2	5
		SP	56.2±2.0	3.46±0.07	0.62±0.06	3.65±0.06	*318.7±15.7	246.9±1.5	76.3± 2.6	5

1 Abpods = aborted pods, those missing or with no marketable peas.
2 Difference between means of each treatment per location are significant at * P = 0.05 or ** P = 0.01 level of probability (ANOVA).

Table 21. (Cont'd) Means (± S.E.M.) of harvest components of individual pea fields in which plots were sprayed (treatment SP) or were not sprayed (treatment NS).

Location	Cultivar	Trt	No. Plants/m^2	No. Pods/Plant	No. Abpods /Plant[1]	No. Peas/Pod	Weight/m^2 (g)	Weight/ 1000 seeds(g)	Height (cm)	n
b) 1986										
Carberry	Century	NS	78.7±2.7	6.19±0.18	2.04±0.17	2.94±0.15	195.9±20.6	175.4±3.12	202.0± 6.8	10
		SP	74.1±3.2	6.78±0.20	2.44±0.22	2.98±0.12	204.3±21.6	181.4±2.47	198.4± 6.4	10
Lowe Farm	Century	NS	79.5±4.8	5.69±0.25	*2.81±0.26	4.06±0.17	237.6±30.9	186.7±4.60	148.4± 8.6	10
		SP	71.4±3.5	5.99±0.27	*3.51±0.18	3.60±0.19	196.7±24.5	177.8±2.97	138.0± 7.8	10
McTavish	Century	NS	92.7±3.8	**2.55±0.15	1.91±0.15	3.44±0.09	125.6± 7.4	196.9±2.78	113.8± 5.6	10
		SP	85.1±6.3	**3.52±0.22	2.17±0.14	3.27±0.11	124.8±12.7	194.3±1.75	116.8± 5.5	10
Plum Coulee	Century	NS	38.8±3.3	**5.38±0.30	**1.74±0.14	**4.26±0.10	200.8±20.2	**149.6±2.70	*109.8± 9.0	10
		SP	41.9±2.5	**6.69±0.11	**2.48±0.14	**3.44±0.14	232.0±19.1	**165.5±2.00	*134.9± 8.0	10
Teulon	Century	NS	58.6±2.6	6.25±0.16	**2.07±0.20	3.20±0.08	297.8±19.6	**186.7±2.60	146.6± 7.0	10
		SP	60.1±3.1	6.69±0.24	**3.06±0.19	3.16±0.14	257.6±13.8	**172.1±1.31	158.8± 5.2	10
St. Jean	Trapper	NS	46.1±3.8	*7.78±0.29	5.99±0.24	3.68±0.18	162.6±16.8	97.9±1.51	162.7±10.7	10
		SP	49.5±3.2	*6.72±0.26	5.67±0.28	3.31±0.13	195.4±29.2	102.2±2.49	156.0±12.3	10
Portage la Prairie	Triumph	NS	47.8±3.4	7.64±0.47	4.65±0.22	3.74±0.10	328.4±34.7	281.3±4.37	101.0± 6.8	10
		SP	48.0±2.9	6.86±0.36	4.58±0.17	3.84±0.11	300.7±17.3	286.5±3.11	114.4± 4.8	10

1 Abpods = aborted pods, those missing or with no marketable peas.
2 Difference between means of each treatment per location are significant at * P = 0.05 or ** P = 0.01 level of probability (ANOVA).

low before this time. This fact, as well as the fact that plant height, a growth characteristic not normally influenced by aphid feeding, was affected, suggests that the yield differences between the two treatments were more a reflection of site variability than aphid damage. The unsprayed site was very close to a field edge and may have been differentially affected by this proximity.

The sprayed plot in the Triumph field near Carberry in 1985 had a significantly greater weight of peas per m^2 than the unsprayed plot; seed weights were also heavier in the sprayed plot, although not significantly so. When aphid numbers surpassed 2 to 3 per plant tip, the pods were in the maturation stage. On the other hand, no significant differences were found in harvest components of the Triumph plots near Portage la Prairie in 1986, even though the published economic threshold in the unsprayed plot was surpassed at flowering (Table 20).

When data from the fields of each cultivar were combined, there were no significant differences between spray treatments in analysis of variance of yield components of Trapper and Triumph peas. However, plants in the spray treatments of both cultivars tended to have increased weights both per m^2 and per 1000 seeds (Table 22). Despite this tendency, none of the linear regressions of harvest components over number of aphids were significant in either cultivar.

In Century peas, however, there were significantly greater numbers of pods per plant and aborted pods per plant in the sprayed plots than in plots which were not sprayed (Table 22). Regression analyses of data combined over both years indicated that the number of

Table 22. Means (± S.E.M.) of harvest components of commercial field pea plots in which pea aphid densities were (treatment SP) or were not (treatment NS) controlled, combined for each cultivar over 1985 and 1986.

Cultivar	Treatment	No. Plants/m^2	No. Pods/Plant	No. Abpods /Plant[1]	No. Peas/Pod	Weight/m^2 (g)	Weight/ 1000 seeds(g)	Height (cm)	n
Century	NS	70.8±2.9	**5.04±0.18[2]	*1.86±0.01	3.75±0.08	242.4±12.1	185.6±2.8	141.5±4.5	65
	SP	66.1±2.2	**5.81±0.16	*2.33±0.12	3.52±0.08	244.1±13.0	184.8±2.3	146.2±3.9	65
Triumph	NS	49.3±2.4	6.19±0.63	3.34±0.52	3.72±0.07	305.0±24.9	268.1±5.8	91.7±5.7	25
	SP	50.7±2.3	5.72±0.49	3.26±0.51	3.78±0.08	306.8+12.5	273.3±5.4	101.7±5.8	25
Trapper	NS	67.3±4.5	6.06±0.32	3.36±0.72	3.89±0.72	239.0±16.1	104.9±1.8	134.0±7.0	15
	SP	72.1±4.6	5.78±0.21	3.27±0.43	3.56±0.08	247.4±18.7	107.1±1.5	129.7±7.7	15
Pooled S.E.		3.7	0.24	0.18	0.13	20.9	2.6	7.0	

1 Abpods = aborted pods, those missing or with no marketable peas.
2 Difference between means of each treatment per cultivar are significant at * P = 0.05 or ** P = 0.01 level of probability (ANOVA).

pods per Century plant were negatively correlated with aphid densities, although not significantly so at the time of peak aphid populations.

Along with a greater number of pods, there was a reduced number of peas per pod in the sprayed plots of Century; number of peas per pod increased with increasing pea aphid densities according to the function $Y=3.41+0.1085x$, $r^2=0.27$, $n=16$, $P\leq 0.05$, for the August 7 sampling period. The decreased numbers of peas per pod tended to offset the increased number of pods per sprayed Century plant so that weights, both per m^2 and per 1000 seeds, were very similar between treatments in the two years (Table 22).

Location by spray treatment interactions in the ANOVA of the data in Table 22 were significant ($P\leq 0.01$) for all harvest components, attesting to the variability inherent in the locations. Various factors may have differentially influenced plant growth and yields between sprayed and unsprayed staked plots. These include uneven crop maturity due to site (Plum Coulee, 1986), variable pea disease infestations (Carberry, 1986), more volunteer cereals in and near the sprayed site than in the unsprayed site (Portage la Prairie, 1986), rodent infestation in the sprayed site (McTavish, 1986), and a double germination of peas (St. Jean, 1986).

4. Discussion

The greater number of pea aphids found in commercial plantings of Trapper field peas than in Century field peas in Manitoba corresponds with results from small test plots (Section I). This difference would have been even larger had aerial spraying not destroyed most of the aphids in the Trapper fields as their populations were rising.

Because fields used in the first year were often not close to the ones used in the second year, location and year were partly confounded. Therefore, how much of the aphid population increase on Trapper as opposed to Century or Triumph plants was attributable to cultivar effects and how much to other factors is not entirely certain. The aphid population figures for the Trapper field in 1986 used in the analysis were from the week preceding spraying. Aphid populations can build up very rapidly in pea fields (Figure 2; Maiteki and Lamb, 1985a). The fact that pea aphid populations were significantly greater on Trapper than Century or Triumph plants in commercial fields in 1985, the large number of aphids in the one sample taken prior to aerial spraying of the Trapper field in 1986, and other evidence (Sections I, II) indicates that, in general, Trapper fields support larger aphid populations than Century fields in Manitoba.

Both whole field and plot plant tip sampling confirmed sweep net findings, although results using plant tips were not significant for either year (Tables 19, 20). In a comparison of methods of sampling alfalfa fields for arthropod populations, the sweep net was found to be an excellent tool for locating light and unevenly distributed insect populations (Fenton and Howell, 1957). Pea aphids generally exhibit a clumped or contagious distribution pattern (Baumgaertner et al., 1983; Maiteki and Lamb, 1987). Thus the lack of significant differences in aphid numbers among cultivars when sampled by plant tip, especially in the staked plots where the number of plants sampled was only ten per treatment per date, was more a reflection of sampling procedure than lack of population differences. Maiteki and Lamb (1987) determined that the decision to control pea aphids chemically should be based on the

aphid numbers found in a sample of at least 20 plant tips, sampled along four well-spaced transects in a field.

The seasonal pattern of abundance of pea aphids on Century peas was generally similar to that reported by Maiteki et al. (1986) on Century peas in southern Manitoba. However, the population decline in August was not as rapid in the present study as the decline reported by these authors. Pea aphid populations decrease rapidly in the late summer because of such factors as migration from hosts of deteriorating quality, and increased predation, parasitism and disease (Cooke, 1963; Hutchison and Hogg, 1985). In this study, no extensive buildup of predators or parasites was observed, although several fields had considerable numbers of diseased aphids by the end of the season. The July and August precipitation in most areas of Manitoba in the course of this study was considerably greater than that of the three years of the study of Maiteki et al. (1986). The rate of plant senescence and aphid migration from the fields may have been slower in this study than in the earlier work.

The seasonal A. pisum population on Trapper plants peaked earlier and declined more rapidly than on Century plants (Figures 7, 8). Laboratory tests indicate that rather than a greater preference, pea aphids have a more rapid developmental rate and greater fecundity on plants of this cultivar than on Century plants (Section IV).

Care should be taken when attempting to draw conclusions about pea aphid populations in commercial Triumph fields, since only one field of Triumph was sampled in each of the two years. However, the high population of A. pisum on Triumph late in the 1985 season as compared to populations on the other two cultivars may be associated

with the tendency of Triumph plants to remain green later in the year than plants of other cultivars. This tendency has also been observed by growers of the cultivar (N. Arbuckle, B.C. Pea Processors Ltd., Portage la Prairie, MB, personal communication). In a comparison of pea aphid numbers on several cultivars in small field plots, Triumph supported the largest population of pea aphids on the last sampling date of the season in two out of three years (Section I, Appendix 3). The occurrence of extensive A. pisum mortality apparently due to disease caused this pattern of elevated aphid numbers late in the year to be absent from the Triumph field sampled in 1986. Further sampling is necessary to confirm the generality of this population pattern in Triumph fields.

In this survey, while aphid populations were above the published economic threshold for Century peas in all fields, aphid population increases in Century fields generally occurred after pods were starting to enlarge and fill. Since Century peas are most vulnerable to aphid damage for a two- to three-week period beginning at pod formation (Maiteki and Lamb, 1985b), significant yield decreases in unsprayed versus sprayed Century plots were not expected and did not occur (Table 22). At densities above the economic threshold, A. pisum reduces the number of pods per plant and peas per pod in Century plants (Maiteki and Lamb, 1985b). In the present investigation, the compensatory increase in the number of peas per pod in infested plots may be a result of the general lateness of the aphid population increase. As the season progresses, pea aphids frequently aggregate and feed on young pods (unpublished observation). This feeding may cause some pods to shrink, malform or abort (Harrington and Searls,

1940). In the process, photosynthate may be diverted to unattacked pods, resulting in the development of more or larger peas. Decreasing the number of pods per pea plant may result in better fruit set (more peas per pod) and larger seeds (Tammes, 1961). If the population increase of A. pisum is early in the season, most flowers and pods will be affected, the number of peas per pod as well as the number of pods per plant will decrease, and yield losses will occur (Maiteki and Lamb, 1985b).

The harvest results indicate that the economic threshold of pea aphids on Trapper plants may be considerably higher than the two to three aphids per plant tip of Century. Pea aphid densities in both Trapper fields near Plum Coulee and West St. Paul were slightly over 9 per plant tip at blooming and pod formation. In the former field the population rose to a maximum of 48.5 $\pm$9.2 aphids per plant tip at pod fill and significant yield decreases were found, while in the latter the aphid population declined after flowering and no yield depression occurred. There is some evidence of tolerance of Trapper plants to feeding by A. pisum (Section IV). Although there was a trend toward reduced seed weight and yield per m^2 with the relatively higher number of aphids in Trapper as opposed to Century fields (Table 22), these yield reductions were not significant and could not be exclusively related to aphid number.

The harvest results from the two fields of Triumph peas were contradictory. If the economic threshold of Century (Maiteki and Lamb, 1985a) is valid for Triumph plants, the low densities of aphids at flowering in 1985 meant that a yield decrease should not have occurred, but it did; while the high aphid densities in 1986 should have affected

yields, but did not (Table 20). Research from small field plots indicates that Triumph plants are susceptible to pea aphid feeding injury later in the season than Century plants (Sections I, II). The lack of significant yield differences in Triumph plots in 1986 may be due to the fact that, while aphid numbers in the sprayed plot remained low for much of the season, at pod maturation they reached 4.9 per plant tip and surpassed densities on unsprayed plants. Thus it appears that, while the economic threshold of pea aphids on Triumph plants may not differ greatly from that of Century plants, the critical period for pea aphid control in plantings of Triumph extends to pod maturation.

The fact that location by treatment interactions were significant for all harvest components was not unexpected, considering the variety of agronomic practices and philosophies of the farmer co-operators involved. However, it is difficult to determine what components of each location contributed to experimental variability. Latitude may be an important determinant of aphid population growth. In this study, fields in southern areas of the Red River Valley tended to have higher A. pisum populations than fields in the Interlake region, 200 km to the north.

Maiteki and Lamb (1985a) point out that their economic threshold of 2 to 3 aphids per plant tip at bloom is a dynamic one, influenced by crop price, control costs, and seed weight, which in turn is affected by weather. Based on the number of aphids on Century plants and the plant yields obtained, there is no evidence in this study to refute these authors' economic threshold. However, in the cultivar Trapper, aphid numbers at bloom in the order of 3 to 4 times that of the Century

economic threshold had variable effects on yield; thus the pea aphid economic threshold on this cultivar may be considerably higher than that on Century. Pea aphid numbers lower than those found on Century in this study caused yield decreases in Triumph plants and it may be that this cultivar is more sensitive to aphid feeding or, at least, is sensitive later in the growing season than is Century. However, this conclusion is tentative and more sampling should be done in commercial Triumph fields to confirm it.

In practical terms, because aphid populations build up quickly in Trapper fields, farmers should monitor for high aphid populations earlier in the season in Trapper than in Century fields. Because Triumph appears susceptible to injury later than the other two cultivars, sampling for A. pisum should continue in this cultivar at least until pod maturation.

Section IV

Antibiosis, Antixenosis, and Tolerance to Pea Aphids, Acyrthosiphon pisum (Harris) (Homoptera: Aphididae), in Cultivars of Field Peas.

Abstract

Life tables, host preference, and tolerance tests were used to assess the resistance to pea aphid, Acyrthosiphon pisum (Harris), of six cultivars of field peas in the laboratory. Antibiosis resistance in the cultivars Tipu and Century was expressed chiefly as decreased aphid fecundity and longevity, since differences in developmental rates of aphids among cultivars was not great. Although differences in the net reproductive rate were considerable, there were only slight differences in the aphids' intrinsic rate of increase, r_m, among cultivars. At 10 days after infestation, Tipu exhibited the most and Triumph the least antixenotic resistance. At 20 days, Triumph was still the preferred cultivar. The cultivar Trapper, on which aphids had the greatest r_m value, appeared to have some tolerance to aphid feeding.

1. Introduction

The mechanisms of host plant resistance are antibiosis, comprised of plant factors detrimental to an insect's biology, antixenosis, comprised of plant factors which decrease an insect's acceptance of the plant as host, and tolerance, comprised of plant factors which enable the plant to withstand or recover from insect feeding (Painter, 1951; Kogan and Ortman, 1978). Parameters used to measure antibiosis resistance of crop plants to aphids include mean relative growth rate of the herbivores (Leather and Dixon, 1984), their number of offspring and lifespan (Markkula and Roukka, 1971), their intrinsic rate of natural increase (Campbell and Mackauer, 1977), their capacity for increase (Laughlin, 1965), and an index of rate of increase (Holt and Wratten, 1986). Most of these measures utilize the developmental time, fecundity, and survival rates of caged virginoparae. Antixenosis is most often measured by recording host selection and acceptance (Ellsbury et al., 1985; Holt and Wratten, 1986). Tolerance is measured by comparison of growth parameters of infested and uninfested plants (Newman and Pimentel, 1974).

Many instances of pea cultivar resistance to the pea aphid Acyrthosiphon pisum (Harris) have been reported. Some studies simply note the greater numbers of A. pisum on one cultivar than another (Searls, 1932; Markkula and Roukka, 1970), while others investigate the basis of the differences in aphid populations (Bintcliffe and Wratten, 1980; Bieri et al., 1983).

In commercial pea fields in Manitoba differences in pea aphid densities have been observed on different field pea cultivars (Section

III, Maiteki et al., 1986). The current study examines the development, fecundity, and survival of pea aphids individually caged on six field pea cultivars, the host preference of aphids in cultivar choice tests, and the growth responses of the six cultivars when infested. The aim of the investigation was to determine if the different densities of A. pisum on various pea cultivars could be explained by differences in the level of resistance among cultivars and the mechanisms of resistance which account for these differences.

2. Materials and Methods

Six cultivars of field peas were tested: Century, Trapper, Lenca, Tara, Triumph, and Tipu. Plants of the first four cultivars are phenotypically similar; Triumph vines have much shorter internodes and possess leaves which are slightly darker green than those of the other cultivars (Ali-Khan, 1973); Tipu plants are semi-leafless, with normal stipules but with leaflets reduced to tendrils (Ali-Khan, 1982).

In all investigations plants were grown in 15 cm plastic pots in a sand:peat:soil mixture. They were grown in a Conviron$^{(R)}$ walk-in growth chamber at a constant temperature of 20.0 ±2.0°C, a 16L:8D diel period, a daytime light intensity averaging 3150 lux supplied by cool white flourescent and incandescent bulbs, and a relative humidity of 50% during the day and 90% at night.

a) Antibiosis

The first investigation was a confinement experiment to determine the antibiosis resistance of the cultivars. The clone of pea aphid used

originated from an apterous adult female aphid which had been swept from an alfalfa field near Glenlea, Manitoba on June 1, 1983. Newborn nymphs were removed from faba bean (Vicia faba L. c.v. 'Diana') stock plants and reared on each of the pea cultivars. When these apterae began producing nymphs they were transferred to clip-on cages of 35 mm diameter (Adams and van Emden, 1972) which confined leaflets of the same cultivar on which they had been feeding. They were allowed to reproduce for 24 hours, during which time from six to 12 nymphs were born per adult. These newborn nymphs were transferred to clip-on cages enclosing one of the penultimate, usually the seventh, pair of leaflets, with one aphid and cage per plant and one plant per pot. When the aphids had been on the leaflets for approximately 10 days, they were again transferred to one of the penultimate pair of leaves of the same plant.

The experiment was conducted as duplicated 5x5 or 6x6 Latin squares, randomized independently, on three different occasions. In the first trial the cultivar Tipu was not included, and the experiment was terminated 20 days after it had begun. In the second trial Lenca was not included, while all six cultivars were included in the third trial. In the two later experiments aphids were monitored until their death.

Cages were examined and progeny, if produced, were counted, usually daily, and removed every second day. Data recorded included the time from birth to first reproduction, the number of progeny produced, the post-reproductive period, and adult lifespan. Data were arranged in the form of a life table (Andrewartha and Birch, 1954). For each two day interval from birth to death (x), the age specific survival (l_x) and the age specific fecundity (m_x) were calculated. The intrinsic rate

of increase (r_m) of the pea aphid under the given conditions was calculated from the equation $\Sigma\, e^{(-r_m x)}\, l_x\, m_x = 1$ by iterative substitution of the values of r_m. This statistic was also calculated from the equation $r_m = 0.74\ (\ln M_d)/TTR$ where M_d = number of young produced in a reproductive period equal to TTR, and TTR is the time from birth to reproduction (Wyatt and White, 1977). The jacknife technique (Meyer et al., 1986; Elliot and Kieckhefer, 1989) was used to estimate standard errors of r_m values. Differences in r_m values between cultivars were compared using Tukey's pairwise comparison test (Steele and Torrie, 1980). The net reproductive rates ($R_o = l_x m_x$) and generation times ($T = \ln R_o/r_m$) were calculated following the procedures of Andrewartha and Birch (1954). Data pertaining to individuals that were lost prior to death or were injured during manipulation were not included in the calculations.

Statistical analysis of fecundity and longevity data was performed using analysis of variance. Means were compared using Tukey's Test at a significance level of $P \leq 0.05$ unless otherwise stated.

b) Antixenosis

The second study consisted of a free choice experiment to examine antixenotic properties of the cultivars. Single field pea seedlings of five cultivars were planted in a circle around the edge of 15 cm plastic pots, with one seedling placed in the pot center, for a total of six cultivars per pot. The arrangement of the seedlings was randomized in each pot independently. Four 40 cm long support wires were embedded in the soil; to their top was glued an inverted 10 cm diameter glass dish. An organdy sleeve was anchored to each pot and

Figure 9. Sleeve cage used to confine pea aphids to pots containing one plant of each of six field pea cultivars.

dish by rubber bands (Figure 9). Late fourth instar and newly emerged adult alatae which had been reared on faba bean (V. faba cv. 'Diana') were placed in a 4 cm wide plastic petri dish and suspended above the plants on a fine wire platform attached to the support wires. At the time of infestation, plants were seedlings of the same age and, except for the shorter Triumph plants, were of approximately the same height. The test was a completely randomized design replicated three times with the number of pots caged being 39, 22, and 11 in the three trials, respectively. In the first trial, five alatae were placed in each sleeve cage; in the second and third trials three alatae were introduced into each cage. In all trials the aphid source was the same as that used in the antibiosis study. As well, in the third trial, four additional pots were infested with aphids originating from one apterous virginopara collected on August 23, 1985, from a Century pea field near Carberry, Manitoba.

Pea aphid preference and colonization were assessed 10 and 20 days after each test began. Aphid populations on each plant were visually scored so as not to disturb or influence aphid settling. A six point rating score (Ellsbury et al., 1985) was used: 1) no aphids; 2) 1 to 5 aphids, one alate adult and a few nymphs; 3) 6 to 20 aphids, 1 to 5 alatae or many nymphs or both; 4) 21 to 50 aphids, 5 to 10 adults and numerous nymphs in several colonies; 5) 51 to 100 aphids in large colonies; and 6) >100 aphids, entire plant heavily infested.

The data were tested for homogeneity of variance by means of Bartlett's test (Steele and Torrie, 1980). The Kruskal-Wallis test for ranked-score data (Hollander and Wolfe, 1973) was used to determine the

significance of differences in aphid preference for the various pea cultivars.

c) Tolerance

In each trial of the antixenosis test, pea plants in several pots were caged but not infested with aphids. There were two of these control pots in the first trial, four in the second, and five in the the third. After scoring the populations on the twentieth day of the antixenosis test, all pots were frozen overnight, plants were cut at soil level and their lengths were measured. They were dried at 70°C for 24 hours and the weights of plants plus any attached aphids were recorded.

The significance of differences in height and weight of aphid-infested plants from control plants within trials over all cultivars combined and also within cultivars was assessed by unpaired t-tests.

3. Results

3.1 Antibiosis

Termination of the first trial 20 days after birth allowed measurement of time to reproduction and fecundity to experiment termination; however, it precluded calculation of lifespan, total fecundity, and other demographic statistics for this trial.

The survivorship (l_x) and fecundity (m_x) patterns of aphids reared on the different cultivars were pooled over Trials 2 and 3, and are illustrated in Figures 10 and 11. The patterns of parameters were generally similar over all cultivars. The survivorship curves

Figure 10. Age-specific survivorship (l_x) patterns for pea aphids confined to clip-cages on six cultivars of field peas (n=18 to 23, except Lenca where n=7).

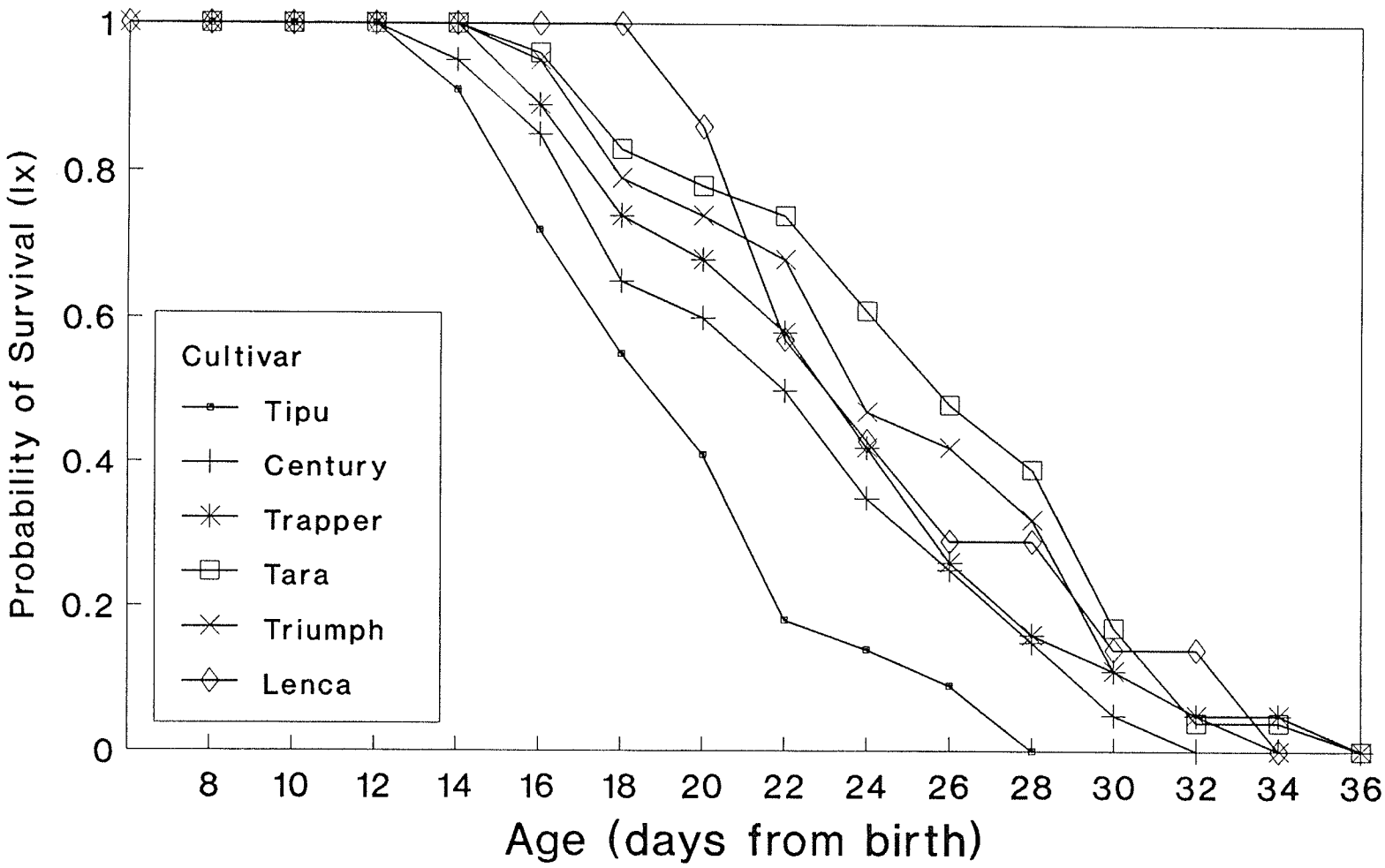
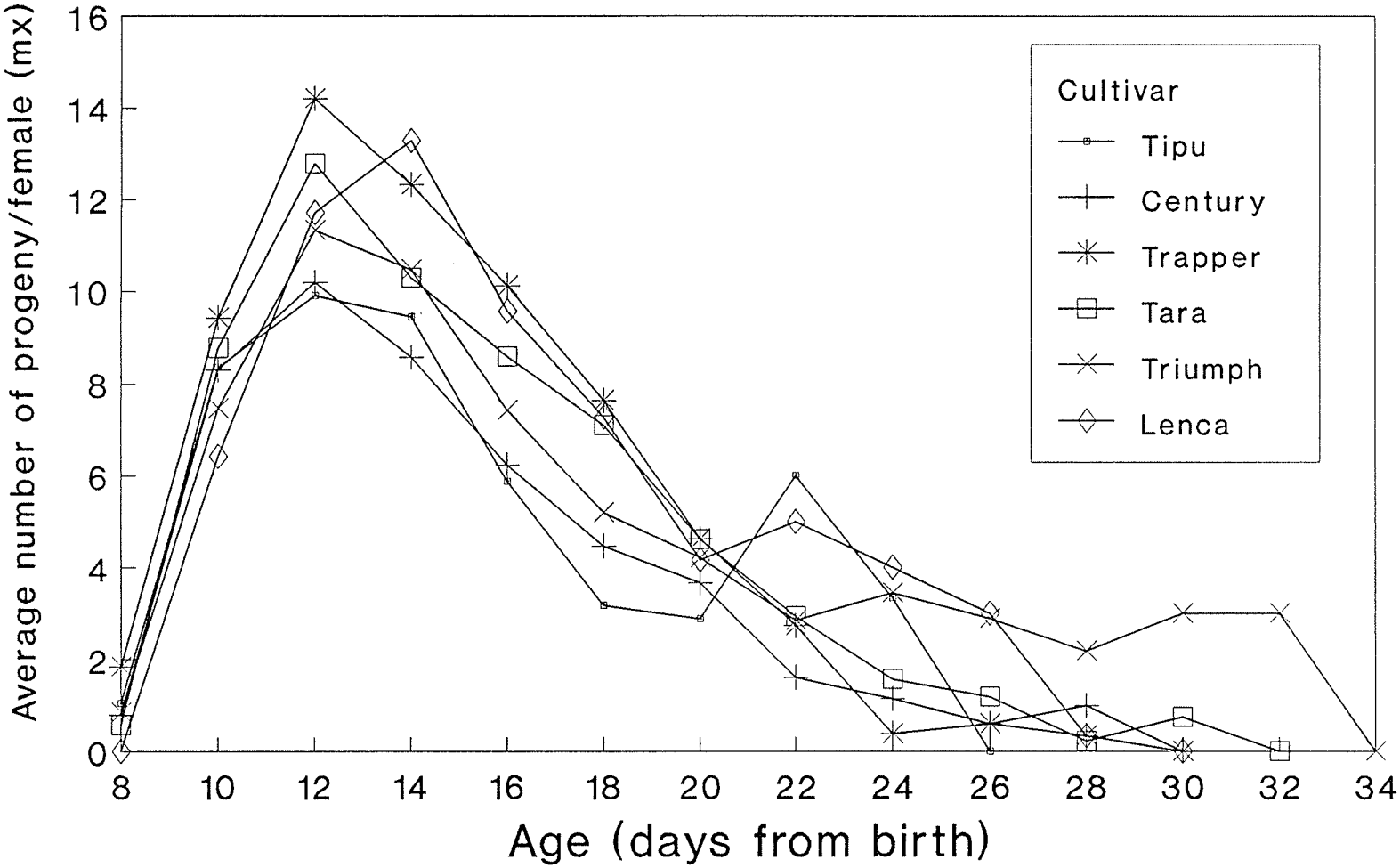

Probability of Survival (lx)
1
0.8
0.6
0.4
0.2
0
Cultivar
Tipu
Century
Trapper
Tara
Triumph
Lenca
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
Age (days from birth)

Figure 11. Age-specific fecundity (m_x) patterns for pea aphids confined to clip-cages on six cultivars of field peas (n=18 to 23, except Lenca were n=7).


Average number of progeny/female (mx)
16
14
12
10
8
6
4
2
0
8
10
12
14
16
18
20
22
24
26
28
30
32
34
Age (days from birth)
Cultivar
Tipu
Century
Trapper
Tara
Triumph
Lenca

(Figure 10) were of the Type 1 form, in which mortality acts most heavily on old individuals (Southwood, 1978). At all life stages, aphids on Tipu exhibited a lower survivorship than aphids on the other cultivars. There was no aphid mortality until after peak reproduction on any cultivar. Fecundity (Figure 11) peaked early on all cultivars, usually within the first quarter of the reproductive period, then gradually declined as adults aged. Peak fecundity occurred two days later in aphids reared on Lenca than on any other cultivar. The aphids on Triumph had the most extended reproductive period.

Data from all life table variables except time to reproduction were normally distributed and their variances were homogeneous among experiments according to F- max and Levene's tests (Snedecor and Cochran, 1980). Data for these variables were, therefore, combined over experiments.

Time to reproduction data were not normally distributed in any of the three trials, and no transformation could be found to normalize them. As well, F- max and Levene's tests (Snedecor and Cochran, 1980) indicated that the variances of this variable were heterogeneous among trials. A Friedman's rank test (Steele and Torrie, 1980) was conducted on data pooled over trials. This test indicated that cultivars did not significantly affect aphid pre-reproductive period (d.f.=5, X^2=10.11, $X^2_{P<0.05}$=11.10). The fact that the null hypothesis was not rejected, despite the absence of data from Tipu in the first trial and Lenca in the second, which tended to exacerbate cultivar differences when data were pooled, lends support to the conclusion drawn from the tests.

Although no significant differences among cultivars were found in the pre-reproductive period of aphids, the time to first reproduction

(TTR) was the shortest for aphids reared on the cultivar Trapper in the first two trials (Table 23). In the third trial the time to reproduction of aphids on this cultivar may have been influenced by the general lack of vigour which most of the Trapper plants in this test exhibited. Overall, however, the range of developmental times of aphids on the six cultivars was not large, especially in the last two trials (Table 23).

Aphids on Lenca had the longest reproductive period (Table 24). Aphids on Tipu, meanwhile, reproduced relatively quickly, over a short period of time, and died soon after producing their last offspring. However, the reproductive and post-reproductive periods were not significantly different among aphids reared on the six cultivars. Post-reproductive period was the most variable parameter measured, with a coefficient of variation of 134.6.

The significant differences ($P \leq 0.01$) in aphid longevity (Table 24) were due primarily to the short lifespan of aphids on Tipu. As well as having a short lifespan, aphids were more restless and spent less time feeding on Tipu than on any other cultivar; they were dislodged from plants more easily, and more were lost or escaped from the clip cages.

Aphids reared on Trapper and Tara had significantly greater numbers ($P \leq 0.0001$) of both total progeny and progeny born up to 20 days after the adult's birth than aphids on Century or Tipu (Table 24). Aphids on Lenca also had significantly greater total numbers of offspring than those on Century or Tipu. A comparison of the two fecundity measurements indicated that aphids on Tipu had virtually completed larviposition in 20 days, while those on Lenca deposited one third of their progeny beyond 20 days of life.

Table 23. Developmental times (± S.E.M.) of pea aphids confined on six different cultivars of field peas (n = 7 to 12).

	Pre-Reproductive Period (TTR) days		
Cultivar	Trial 1	Trial 2	Trial 3
Trapper	9.9 ±0.27	8.4 ±0.02	9.9 ±0.22
Tara	10.8 ±0.42	8.6 ±0.15	9.6 ±0.23
Triumph	10.5 ±0.27	8.9 ±0.29	9.6 ±0.20
Lenca	10.9 ±0.28	--	9.6 ±0.20
Century	11.0 ±0.39	8.8 ±0.17	9.2 ±0.45
Tipu	--	8.8 ±0.35	9.1 ±0.16

Table 24. Mean (± S.E.M.) life-table characteristics of pea aphids confined on six field pea cultivars in the laboratory.

Cultivar	n	Reproductive[1] Period (days)	Post-Reproductive Period (days)	Lifespan (days)	Total Fecundity	n	Total Fecundity to 20 days After Birth
Trapper	19	12.4 ±0.80 a[2]	2.9 ±0.80 a	24.4 ±1.68 ab	57.6 ±4.01 a	29	51.8 ±2.59 a
Tara	23	13.8 ±0.96 a	3.3 ±0.53 a	25.9 ±1.54 a	54.0 ±4.32 a	33	45.2 ±2.87 ab
Triumph	19	13.8 ±1.27 a	2.5 ±0.70 a	25.6 ±1.68 a	50.6 ±6.55 abc	29	42.6 ±3.62 bc
Lenca	7	14.9 ±1.11 a	2.1 ±1.53 a	25.4 ±2.03 ab	57.4 ±6.17 ab	17	33.4 ±3.62 bcd
Century	20	14.6 ±0.85 a	2.2 ±0.70 a	22.9 ±1.56 ab	39.6 ±2.98 bc	30	32.2 ±2.59 cd
Tipu	22	11.3 ±1.00 a	1.0 ±0.47 a	20.0 ±1.24 b	36.6 ±3.17 c	22	35.1 ±2.95 d

[1] Data for reproductive period, post-reproductive period, lifespan and total fecundity are the means of two trials: Feb-Mar '87 and Apr-Jun '87, while data for fecundity for 20 days after birth are means three trials: Feb-Mar '85, Feb-Mar '87 and Apr-Jun '87.

[2] Means within columns followed by the same letter are not significantly different at $P \leq 0.05$ (Tukey's Test).

Net reproductive rate, R_o, was considerably lower in aphids feeding on Century and Tipu than those reared on the other cultivars (Table 25). However, differences in the intrinsic rate of population increase, r_m, were relatively small among cultivars, with Trapper having the largest r_m value, and Tipu the smallest. None of the differences in aphid r_m values on the various cultivars was significant ($P \leq 0.05$, Tukey's pairwise comparison test [Steele and Torrie, 1980]). Both methods of r_m calculation, that of Andrewartha and Birch (1954) where $\Sigma\, e^{(-r_m x)} l_x m_x = 1$ (method 1), and that of Wyatt and White (1977) where $r_m = 0.74(\ln M_d)/TTR$ (method 2), resulted in approximately similar rankings. Mean generation times ($T = \ln R_o / r_m$) were also similar among aphids reared on the various cultivars; those aphids reared on Tipu had the shortest T, while those on Lenca had the longest.

3.2 Antixenosis

The variances of the mean visual scores of pea aphid numbers in the choice test were heterogeneous among experiments and data were not pooled.

There were significant differences in colonization and reproduction of pea aphids on the various cultivars 10 days after initiation in the first and third trials ($P \leq 0.0001$ and 0.05, respectively) (Figure 12a). In all three trials after 10 days, Triumph and Trapper had the highest population scores and Tipu generally had the lowest score. Population scores on Century were generally in the middle range, while aphid scores on Tara were low. Populations on Lenca, meanwhile, were variable; at 10 days aphids on this cultivar

Table 25. Demographic statistics derived from the life table study of individual pea aphids confined on six cultivars of field peas.

Cultivar	Net Reproductive Rate (R_o)[1]	Intrinsic rate of Increase (r_m)[2] Method 1[3]	Method 2[4]	Generation Time (T)(Days)[5]
Trapper	57.09	0.319±0.009[6]	0.318	12.72
Tara	55.70	0.307±0.005	0.308	13.05
Triumph	53.81	0.304±0.010	0.296	13.46
Lenca	57.42	0.297±0.008	0.300	13.50
Century	41.45	0.299±0.008	0.292	12.76
Tipu	37.55	0.296±0.008	0.288	12.59

[1] R_o = females/female/generation

[2] r_m = females/female/day

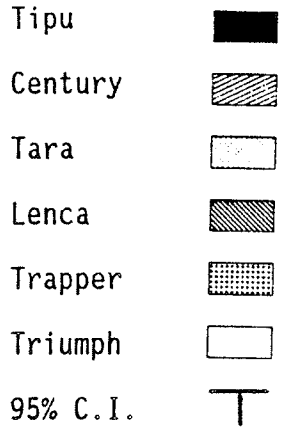
[3] r_m Method 1 = $\exp^{(-r\,x)}\ l_x\ m_x = 1$

[4] r_m Method 2 = $0.74\ (\ln M_d)/TTR$

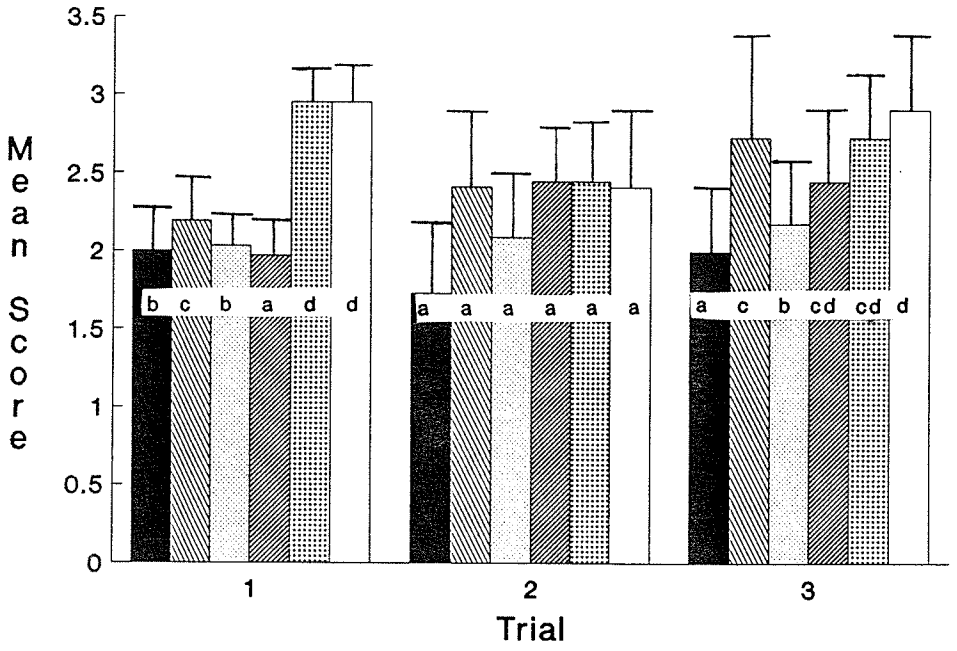
[5] $T = \ln R_o/r_m$; r_m determined by Method 2

[6] Standard error of the mean.

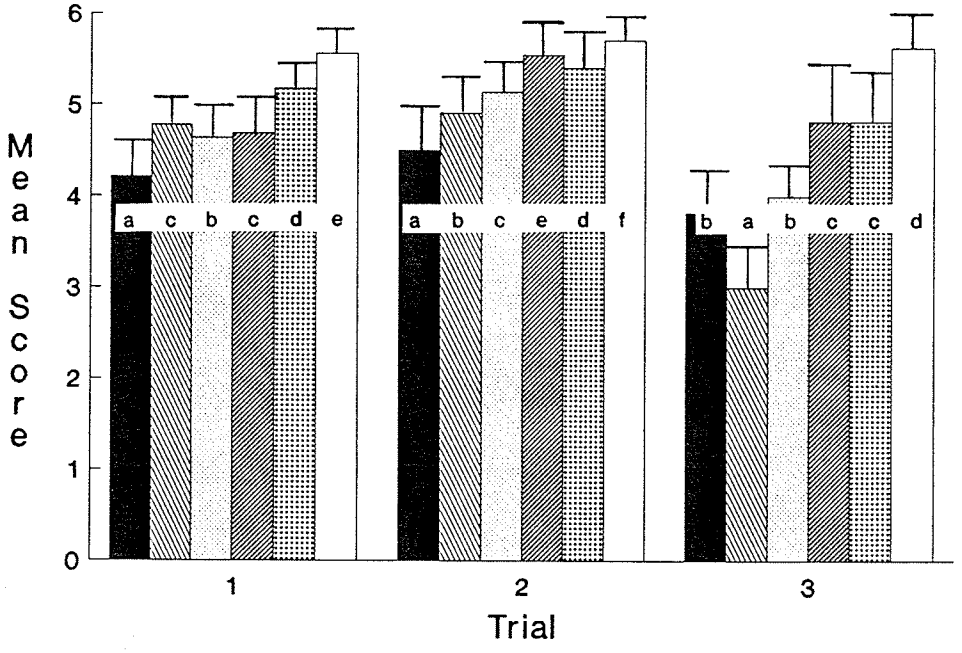
Figure 12. Mean visual scores of pea aphid populations, Glenlea clone, on six cultivars of field peas. Rating scale from 1 (no aphids per plant) to 6 (>100 aphids per plant); initial infestation: trial 1 = 5 aphids per cage, trial 2 and 3 = 3 aphids per cage. Ranked population scores for columns with the same letter do not differ significantly within each observation level (Kruskal-Wallis test, $P \leq 0.05$) (n=11 to 39).



a) Aphid population scores at 10 days



b) Aphid population scores at 20 days



scored the lowest in the first trial, the highest in the second trial, and midway in between in the third trial.

Twenty days after infestation the greatest number of aphids were found on Triumph, while Tipu had the fewest aphids in two trials and the second lowest number in the final trial (Figure 12b). Population scores on Century and Tara were generally low, while populations on Lenca and Trapper at 20 days after infestation were in the middle to high range in all three trials.

Scoring the numbers of aphids on the plants at 10 days allowed for maximum expression of antixenosis with minimum confounding by antibiosis factors of the cultivars. The fertility of the original colonizers was largely determined by the host plant on which they were raised, i.e., faba beans (Adams and van Emden, 1972). Antibiosis factors of the peas affected the growth rate of the aphid offspring growing on them. However, the vast majority of nymphs on all cultivars did not start reproducing until after the 10 day population assessment. Thus assessment at 10 days allowed for maximum nymph production by the colonizers and distribution of aphids on the plants, the latter representing antixenosis, without differential fecundity of the nymphs on the various cultivars, or antibiosis, affecting aphid numbers.

Population scores on the plants at 20 days depended not only on plant preference of the original colonizers and their offspring, but on their reproductive capability which, in the case of the nymphs, was a measure of antibiosis of the peas on which they grew. To detect whether the antixenotic effects of the cultivars were real after 20 days, allowance was made for the effect of rate of increase in the aphid populations on the various cultivars. N_t, the number of reproducing

individuals at time t, is a function of $N_o e^{r t}$, where N_o is the number of reproducing individuals at time t_o and r_m is the intrinsic rate of population increase (Andrewartha and Birch, 1954). Since many of the aphids when placed in the cages were not reproductively mature, a two day delay in reproductive capability was assumed, i.e., t=8 and 18. Using the r_m's calculated by method 2 from the antibiosis test (Table 25), the theoretical aphid population score after 10 days was 5, or from 51 to 100 aphids, for all cultivars in the first trial, where N_o=5, and 4, or from 21 to 50 aphids, in the second and third trials in which N_o=3. The theoretical aphid population scores for all cultivars in all trials after 20 days was 6, with calculated aphid numbers varying between 618 for aphids in Tipu in trials 2 and 3, and 1560 for aphids on Trapper in trial 1.

Because population levels never approached these theoretical values the conditions of the test, most probably crowding of plants and aphids, imposed some limitations to aphid population growth not experienced in the experiment in which r_m's were calculated. To estimate what part antibiosis and antixenosis played in the population scores of Figure 12b, it was assumed that these population limitations were expressed uniformly across all cultivars. Had these limitations not occurred, according to the N_t values calculated from $N_t=N_0 e^{r_m t}$, aphid populations on Trapper would have grown 1.43 times faster than on Century because of factors of antibiosis present in the latter cultivar. An antibiosis index, expressed as the ratio of the theoretical aphid population on Trapper to the population of each of the other cultivars at 18 days of reproduction, was calculated for all cultivars (Table 26). Trapper was chosen as the standard because aphids

Table 26. Theoretical pea aphid population levels (N_t) at t=18 after reproductive maturity of 5 or 3 aphids on six cultivars of field peas and the antibiosis index of each cultivar.

Cultivar	r_m	$e^{r_m t}$	N_t[1]		Antibiosis Index (I)[2]
			$N_o=5$	$N_o=3$	
Trapper	0.319	312	1559	935	1.00
Tara	0.307	251	1256	753	1.24
Triumph	0.304	238	1190	712	1.31
Century	0.299	218	1088	652	1.43
Lenca	0.297	210	1049	629	1.49
Tipu	0.296	206	1030	618	1.51

[1] $N_t = N_o e^{r_m t}$

[2] $I = \frac{N_t \text{ (Trapper)}}{N_t \text{ (Cultivar)}}$

on this cultivar had the highest intrinsic rate of reproduction. To compensate for antibiosis factors in the cultivars, the mean aphid population scores after 20 days were upwardly adjusted for all plants in all trials by the antibiosis indices. When the adjusted population scores from each trial were ranked by cultivar, a Kruskal-Wallis nonparametric test on each trial and on data combined over trials indicated that there were significant differences in the ranks of mean aphid population scores among cultivars ($H \geq 20.9$, $P \leq 0.05$). Mean adjusted aphid population ranks are listed in Table 27. Trends among the trials were similar to each other and to the results of the original analysis, with Triumph having high adjusted aphid populations and with Tipu being generally avoided. However, with adjustment, Tara scored lowest in population ranks in all three trials; this cultivar and Tipu had significantly greater antibiosis properties than Triumph, Century or Lenca.

As Appendix 7 indicates, the differences among cultivars in numbers of aphids from the Carberry clone were not significant at either 10 or 20 days after placement, probably because of the small size of the experiment. However, trends at 10 days were similar to those of the trials using the clone from Glenlea (Figure 12a), with numbers of the Carberry clone lowest on Tipu plants and highest on Triumph, Trapper and Century plants. At 20 days the pattern was somewhat different than that of Figure 12b, with the greatest number of aphids found on Tara, although Tipu had the lowest number of aphids. The Carberry aphid clone, while having similar relative scores on the cultivars as that from Glenlea, had lower absolute numbers per pot.

Table 27. Average population ranks of pea aphids on six cultivars of field peas at 20 days after infestation, adjusted to remove the effect of antibiosis on cultivars. (n_{Trial1}=39; n_{Trial2}=22, n_{Trial3}=11; $n_{Combined}$=72)

Cultivar	Adjusted Average Population Rank			
	Trial 1	Trial 2	Trial 3	Combined
Triumph	146.3 a[1]	74.0 ab	46.1 a	259.2 a
Century	142.9 ab	69.1 ab	44.0 a	248.3 a
Lenca	128.6 abc	82.2 a	41.1 a	248.1 a
Trapper	117.0 abc	62.2 ab	29.3 ab	201.4 ab
Tipu	100.0 bc	53.1 ab	25.7 ab	176.4 b
Tara	85.4 c	48.1 b	16.8 b	157.6 b

[1] Population rank scores within each column followed by the same letter are not significantly different at $P \leq 0.05$ (Kruskal-Wallis Rank Sum Comparisons).

This slower population growth was noticed in the faba bean stock culture as well.

3.3 Tolerance

Infested plants generally decreased in weight and height compared to controls, significantly so for weight in Trial 2 (d.f.=154, t=2.50, $P \leq 0.05$) (Table 28). However, unpaired t-tests indicated that these weight decreases were not significant for any particular cultivar. While plant heights decreased randomly among cultivars, there was a trend within trials for decreases in plant weights to be proportional to absolute aphid population scores (i.e., not adjusted for antibiosis) after 20 days. Thus, infested Triumph plants, which had the largest number of aphids after 20 days, also had the greatest weight decrease from the controls, while infested Tipu plants, which had the fewest aphids, generally had the smallest weight decreases (Table 28). Trapper plants were the exception to this trend; in two of the three trials the average weight of infested Trapper plants was greater than that of uninfested controls, even though aphid populations on infested plants were high. This suggests that, in the conditions of this test, Trapper was more tolerant of aphid feeding than are the other cultivars. However, with only three values per cultivar, weight and height differences between treatments among trials were not closely related to mean population scores of aphids on the cultivars. Further research is needed to verify that Trapper is more tolerant of similar aphid populations than the other cultivars tested.

Table 28. Mean visual scores of pea aphid populations on six cultivars of field peas 20 days after infestation and growth parameters of seedling field peas infested with pea aphids for 20 days expressed as a percentage of the parameters of uninfested plants.

	Trial 1			Trial 2			Trial 3		
		% of Control			% of Control			% of Control	
Cultivar	Pop'n Score	Wt.	Ht.	Pop'n Score	Wt.	Ht.	Pop'n Score	Wt.	Ht.
Triumph	5.56	70.0	97.0	5.71	61.9	69.0	5.64	63.7	83.4
Trapper	5.18	102.5	83.5	5.40	101.7	86.0	4.82	83.3	100.5
Century	4.78	74.2	79.2	4.91	86.0	93.3	3.00	89.6	117.3
Lenca	4.69	79.0	90.6	5.45	76.6	92.3	4.82	102.3	100.7
Tara	4.64	80.0	89.1	5.14	63.6	90.0	4.00	105.4	97.2
Tipu	4.21	129.2	97.0	4.50	72.9	93.4	3.82	97.2	90.5

4. Discussion

4.1 Antibiosis

Patterns of longevity and fecundity similar to those of this study have been found in other investigations of A. pisum on a variety of hosts (Mackauer, 1973; Campbell and Mackauer, 1977; Hutchison and Hogg, 1984). The slope of the survival curve of aphids on Tipu, however, is steeper than those illustrated in the literature, and indicates an adverse reaction of the aphid to this cultivar. If the degree of antibiosis resistance of the plant is reflected in the life history of the pea aphid, then the reduced longevity of aphids on Tipu is a result of proportionately greater resistance of Tipu plants. Conversely, the more extended fecundity of aphids on Triumph is an indication of this cultivar's susceptibility to the aphid. This extended fecundity may be a reflection of the slower rate of senescence of this as opposed to other cultivars, for Triumph plants remained greener longer than those of other cultivars.

Calculation of the intrinsic rate of population increase, r_m, by iterative substitution of data from detailed lifetables, is a lengthy process. The much simpler method of Wyatt and White (1977) utilizes the fact that the first few days of aphid reproduction contribute most to the population increase rate (Hutchison and Hogg, 1984). Since aphids do not have to be monitored until their deaths, a considerable amount of time is saved in utilizing this method of r_m determination. The close agreement between the two methods of calculating r_m is confirmed in this study by a correlation coefficient of 0.958 and a residual standard deviation of 0.04.

Although the differences in r_m among all cultivars were small and not significant, because populations increase exponentially, small initial differences in r_m may lead to considerable disproportionalities at the end of a growing season. Thus, a decrease in r_m of 0.023 could result in a significant reduction in aphid populations in Tipu as opposed to Trapper fields. For example, 50 days after infestation by one reproducing pea aphid, populations on Trapper plants may potentially reach over 8 million aphids, while those on Tipu would be below 1.8 million, a difference of 350%.

The r_m is a complex statistic derived by combining the duration of the pre-reproductive period and daily fecundity. These components may enhance or counteract each other. While the statistic itself is an indication of the relative population growth of a species, a consideration of the components of r_m leads to an understanding of how that growth may occur.

In populations of species such as A. pisum which are capable of rapid increase, developmental rate is probably the single most important factor influencing r_m; increases in developmental rate in the order of 10% are approximately equivalent to fertility increases in the order of 100% (Lewontin, 1965). The short developmental period of aphids on Trapper was coupled with the highest fecundity, making this cultivar the most amenable to aphid population increase of the six tested. The rapid development of aphids on Tipu was offset by very low fecundity, giving rise to a low r_m value. However, the rapid developmental rate means that, under favourable conditions for an extended period, the potential for pea aphid population build-up in Tipu fields may be considerable. Although aphids on Lenca had the

highest net reproductive rate of the six cultivars tested, their relatively long pre-reproductive period and protracted reproduction in comparison with those on other cultivars is an indication that pea aphid population build-up on Lenca in the field may be slow.

In this study, differences in developmental rates were as great among trials as among cultivars. More precise determination of the time to reproduction such as to the nearest hour, rather than to the nearest day, might have alleviated this problem (Barker and Tauber, 1951a). However, variation in plant quality also affects aphid growth rates, sometimes inexplicably. The rates of aphid and mite development and reproduction are inversely proportional to the ages of tissues to which they are confined, independent of cultivar (Harrington et al., 1943; Bintcliffe and Wratten, 1980; Trichilo and Leigh, 1985). In a study of the effect of garden pea nutrient deficiencies on pea aphid population growth, Barker and Tauber (1954) found an unaccountable reduction in aphid fecundity on plants grown in full nutrient solution. In the present study, although extraneous variables were controlled as much as possible, the 2°C variation in temperature control may have led to variation in plant as well as aphid growth among trials; the intrinsic rate of increase of pea aphids rises with temperatures to about 26°C (Campbell and Mackauer, 1977). As well, the seed sources for the first antibiosis trial were different from those of the second and third trials which may have contributed to variability of cultivars among trials.

Variation in aphid fecundity, especially in the first 20 days after birth, was the clearest expression of antibiosis resistance among the parameters tested. By this parameter Tipu and Century are more

resistant or less suitable for pea aphids than is the cultivar Trapper. The short lifespans of aphids on Tipu and Century further attest to the antibiosis resistance of these cultivars.

4.2 Antixenosis

Because offspring of the original colonizers were not yet reproductive at the time of the first assessment, cultivar population scores at 10 days after infestation were an indication of the relative degree of antixenosis each cultivar possessed. The alate colonizers flew to the host plant of their choice; as the test progressed the small size of the pots resulted in leaves of the various cultivars touching, so that apterae were free to walk from cultivar to cultivar. The low population scores of Tipu and Tara at 10 days after infestation were an indication of the antixenosis qualities of these cultivars. The irritability of aphids on Tipu which was observed in the antibiosis experiment and the fact that more aphids were lost from this cultivar than any other was further evidence of this cultivar's antixenotic qualities. The population scores on Century plants indicated that, at 10 days, this cultivar was preferred over Tipu and Tara, which was unexpected since, according to the lifetable values in Tables 23 to 25, Tara was a more suitable host for the aphids than was Century. While Trapper was the least resistant cultivar in terms of antibiosis, Triumph superseded it in terms of A. pisum preference. The physical attributes of Triumph plants, that is their shorter, thicker stature and darker green colour, may have played a role in pea aphid host choice.

Assessment of aphid populations 20 days after infestation confounded antibiosis effects with antixenosis ones. The values represented in Figure 12b are an indication of the combined effects of the two types of resistance on aphid population growth. Clearly the cultivars varied in their degrees of combined resistance to the pea aphids. The results were similar to those found in open field and field cage tests (Sections I, II); that is, populations of pea aphids on Tipu and Century were significantly smaller than populations on Trapper and Triumph.

Comparison of the population patterns among cultivars in Figure 12b, representing antixenosis plus antibiosis, with the values in Table 26, representing antixenosis, allowed inferences regarding which mechanism was predominant in which cultivar. Thus, Triumph expressed little evidence of either type of resistance. Trapper had relatively little antibiosis resistance, but was among the less preferred cultivars. Lenca was variable in all tests, but tended to have relatively low levels of both types of resistance. Tara had little antibiosis resistance but, according to the adjusted population ranks, its antixenosis resistance was the highest of any cultivar. Aphids remained on Century, even though it possessed considerable antibiosis resistance. Finally, Tipu expressed relatively large amounts of both types of resistance.

The data in Table 27 were biased against cultivars such as Triumph with greater numbers of aphids before adjustment. That is, when populations were adjusted upwards by their appropriate antibiosis indices, plants which initially had over 100 aphids still retained an adjusted score of 6. Despite this bias, the fact that Triumph had the

greatest adjusted population ranks attests to the preference of pea aphids for this cultivar. After 20 days Triumph plants were often the only ones whose height was not restricted by the size of the cage, which may have influenced aphid choice.

4.3 Tolerance

In the view of Maxwell et al. (1972), antibiosis and antixenosis are the main mechanisms of resistance of alfalfa cultivars to pea aphids, with tolerance involved to a much lesser degree. The work of Newman and Pimentel (1974), in which only 3 of 1250 pea races were thought to have more tolerance than antibiosis resistance, suggests that this conclusion may be true for peas as well. In the current study there was a trend for Trapper plants to be more tolerant than other cultivars, in terms of plant dry weight, to pea aphid feeding. Since Trapper possessed little antibiosis resistance and was more preferred than cultivars such as Tipu and Tara, tolerance may be the reason that there was little effect of aphid feeding on yield of this cultivar in small plot and commercial field tests (Sections I, III).

This study substantiates field observations that Trapper supports greater pea aphid populations than Century (Sections I to III, Maiteki et al,. 1986). Given equal infestation levels, aphid populations on Trapper and Triumph will flourish relative to other cultivars. Triumph shows little resistance of any type to the pea aphid. However, Trapper may exhibit tolerance to aphid feeding so that crop damage may be less in this cultivar than in Triumph. Aphid populations on Tipu and Century may be relatively small, for both cultivars possess antibiosis qualities while Tipu has antixenosis resistance as well.

CHAPTER IV

GENERAL DISCUSSION

This series of experiments was prompted by the concern that field pea cultivars grown in Manitoba may support different levels of pea aphid populations. If this were true, then A. pisum control recommendations (Maiteki and Lamb, 1985b; Smith et al., 1988) should be re-evaluated.

In all four studies for this project the patterns of aphid population build-up among cultivars were generally similar to each other and to that reported by Maiteki et al. (1986) for fields of Century. Pea aphid populations increased rapidly from low levels from about the middle of July, peaked in late July or early August, and declined rapidly with the onset of plant senescence in middle to late August. While patterns of pea aphid population growth were similar among cultivars, variability was found in the peak number of pea aphids which the cultivars supported. That is, larger populations of pea aphids occurred over time on the cultivars Triumph or Trapper than on Century or Tipu. These trends held whether plants sampled were in the growth chamber, in field cages, in open field plots, or in Century, Trapper or Triumph commercial pea fields.

A comparison of the results from the field cage study (Section II) with those from the other experiments leads to the conclusion that predators and parasitoids were not the main instrument in achieving the different aphid population levels found on the cultivars, with the possible exception of such control agents in Tipu. The higher than

expected numbers of aphids in the Tipu field cages may be due to increased levels of predation or parasitism on this over other cultivars in the field. However, the low aphid population levels on Tipu in the confinement study of Section IV were comparable to those found in the subplots in the field (Section I). This suggests that, rather than differential predation or parasitization, perhaps there was a response of this cultivar to the caging process which encouraged aphid population growth more so than on the other caged cultivars. Mueke et al. (1978) found conflicting results in pea aphid populations following chemical application between greenhouse, cage and open field experiments.

Raworth et al. (1984) suggested that laboratory measures of developmental time, fecundity and longevity of Brevicoryne brassicae (L.) are different from field measures due to differences in plant quality. Pea aphid growth parameters were not measured in field experiments of this project. Although absolute measures of l_x, m_x, R_o, r_m and other life statistics may vary between the laboratory and the field, the fact that the patterns of aphid population development on the respective cultivars in the field (Figures 1-3, 5) paralleled those in the growth chamber suggests that the relative values of life table parameters determined on the cultivars in the laboratory hold true for Manitoba field conditions as well.

Growth statistics and preference studies provided evidence for the underlying reasons for differential aphid populations on the cultivars. The short development times and high fecundity of pea aphids on Trapper in the laboratory resulted in rapid population buildup on this cultivar, as was seen in commercial fields. The lack of antibiosis

factors in the cultivar Triumph and the preference of aphids for Triumph plants in the laboratory resulted in high populations of aphids, which were also seen in subplots in the field. Tipu's generally low populations of aphids in the field were mirrored in the laboratory, where antibiosis and antixenosis factors of the cultivar predominated. Century plants were antibiotic for the laboratory aphids, Tara plants were antixenotic, while Lenca plants did not elicit a consistent response in either the laboratory or the field.

The disparities in response of the aphids to the plants is remarkable when the lack of genetic diversity among the cultivars is considered. Tipu, Lenca and Tara have varying degrees of Century in their pedigree (Ali-Khan, 1978, 1980, 1982), while Century and Trapper each have the cultivar Chancellor in their background (Anonymous, 1976). Triumph was developed from the world pea collection (Anonymous, 1976), and is the only cultivar which does not have Century or Chancellor in its background.

Although most of the cultivars tested share genetic material, the expression of different types of resistance in them suggests that different resistance genes may be involved. Despite some success in breeding for resistance (e.g., Maltais, 1949), the genetics of field pea resistance to the pea aphid are not well known. However, the use of multiline cultivars or cultivar composites with similar agronomic characters but with different resistance genes is one method of providing durable resistance to an insect pest (Dahms, 1972).

While cultivar effects on aphid populations were relatively straightforward to delineate, determining the effects of aphid populations on cultivar yields was not.

Both the yield of field peas and crop losses due to pea aphids are complex functions of a large number of variables. Several studies have found that crop losses caused by aphids vary under different cropping and environmental conditions (e.g., Barker and Tauber, 1951b; Hobbs et al., 1961; Maiteki and Lamb, 1985a; Wise, 1988). This suggests that damage relations are unlikely to be well correlated with aphid abundance (Wellings et al, 1989). In a chemical control study, Wise (1988) found that, even with pre-spray infestation levels as high as 9 to 16 pea aphids per Century shoot tip, none of the nine treatments applied significantly enhanced yield, and yield was not significantly correlated with mean aphid numbers per assessment date.

The timing of the aphid population buildup in fields in relation to crop phenology is critical in determining whether crop loss will occur. Some yield reductions occurred in infested subplots in 1984 (Section I); this was not the case in 1986, when the population size of aphids were similar to that in 1984 but developed later in the season than in 1984. Indeed, in most of the subplots described in Section I aphid infestation did not have a great effect on cultivar yield. Aphid suppression in the control plots of this experiment was less than optimal, especially in 1985; however, there was excellent aphid control in the sprayed sections of farmers' fields (Section III), but few general cultivar differences in yield between infested and sprayed plots were found in this experiment either. In contrast, considerable reduction in yield components was found in several cultivars in the field cage experiment (Section II). The pea aphid population levels reached in the cages were comparable to those reached in the field plots in 1985 (Figures 3 and 5). However, the increase in A. pisum

numbers occurred at the most susceptible stages of plant growth in the cages, from flowering to pod elongation (Maiteki and Lamb, 1985a), while in the 1985 field experiment aphid numbers rose as pods were filling to maturing. Thus, the disparities in the severity of yield loss in the two experiments were in large measure attributable to the timing of the aphid increase in number. Similarly, several of the farmers' fields surveyed had high aphid numbers late in the year, but no yield reductions in unsprayed plots occurred. Seeding early may be the best precaution a farmer can take to minimize field pea yield losses due to pea aphid infestation.

In the present investigations, even with similar initial aphid infestation rates on the cultivars, such as in the field and growth chamber cage studies, the variable aphid population growth rates resulted in differences in aphid populations on the cultivars at the end of the studies. Therefore, it was difficult to dissociate innate yield response of the cultivars from the effects of varying aphid densities.

However, the linear regression data presented in Section I indicates that the seed weight of Century is decreased the most and that of Trapper the least with a given aphid density. Although the trend was not significant, the tolerance test of Section IV indicated that dry matter weight loss of infested Trapper plants was less than that of plants of the other cultivars. Analysis of the data from Maiteki and Lamb (1985b), in which growth and yield parameters are presented for field peas infested with pea aphids, results in a strong correlation ($n=15$, $r=0.729$, $P \leq 0.01$) of dry matter weight with thousand seed weight of Century peas. Therefore, the relative lack of seed

weight loss of Trapper peas under aphid infestation may be related to the ability of this cultivar to retain dry matter when fed upon.

Regardless of why Trapper is not as severely affected by aphid feeding as the other cultivars, in seven out of a total of eight different locations in three years, pea aphids on Trapper plants surpassed the published economic threshold for pea aphids on field peas in Manitoba. However, in only two of these tests, the cage study (Section II) and one farmers' field (Section IV), did yield decreases occur in infested plots. Since the aphid populations at these two locations at the time of flowering to pod formation were three to four times the economic threshold and subsequently peaked at very high numbers, this is strong evidence that the economic threshold of Trapper peas is higher than that estimated for Century peas.

On the other hand, the cultivar Triumph appears generally susceptible to pea aphids. Although the regression coefficient of seed weight over aphid density for this cultivar was lower than that of Century (Section I), infestations were usually higher, so that significant yield decreases occurred in four of six plantings of Triumph peas. In most of these plantings, Triumph plants senesced at a slower rate than those of other cultivars. This slow senescence may make plants of this cultivar sensitive to aphid infestation later in their phenology than those of other cultivars, as occurred in the commercial field near Carberry in 1985 (Section IV).

For a given aphid infestation level Century had the steepest slope of seed weight over aphid number. However, Century plants exert considerable antibiosis towards pea aphids (Section IV), and by the time field populations of aphids were large enough to cause injury to

the plants, most of these were beyond the susceptible stage. In none of the 13 tests in which pea aphids were sampled on Century did aphid levels exceed three per plant tip at the time of flowering, and in none were yield decreases in infested plots clearly attributable to aphid infestation.

Effective insect control requires knowledge of the pest's population dynamics and the crop's response to the pest. The present study suggests that crop response varies with the cultivar grown. The economic threshold of pea aphids on Century field peas (Maiteki and Lamb, 1985a) is an important step in the development of a comprehensive control program for this insect in Manitoba pea fields. However, the current research indicates that refinement of the published economic threshold may be required when aphid control recommendations are made for cultivars other than Century. In the Manitoba Insect Control guide (Smith et al., 1988), there are no references to particular cultivars in the economic thresholds of crops to insects. As chemical costs escalate and as host plant resistance becomes an attractive means of pest control, the extent of universality of economic thresholds of crop cultivars towards important insect pests needs to be determined.

CHAPTER V

SUMMARY AND CONCLUSIONS

This study found that the pattern of pea aphid population growth does not vary significantly on six cultivars of field peas over the summer season in Manitoba. A. pisum populations build rapidly on all cultivars during the middle of July, peak at the end of July or the beginning of August, and decrease rapidly as the crops senesce in mid- to late-August. However, the magnitude of aphid populations at their peak is dependent upon the cultivar grown. Pea aphid population peaks are larger in plots of Triumph or Trapper than in those of Century or Tipu.

The timing of the pea aphid infestation is critical to cultivar yield response. Infestation after pod initiation and filling generally does not affect seed yields. The cultivar Triumph, however, may be susceptible to injury from pea aphids until maturation of pods.

Cultivar yield response to pea aphid feeding in the most part reflects pea aphid population levels on the cultivars. In naturally infested field plots Triumph, with generally the highest aphid numbers, had significant decreases in 1000 seed weights in two years out of three. Century, with generally low pea aphid populations, did not have significant yield decreases attributable to aphids in any of the field plots, field cages or commercial fields in which it was tested. Trapper peas had little yield loss despite the relatively high pea aphid populations which occurred on this cultivar.

In small field plots, the yield component most sensitive to pea aphid feeding is weight of 1000 seeds. Linear regressions of seed weight over aphid density indicates that Trapper peas are least sensitive and Century peas the most sensitive to aphid numbers. Thus, of the six cultivars tested, Century has the greatest potential for seed weight decrease with aphid feeding.

Laboratory tests indicate that pea aphid populations are low on Tipu plants because this cultivar exerts antibiotic and antixenotic properties towards them. Century also has properties antibiotic to the pea aphid, and Tara may exhibit antixenosis. Triumph has little resistance of any type to A. pisum, while Trapper supports pea aphid development and population growth, but may be tolerant of aphid feeding.

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APPENDIX 1. Growth stage description of the pea plant Pisum sativum L. combined from Gane et al. (1984) and Maiteki (1985).

Stage	Stage Name	Description
VEGETATIVE		
	Emergence	50% or more shoots above ground. Rows clearly visible.
V_1	1st node	Fully expanded simple leaf; no tendril.
V_2	2nd node	Fully expanded simple leaf with simple tendril.
	|	
$V_{(n)}$	nth node	Any number of nodes on the main stem with fully expanded leaves according to the cultivar. Compound leaves on later nodes.
REPRODUCTIVE		
R_1	Bud stage	At least 50% of plants have buds inside rolled terminal leaves. In the cultivar Century most buds become visible when plants have 14 to 15 nodes. Leaves at lowermost nodes start to senesce.
R_2	Flower	At least 10% of plants have one open flower at uppermost node. At full bloom 90% of plants have 1-4 open flowers on main stem.
R_3	Pod formation and enlargement	At least 10% of plants have small pods (2 cm long, 0.5 cm wide) and enlarged flat pods (2-6 cm long, 0.5-1.3 cm wide) at upper most 3 nodes, but no pods with apparent seeds.
R_4	Pod swelling and filling	At least 10% of plants have a pair of pods at one of the uppermost five nodes with seeds which can be felt. Pods are succulent and have sweet tasting seeds.
R_5	Pod maturity	At least 10% of plants have fully distended pods with hard seeds. Pods turning yellow at one ofl the uppermost five nodes and 70% of mainstem nodes have senescent leaves.
R_6	Pod drying	At least 50% of plants have dry pods. Leaves are dry at almost all nodes. Peas are ready to harvest within 10 days.

APPENDIX 2. Temperature and precipitation statistics for the months of May to September, 1984 to 1986, and 30 year normals, at Glenlea Research Station, Glenlea, Manitoba.

	1984						1985					
Month	$\bar{X}$ Max Temp°C	$\bar{X}$ Min Temp°C	$\bar{X}$ Temp °C	Accum. ° Days[1]	Rainfall (mm)	Rainy Days	$\bar{X}$ Max Temp°C	$\bar{X}$ Min Temp°C	$\bar{X}$ Temp °C	Accum. ° Days	Rainfall (mm)	Rainy Days
May	18.0	2.0	10.0	266.3	42.4	6	33.0	4.6	18.9	341.2	62.3	13
June	22.0	11.0	16.5	609.8	182.5	12	19.7	7.6	13.7	721.9	84.1	14
July	26.0	11.5	19.0	1040.8	63.4	10	25.4	10.3	17.9	1123.1	22.4	8
August	28.0	13.0	10.5	1511.8	40.1	6	21.4	9.9	15.7	1451.1	173.5	14
September	17.0	3.0	10.0	1687.8	35.6	7	14.7	4.9	9.8	1592.1	27.6	9

	1986						30 Year Normal					
Month	$\bar{X}$ Max Temp°C	$\bar{X}$ Min Temp°C	$\bar{X}$ Temp °C	Accum. ° Days	Rainfall (mm)	Rainy Days	$\bar{X}$ Max Temp°C	$\bar{X}$ Min Temp°C	$\bar{X}$ Temp °C	Accum. ° Days	Rainfall (mm)	Rainy Days
May	20.4	6.4	13.4	305.7	43.9	6	18.0	4.7	11.4	255.0	56.1	10
June	21.7	9.0	15.4	598.0	150.7	10	23.2	10.4	16.9	610.6	88.4	12
July	24.4	13.8	19.1	1023.0	189.6	16	26.1	13.0	19.6	1061.1	73.9	12
August	23.5	9.5	16.5	1380.5	13.0	6	25.0	11.4	18.3	1570.0	60.5	11
September	17.0	5.0	11.0	1571.2	72.6	14	18.6	5.8	12.2	1787.4	50.1	13

[1] Minimum threshold for accumulated degree days is 5°C.

APPENDIX 3. Pea aphid populations (± S.E.M.) in field plots of field peas at Glenlea, 1984-1986.

1984

Spray Regime	N	Cult.	Mean No. Aphids/Plant Tip, Sample Date: July 13	July 20	July 27	Aug 3	Aug 10	Aug 16
Spray	40	Century	4.22 ±0.43	2.50 ±0.76	2.75 ±1.06	0.98 ±0.40	0.98 ±0.19	1.38 ±0.31
		Lenca	2.52 ±0.99	3.75 ±1.26	5.98 ±0.46	4.18 ±2.20	2.92 ±1.05	3.50 ±0.47
		Tara	5.52 ±0.55	2.78 ±1.06	3.35 ±1.64	2.05 ±0.73	2.40 ±0.70	3.70 ±0.70
		Trapper	3.10 ±0.79	3.55 ±1.82	2.90 ±1.16	1.78 ±0.57	1.30 ±0.20	2.75 ±0.69
		Triumph	3.88 ±0.72	3.35 ±0.93	2.98 ±1.12	4.38 ±1.27	5.00 ±1.51	5.62 ±1.33
Non-Spray	40	Century	2.90 ±0.88	0.98 ±0.31	3.00 ±1.01	4.70 ±0.72	2.55 ±0.73	2.72 ±0.81
		Lenca	3.12 ±0.74	2.00 ±0.36	4.60 ±1.90	10.60 ±1.28	5.18 ±0.51	4.72 ±0.61
		Tara	4.60 ±1.23	4.42 ±1.72	5.18 ±1.99	7.42 ±1.14	10.48 ±3.01	4.40 ±0.48
		Trapper	4.10 ±0.69	2.78 ±0.62	5.80 ±1.24	14.30 ±1.63	7.75 ±1.38	3.68 ±0.54
		Triumph	4.65 ±1.37	4.18 ±1.36	22.05 ±6.76	39.25 ±6.25	13.82 ±2.29	7.32 ±1.01

Spray Regime	N	Cult.	Mean No. Alate Aphids/Plant Tip, Sample Date: July 13	July 20	July 27	Aug 3	Aug 10	Aug 16
Spray	40	Century	0.92 ±0.17	0.18 ±0.08	0.28 ±1.06	0.05 ±0.03	0.12 ±0.08	0.00 ±0.00
		Lenca	0.75 ±0.34	0.12 ±0.02	0.18 ±0.09	0.10 ±0.07	0.77 ±0.12	0.03 ±0.02
		Tara	0.85 ±0.21	0.18 ±0.18	0.19 ±0.00	0.08 ±0.05	0.55 ±0.13	0.00 ±0.00
		Trapper	0.60 ±0.26	0.08 ±0.02	0.08 ±0.08	0.02 ±0.02	0.28 ±0.13	0.00 ±0.00
		Triumph	0.55 ±0.38	0.10 ±0.04	0.28 ±0.02	0.20 ±0.07	1.15 ±0.22	0.10 ±0.00
Non-Spray	40	Century	0.32 ±0.14	0.98 ±0.31	0.10 ±0.04	0.10 ±0.04	0.35 ±0.25	0.00 ±0.00
		Lenca	0.65 ±0.24	0.00 ±0.36	0.02 ±0.02	0.32 ±0.05	0.45 ±0.12	0.05 ±0.05
		Tara	0.82 ±0.29	0.42 ±1.72	0.12 ±0.08	0.10 ±0.04	0.70 ±0.27	0.00 ±0.00
		Trapper	0.62 ±0.15	0.78 ±0.62	0.25 ±0.10	0.45 ±0.22	0.68 ±0.18	0.08 ±0.02
		Triumph	1.02 ±0.27	0.18 ±1.36	0.30 ±0.04	0.75 ±0.21	0.78 ±0.07	0.22 ±0.13

APPENDIX 3. (Cont'd) Pea aphid populations (± standard error of mean) in field plots of field peas at Glenlea, 1984-1986.

1984

Mean No. Apterous Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 13	July 20	July 27	Aug 3	Aug 10	Aug 16
Spray	40	Century	0.22 ±0.08	0.72 ±0.19	0.18 ±0.05	0.20 ±0.06	0.12 ±0.48	0.00 ±0.00
		Lenca	0.05 ±0.05	1.18 ±0.41	0.42 ±0.05	0.62 ±0.29	0.17 ±0.12	0.10 ±0.04
		Tara	0.25 ±0.05	0.98 ±0.68	0.42 ±0.27	0.35 ±0.10	0.02 ±0.02	0.00 ±0.00
		Trapper	0.20 ±0.09	1.00 ±0.29	0.30 ±0.12	0.30 ±0.12	0.18 ±0.11	0.05 ±0.05
		Triumph	0.48 ±0.16	0.85 ±0.20	0.38 ±0.21	0.22 ±0.08	0.28 ±0.13	0.08 ±1.08
Non-Spray	40	Century	0.10 ±0.07	0.35 ±0.12	0.22 ±0.10	0.75 ±0.18	0.00 ±0.00	0.05 ±0.05
		Lenca	0.35 ±0.09	0.48 ±0.09	0.89 ±0.28	1.08 ±0.28	0.18 ±0.10	0.00 ±0.00
		Tara	0.18 ±0.07	1.05 ±0.40	0.88 ±0.33	0.75 ±0.13	0.58 ±0.38	0.25 ±0.10
		Trapper	0.20 ±0.04	1.28 ±0.33	0.42 ±0.06	1.48 ±0.20	0.58 ±0.16	0.20 ±0.20
		Triumph	0.35 ±0.10	1.28 ±0.38	2.08 ±0.69	2.55 ±0.54	0.49 ±0.11	0.25 ±0.19

Mean No. Nymphal Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 13	July 20	July 27	Aug 3	Aug 10	Aug 16
Spray	40	Century	3.08 ±0.34	1.60 ±0.57	2.30 ±0.93	0.72 ±0.34	0.72 ±0.16	1.38 ±0.31
		Lenca	1.72 ±0.70	2.45 ±0.92	5.38 ±0.49	3.45 ±1.84	1.97 ±1.00	3.37 ±0.51
		Tara	4.42 ±0.53	1.62 ±0.98	2.82 ±1.40	1.62 ±0.71	1.82 ±0.59	3.48 ±0.82
		Trapper	2.30 ±0.56	2.48 ±1.66	2.52 ±1.01	1.55 ±0.48	0.85 ±0.16	2.70 ±0.67
		Triumph	3.12 ±0.28	2.40 ±0.88	2.32 ±0.91	3.95 ±1.17	3.58 ±1.56	5.58 ±1.24
Non-Spray	40	Century	2.48 ±0.84	0.58 ±0.24	2.75 ±0.90	3.85 ±0.73	1.32 ±0.33	2.68 ±0.76
		Lenca	2.15 ±0.51	1.45 ±0.26	3.68 ±1.67	9.22 ±1.53	4.55 ±0.43	4.68 ±0.62
		Tara	3.60 ±0.99	3.25 ±1.65	4.18 ±1.61	6.58 ±1.13	9.20 ±2.49	4.15 ±0.52
		Trapper	3.28 ±0.60	1.47 ±0.59	5.12 ±1.26	12.38 ±1.63	6.48 ±1.20	3.40 ±0.67
		Triumph	3.28 ±1.14	3.48 ±0.81	19.67 ±6.08	35.92 ±5.79	12.56 ±2.23	6.85 ±0.74

APPENDIX 3. (Cont'd) Pea aphid populations (± standard error of mean) in field plots of field peas at Glenlea, 1984-1986.

1985

Mean No. Aphids/Plant Tip

Spray Regime	N	Cult.[1]	Sample Date: July 3	July 10	July 16	July 22	July 29	Aug 3	Aug 15	Aug 22
Spray	50	Tipu	0.02±0.02	0.02±0.02	0.16±0.11	0.08±0.04	1.60±0.43	18.14± 2.28	4.64± 1.14	1.38±0.64
		Cent	0±0	0.02±0.02	0.14±0.14	0.22±0.05	2.76±0.33	41.72± 6.70	12.12± 4.58	0.64±0.22
		Lenca	0±0	0.02±0.02	0.08±0.04	0.14±0.07	3.44±0.55	37.30± 2.69	11.10± 1.45	1.12±0.38
		Tara	0.08±0.06	0.08±0.08	0.70±0.60	0.16±0.09	2.64±1.15	49.78±14.02	13.90± 3.12	2.36±0.88
		Trap	0.04±0.02	0.02±0.02	1.00±0.50	0.16±0.05	7.02±3.45	66.06±16.93	10.78± 4.46	1.62±0.52
		Tri	0±0	0.02±0.02	0.34±0.20	0.20±0.10	4.00±0.74	44.42±10.05	15.28± 6.29	2.22±0.90
Non-Spray	50	Tipu	0±0	0.16±0.12	0.48±0.23	0.58±0.53	12.50±5.22	30.30± 3.22	35.70± 6.42	8.92±2.07
		Cent	0±0	0.04±0.02	0.44±0.17	0.20±0.07	4.14±1.67	48.34± 5.60	32.64± 3.95	5.96±1.47
		Lenca	0±0	0.12±0.12	0.28±0.17	0.28±0.21	5.92±2.15	57.76± 2.21	68.32±13.93	8.94±1.88
		Tara	0±0	0.30±0.28	0.40±0.26	0.52±0.22	8.84±3.07	69.00±11.57	61.00±11.43	5.02±1.32
		Trap	0.06±0.06	0.23±0.28	0.58±0.18	0.52±0.16	15.56±5.03	104.62±11.34	69.94± 9.38	6.22±0.96
		Tri	0.16±0.16	0±0	0.22±0.07	0.88±0.31	5.32±0.55	49.88±10.17	63.32± 8.86	9.56±2.45

Mean No. Alate Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 3	July 10	July 16	July 22	July 29	Aug 3	Aug 15	Aug 22
Spray	50	Tipu	0±0	0±0	0.02±0.02	0.08±0.04	0.38±0.16	4.36± 0.71	3.22± 0.93	0.04±0.02
		Cent	0±0	0±0	0±0	0.14±0.02	0.76±0.15	16.96± 5.13	9.98± 3.49	0.02±0.02
		Lenca	0±0	0.02±0.02	0.04±0.02	0.06±0.02	0.56±0.19	12.02± 3.26	8.60± 1.47	0±0
		Tara	0±0	0±0	0.04±0.02	0.08±0.04	0.80±0.21	12.62± 2.30	10.94± 2.53	0.08±0.04
		Trap	0.04±0.02	0±0	0.08±0.05	0.06±0.04	1.08±0.49	10.68± 3.03	8.72± 4.27	0±0
		Tri	0±0	0.02±0.02	0.06±0.04	0.18±0.09	1.14±0.25	11.46± 2.48	11.34± 4.92	0.02±0.02
Non-Spray	50	Tipu	0±0	0±0	0.06±0.04	0.08±0.04	1.16±0.34	6.58± 1.62	4.92± 1.14	0.02±0.02
		Cent	0±0	0±0	0.18±0.16	0.14±0.05	1.28±0.71	15.56± 2.99	11.96± 1.12	0.02±0.02
		Lenca	0±0	0±0	0.04±0.04	0.12±0.07	0.76±0.25	10.12± 1.19	7.14± 1.18	0±0
		Tara	0±0	0±0	0.06±0.06	0.14±0.05	0.82±0.19	11.76± 3.10	8.36± 1.25	0.50±0.48
		Trap	0.02±0.02	0±0	0.06±0.04	0.14±0.04	1.22±0.39	9.54± 2.62	6.12± 1.76	0.06±0.02
		Tri	0.04±0.04	0±0	0.04±0.02	0.24±0.09	0.90±0.24	8.68± 1.29	7.52± 1.93	0.08±0.06

[1] Cent = Century; Trap = Trapper; Tri = Triumph.

APPENDIX 3. (Cont'd) Pea aphid populations (± standard error of mean) in field plots of field peas at Glenlea, 1984-1986.

1985

Mean No. Apterous Aphids/Plant Tip

Spray Regime	N	Cult.[1]	Sample Date: July 3	July 10	July 16	July 22	July 29	Aug 3	Aug 15	Aug 22
Spray	50	Tipu	0±0	0±0	0.02±0.02	0±0	0.02±0.02	1.98±0.28	0.34± 0.17	0.04±0.04
		Cent	0±0	0±0	0±0	0±0	0±0	1.10±0.50	0.28± 0.15	0±0
		Lenca	0±0	0±0	0±0	0±0	0.16±0.10	2.66±0.65	0.54± 0.39	0.02±0.02
		Tara	0±0	0.04±0.04	0.04±0.04	0±0	0.06±0.06	2.08±0.61	0.42± 0.21	0.04±0.02
		Trap	0±0	0.02±0.02	0.08±0.06	0.02±0.02	0.20±0.11	5.30±1.70	0.44± 0.28	0±0
		Tri	0±0	0±0	0.02±0.02	0±0	0±0	2.76±0.94	0.60± 0.25	0.02±0.02
Non-Spray	50	Tipu	0±0	0.02±0.02	0.02±0.02	0.06±0.06	1.36±0.52	3.52±0.52	4.68± 0.56	0.52±0.09
		Cent	0±0	0.02±0.02	0.08±0.04	0±0	0.16±0.07	3.56±1.02	3.20± 0.49	0.46±0.04
		Lenca	0±0	0.02±0.02	0.02±0.02	0.04±0.02	0.48±0.21	8.54±0.32	7.12± 1.48	0.26±0.11
		Tara	0±0	0.06±0.06	0.06±0.04	0.04±0.04	0.68±0.36	5.52±0.93	6.84± 0.97	0.18±0.04
		Trap	0±0	0.08±0.08	0.14±0.10	0.06±0.02	1.32±0.55	13.48±3.78	7.58± 0.57	0.14±0.07
		Tri	0±0	0±0	0.02±0.02	0±0	0.52±0.16	4.22±1.74	7.28± 0.90	0.52±0.17

Mean No. Nymphal Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 3	July 10	July 16	July 22	July 29	Aug 3	Aug 15	Aug 22
Spray	50	Tipu	0.02±0.02	0.02±0.02	0.12±0.10	0±0	1.20±0.28	11.80± 1.67	1.08± 0.36	1.30±0.58
		Cent	0±0	0.02±0.02	0.14±0.14	0.08±0.04	2.00±0.31	23.66± 3.02	1.86± 1.03	0.62±0.22
		Lenca	0±0	0±0	0.04±0.02	0.08±0.08	2.72±0.39	22.62± 2.45	1.96± 0.47	1.10±0.36
		Tara	0.08±0.06	0.04±0.04	0.62±0.55	0.08±0.06	1.78±5.60	35.08±12.33	2.54± 0.70	2.24±0.84
		Trap	4±0	0±0	0.84±0.47	0.08±0.06	5.74±2.88	50.08±13.67	1.62± 0.54	1.62±0.52
		Tri	0±0	0±0	0.26±0.17	0.02±0.02	2.86±0.62	30.20± 7.58	3.34± 1.37	2.18±0.90
Non-Spray	50	Tipu	0±0	0±0	0.06±0.04	0.44±0.44	9.98±4.40	20.20± 1.84	26.10± 4.88	8.38±2.03
		Cent	0±0	0±0	0.18±0.16	0.06±0.02	2.70±0.93	29.22± 2.42	17.48± 4.04	5.48±1.45
		Lenca	0±0	0±0	0.04±0.04	0.12±0.12	4.68±1.75	39.10± 2.19	54.06±11.88	8.68±1.79
		Tara	0±0	0±0	0.06±0.06	0.34±0.17	7.34±2.66	51.72± 7.98	45.80±10.55	4.34±1.20
		Trap	0.02±0.02	0±0	0.06±0.04	0.32±0.16	13.02±4.21	81.60± 9.06	56.24± 7.39	6.02±0.94
		Tri	0.04±0.04	0±0	0.04±0.02	0.64±0.36	3.90±0.41	36.98± 7.99	48.52± 8.86	8.96±2.31

[1] Cent = Century; Trap = Trapper; Tri = Triumph.

APPENDIX 3. (Cont'd) Pea aphid populations (± standard error of mean) in field plots of field peas at Glenlea, 1984-1986 .

1986

Spray Regime	N	Cult.	Mean No. Aphids/Plant Tip Sample Date July 3	July 15	July 22	Aug 1	Aug 8	Aug 14	Aug 20
Spray	50	Tipu	0±0	0±0	0.06±0.04	0.12±0.07	1.22±0.81	2.40±0.65	1.65±0.25
		Century	0±0	0±0	0.20±0.15	0.18±0.09	0.12±0.08	1.85±1.01	1.47±0.57
		Lenca	0±0	0.02±0.02	0.24±0.15	0.50±0.29	0.28±0.17	0.67±0.34	2.97±1.51
		Tara	0±0	0.06±0.06	1.04±0.94	1.42±0.73	0.46±0.44	1.35±0.90	2.98±1.37
		Trapper	0±0	0.02±0.02	0.36±0.22	0.54±0.49	0.62±0.24	3.32±2.24	2.60±0.50
		Triumph	0±0	0±0	0.04±0.02	1.66±0.81	1.34±0.69	1.76±0.80	3.38±1.01
Non-Spray	50	Tipu	0±0	0.04±0.04	0.10±0.08	1.94±0.79	6.80±2.22	14.10±5.86	2.68±1.61
		Century	0±0	0.06±0.04	0.08±0.04	0.52±0.20	9.90±2.99	12.28±4.18	5.36±2.00
		Lenca	0±0	0.06±0.04	0.24±0.16	2.40±0.69	8.12±2.44	18.48±3.88	7.75±2.13
		Tara	0±0	0.02±0.02	0.30±0.19	3.14±0.94	12.00±4.18	21.12±4.64	8.62±5.03
		Trapper	0±0	0.16±0.16	0.12±0.06	4.10±1.86	14.88±3.89	18.20±5.65	5.03±2.81
		Triumph	0.12±0.12	0±0	0.48±0.16	5.72±2.23	13.44±4.90	19.62±4.51	7.00±2.94

Spray Regime	N	Cult.	Mean No. Alate Aphids/Plant Tip Sample Date July 3	July 15	July 22	Aug 1	Aug 8	Aug 14	Aug 20
Spray	50	Tipu	0±0	0±0	0.04±0.04	0.02±0.02	0.04±0.02	0.02±0.02	0±0
		Century	0±0	0±0	0.04±0.04	0.02±0.02	0.02±0.08	0.02±0.02	0.07±0.07
		Lenca	0±0	0±0	0±0	0.02±0.02	0±0	0±0	0±0
		Tara	0±0	0±0	0.04±0.02	0.08±0.06	0±0	0.08±0.05	0.02±0.02
		Trapper	0±0	0.02±0.02	0.06±0.04	0.06±0.04	0.04±0.02	0.05±0.05	0±0
		Triumph	0±0	0±0	0.04±0.02	0.08±0.08	0.02±0.02	0.06±0.04	0.04±0.04
Non-Spray	50	Tipu	0±0	0±0	0±0	0.16±0.12	0.06±0.06	0.05±0.03	0±0
		Century	0±0	0.02±0.02	0±0	0.02±0.02	0.16±0.04	0.02±0.02	0.07±0.03
		Lenca	0±0	0.04±0.04	0±0	0.10±0.03	0.04±0.02	0.18±0.06	0±0
		Tara	0±0	0.02±0.02	0.04±0.04	0.08±0.04	0.20±0.09	0.12±0.02	0.07±0.05
		Trapper	0±0	0±0	0.06±0.04	0.14±0.12	0.42±0.25	0.22±0.13	0.03±0.03
		Triumph	0±0	0±0	0.10±0.05	0.10±0.05	0.50±0.43	0.25±0.09	0.08±0.05

APPENDIX 3. (Cont'd) Pea aphid populations (± standard error of mean) in field plots of field peas at Glenlea, 1984-1986.

1986

Mean No. Apterous Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 3	July 15	July 22	Aug 1	Aug 8	Aug 14	Aug 20
Spray	50	Tipu	0±0	0±0	0±0	0.06±0.04	0.18±0.12	0.25±0.10	0.25±0.05
		Century	0±0	0±0	0.06±0045	0.02±0.02	0±0	0.22±0.17	0.17±0.07
		Lenca	0±0	0±0	0.04±0.04	0.10±0.14	0.08±0.06	0.13±0.13	0.33±0.15
		Tara	0±0	0±0	0.06±0.06	0.28±0.05	0.04±0.04	0.25±0.18	0.28±0.05
		Trapper	0±0	0±0	0.08±0.06	0.10±0.10	0.10±0.05	0.38±0.25	0.25±0.05
		Triumph	0±0	0±0	0±0	0.28±0.12	0.16±0.10	0.20±0.05	0.46±0.12
Non-Spray	50	Tipu	0±0	0±0	0.02±0.02	0.36±0.17	1.06±0.36	1.58±0.68	0.18±0.09
		Century	0±0	0±0	0±0	0.10±0.04	1.56±2.99	1.80±0.83	0.57±0.24
		Lenca	0±0	0±0	0±0	0.30±0.08	1.62±2.44	2.72±0.99	0.58±0.13
		Tara	0±0	0±0	0.02±0.02	0.48±0.16	1.64±4.18	2.22±0.41	0.82±0.63
		Trapper	0±0	0±0	0±0	0.54±0.21	1.76±3.89	1.72±0.57	0.27±0.09
		Triumph	0±0	0±0	0±0	0.84±0.23	2.04±4.90	1.58±0.42	0.92±0.29

Mean No. Nymphal Aphids/Plant Tip

Spray Regime	N	Cult.	Sample Date: July 3	July 15	July 22	Aug 1	Aug 8	Aug 14	Aug 20
Spray	50	Tipu	0±0	0±0	0.02±0.02	0.04±0.02	1.00±0.67	2.12±0.60	1.40±0.30
		Century	0±0	0±0	0.10±0.10	0.14±0.07	0.10±0.08	1.60±0.93	1.23±0.55
		Lenca	0±0	0.02±0.02	0.20±0.12	0.38±0.26	0.20±0.13	0.53±0.27	2.57±1.37
		Tara	0±0	0.06±0.06	0.94±0.84	1.06±0.57	0.42±0.40	1.02±0.70	2.68±1.33
		Trapper	0±0	0±0	0.22±0.14	0.38±0.36	0.52±0.22	2.90±2.01	2.35±0.45
		Triumph	0±0	0±0	0±0	1.30±0.72	1.16±0.60	1.50±0.73	2.88±0.95
Non-Spray	50	Tipu	0±0	0.04±0.04	0.08±0.08	1.42±0.76	5.68±1.92	12.48±5.38	2.50±1.53
		Century	0±0	0.04±0.04	0.08±0.04	0.40±0.17	8.16±2.42	10.45±3.38	4.73±1.80
		Lenca	0±0	0±0	0.24±0.16	2.00±0.61	6.46±1.84	15.58±3.20	7.18±2.15
		Tara	0±0	0±0	0.24±0.17	2.58±0.77	10.16±3.62	18.78±4.31	7.72±4.37
		Trapper	0±0	0.16±0.16	0.06±0.04	3.42±1.60	12.70±3.49	16.26±5.26	4.73±2.77
		Triumph	0±0	0±0	0.38±0.13	4.78±1.98	10.90±3.97	17.80±4.06	6.00±2.62

APPENDIX 4. Analysis of variance mean square values for spray regime and cultivar effects on the mean number of various aphid morphs per plant tip at flowering-pod initiation and at the time of peak aphid populations, Glenlea, 1984-1986.

a) 1984

Source of Variation	Degrees of Freedom	Mean Square Values[1]					
		Jul 27			Aug 3		
		Alatae	Apterae	Nymphs	Alatae	Apterae	Nymphs
Spray Regime	1	0.00	0.91*[2]	5.00*	0.69*	3.19**	141.99**
Replicate	3	0.02	0.17	0.88	0.04	0.00	1.15
Spray*Rep[3]	3	0.01	0.08	0.37	0.07	0.11	0.36
Cultivar	4	0.06	0.31**	2.32*	0.19**	0.15	7.27**
Cult*Spray[4]	4	0.04	0.18	3.28**	0.07	0.24*	2.99**
Error[5]	24	0.03	0.07	0.58	0.03	0.07	0.32
	39						
r^2		0.381	0.696	0.692	0.742	0.754	0.919
C.V.		41.62	35.01	38.34	43.40	32.14	24.10
Pooled S.E.		0.09	0.13	0.38	0.09	0.13	0.28

1 Analysis of variance and standard error based on $\sqrt{x + 0.05}$ transformed data.

2 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).

3 Spray regime * replicate, error term applicable to to main plot comparisons.

4 Cultivar * spray regime interaction.

5 Experimental error applicable to subplot comparisons.

APPENDIX 4. (Cont'd) Analysis of variance mean square values for spray regime and cultivar effects on the mean number of various aphid morphs per plant tip at flowering-pod initiation and at the time of peak aphid populations, Glenlea, 1984-1986.

b) 1985

Source of Variation	Degrees of Freedom	Mean Square Values[1]								
		Jul 27			Aug 6[6]			Aug 15[7]		
		Alatae	Apterae	Nymphs	Alatae	Apterae	Nymphs	Alatae	Apterae	Nymphs
Spray Regime	1	0.03	0.03	0.53	0.12	11.62*	23.02*	0.11	49.71**	355.14**
Replicate	4	0.01	0.01	0.16	2.05**	0.19	3.47	2.46	0.39	2.98
Spray*Rep[3]	4	0.02	0.01	0.15	0.07	0.94	2.87	0.93	0.32	4.32
Cultivar	5	0.03	0.01	0.04	2.85**	2.77**	17.63**	2.02**	0.49**	5.54**
Cult*Spray[4]	5	0.01	0.00	0.07	0.19	0.45	0.88	0.46	0.26	3.66**
Error[5]	40	0.02	0.00	0.07	0.66	0.34	1.24	0.55	0.13	0.65
	59									
r^2		0.263	0.563	0.469	0.475	0.703	0.740	0.544	0.915	0.943
C.V.		36.69	23.87	65.61	25.53	29.75	19.39	26.98	23.76	21.47
Pooled S.E.		0.06	0.03	0.12	0.36	0.26	0.50	0.33	0.16	0.36

1 Analysis of variance and standard error based on $\sqrt{x + 0.05}$ transformed data.

2 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).

3 Spray regime * replicate, error term applicable to main plot comparisons.

4 Cultivar * spray regime interaction.

5 Experimental error applicable to subplot comparisons.

6 Aphid population peaks on Trapper, Tara and Century.

7 Aphid population peaks on Lenca, Triumph and Tipu.

APPENDIX 4. **(Cont'd) Analysis of variance mean square values for spray regime and cultivar effects on the mean number of various aphid morphs per plant tip at flowering-pod initiation and at the time of peak aphid populations, Glenlea, 1984-1986.**

c) 1986

Source of Variation	Degrees of Freedom	Mean Square Values[1]					
		Aug 1			Aug 14		
		Alatae	Apterae	Nymphs	Alatae	Apterae	Nymphs
Spray Regime	1	0.06	0.89**	7.80**	0.03	3.76*	32.07*
Replicate	4	0.06	0.35*	2.83	0.02	0.36	1.10
Spray*Rep[3]	4	0.02	0.04	0.44	0.04	0.21	2.33
Cultivar	5	0.01	0.18**	1.22**	0.03	0.06	0.77
Cult*Spray[4]	5	0.01	0.03	0.23	0.02	0.06	0.68
Error[5]	40	0.02	0.03	0.23	0.02	0.12	1.00
	59						
r^2		0.372	0.728	0.755	0.551	0.766	0.780
C.V.		44.38	35.87	49.79	38.11	37.95	40.83
Pooled S.E.		0.06	0.08	0.21	0.06	0.15	0.45

1 Analysis of variance and standard error based on $\sqrt{x + 0.05}$ transformed data.

2 * ** Significant at $P \leq 0.05$ and 0.01, respectively (variance ratio F test).

3 Spray regime * replicate, error term applicable to to main plot comparisons.

4 Cultivar * spray regime interaction.

5 Experimental error applicable to subplot comparisons.

APPENDIX 5. Correlation coefficients of field pea yield per subplot with other harvest components, Glenlea, 1984.

Cultivar	N	Correlation Coefficients						
		No. Plants /Row	No. Pods /Plant	No. Peas /Pod	No. Seeds /Row	Weight/ 250 Seeds	Weight/ 1000 Seeds	Weight/ Row
Century	8	0.572	-0.648	-0.184	0.732*[1]	0.504	0.687	0.806*
Lenca	8	0.390	-0.595	0.111	0.019	0.671	0.635	-0.125
Tara	8	-0.123	0.675	0.388	0.636	0.265	0.247	0.722*
Trapper	8	-0.244	-0.290	0.105	-0.499	0.381	0.702	-0.313
Triumph	8	-0.538	0.828*	-0.472	-0.030	0.322	0.313	0.034
All[2]	40	-0.138	0.213	0.162	-0.000	0.105	0.191	0.230

[1] *Significant at $P \leq 0.05$.

[2] Data from all cultivars combined.

APPENDIX 6. Correlation coefficients of field pea yield per row with other harvest components, Glenlea, 1984 to 1986.

Cultivar	N	Correlation Coefficients					
		No.Plants /Row	No.Pods /Plant	No.Peas /Pod	No.Seeds /Row	Weight /250 Seeds	Weight /1000 Seeds
a) 1984							
Century	8	0.882	-0.785*[1]	-0.398	0.983***	-0.047	0.245
Lenca	8	0.084	0.256	-0.048	0.917***	-0.407	-0.427
Tara	8	0.390	0.566	0.218	0.980***	-0.128	-0.131
Trapper	8	0.037	0.718*	0.647	0.957***	0.734	0.004
Triumph	8	0.602	0.317	0.309	0.940***	0.017	0.004
All[2]	40	0.290	0.276	0.173	0.648***	0.115	0.063

1 * ** *** Significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

2 Data from all cultivars combined.

APPENDIX 6. (Cont'd) Correlation coefficients of field pea yield per row with other harvest components, Glenlea, 1984 to 1986.

Cultivar	N	Correlation Coefficients: No.Plants /Row	No.Pods /Plant	No.Peas /Pod	No.Seeds /Row	Weight /250 Seeds	Weight /1000 Seeds	Height
b) 1985								
Century	10	0.581	-0.325*	-0.011	0.384	0.601	0.514	0.142
Lenca	10	0.462	0.138	0.349	-0.133	0.691*	0.324	0.059
Tara	10	0.660*	0.847**	0.779**	0.045	0.808**	0.417	0.622
Trapper	10	0.701*	0.275	-0.423	0.400	0.826**	0.554	--
Triumph	10	0.190	0.560	0.362	-0.116	0.750*	0.556	0.219
Tipu	10	-0.101	0.611	0.241	0.540	0.740*	0.754*	--
All[2]	60	-0.064	0.279*	0.101	0.158	0.485***	0.416***	-0.177
c) 1986								
Century	8	0.601	0.699	0.029	0.785*	0.548	0.310	0.158
Lenca	8	0.437	0.904***	0.895**	0.583	0.713*	0.614	0.788**
Tara	8	0.614	0.366	0.008	-0.138	0.449	0.378	0.601
Trapper	8	-0.154	0.824**	0.550	0.706*	0.886**	0.711*	0.796*
Triumph	8	0.419	-0.144	-0.217	0.446	0.588	0.692*	0.172
Tipu	8	0.125	0.859**	0.782*	0.609	0.791*	0.768*	0.546
All[2]	52	-0.057	0.494***	0.224	0.387**	0.626***	0.611***	0.126

[1] * ** *** Significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

[2] Data from all cultivars combined.

APPENDIX 7. Mean visual scores (± S.E.M.) of pea aphid populations, Carberry clone, on six cultivars of field peas. Rating scale from 1 (no aphids) to 6 (>100 aphids per plant). Initial infestation rate was 3 aphids per cage; n=4.

Cultivar	Mean Score	
	10 days	20 days
Triumph	2.25 ±0.48[1]	4.00 ±0.41
Trapper	2.25 ±0.48	3.00 ±0.58
Lenca	2.00 ±0.41	3.75 ±0.48
Tara	1.75 ±0.25	4.25 ±0.65
Century	2.25 ±0.48	4.00 ±0.41
Tipu	1.50 ±0.29	3.00 ±0.41

[1] Means within each column are not significantly different from each other at $P \leq 0.05$ (Kruskal-Wallis Test).