SEASONAL DISPERSAL OF THE PEA APHID PARASITOID, APHIDIUS ERVI HALIDAY

BY

BARBARA A. DENEKA

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

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ABSTRACT

Barbara Deneka, M. Sc. University of Manitoba, April 1992

Seasonal Dispersal of the pea aphid parasitoid, Aphidius ervi Haliday

Aphidius ervi Haliday is a potential biological control agent for the pea aphid, Acyrthosiphon pisum (Harris), which is a significant pest of field peas in Manitoba. The parasitoid's dispersal abilities were examined, as this is essential information to enable the manipulation of the parasitoid to control the pea aphid. The life stage dispersing, pattern of dispersal and stimuli leading to dispersal were examined.

Field experiments during the summers of 1990 and 1991 explored the life stage, pattern and extent of dispersal. To the limited extent that the parasitoid disperses, it is the adult which is responsible. Most A. ervi remain in alfalfa, which is their overwintering site and has a supply of hosts. Laboratory studies suggest that the adult is stimulated to disperse, in part, by a lack of hosts.

A biological control program for the pea aphid in field peas would require, at the least, annual releases of A. ervi. The particulars of these releases require further investigation.

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1. INTRODUCTION

Peas are an important crop in Manitoba, and were grown on 36 000 and 56 700 hectares in 1990 and 1991 respectively; Manitoba's pea crop represents thirty percent of the dry pea production in Canada (Anon., 1991). This crop is subject to attack by Acrythrosiphon pisum (Harris), the pea aphid, which is a proven and significant pest (Maiteki and Lamb, 1985). Most pea crops require aphid control measures to be taken; these involve aerial spraying of chemical pesticides. Malathion or dimethoate is usually used (Kolach and McCullough, 1991). Alternatives to chemical control would be advantageous as the use of chemicals is expensive, possibly harmful to the environment and may lead to insecticide resistance. One alternative to chemical pesticides is biological control.

Aphid control has been achieved in several instances with aphidiid parasitoids (Cameron et al., 1981; Hughes et al., 1987; Kfir et al., 1985; Olkowski et al., 1982; van den Bosch et al., 1979). Biological control of aphids has been successful in all of these instances; however they all involved perennial or semi perennial crops. A semi perennial crop is one which grows for two or more years without being disturbed, as opposed to perennial crops such as orchards, which are rarely radically disturbed. In contrast, field peas are an annual crop. Proficient dispersal is vital to a biological control agent used against a pest of an annual crop because it must recolonize the crop every year. Detailed information concerning dispersal patterns may allow the effective manipulation of the biological control agent.

In Manitoba, the most common pea aphid parasitoid is Aphidius ervi Haliday

(Matheson, 1989), and it may have the greatest potential to control the pea aphid. A. ervi overwinters primarily in cultivated alfalfa as well as other wild perennial legumes and disperses into annual peas from there. This study was designed to investigate the dispersal patterns out of alfalfa and into annual peas. With information about the dispersal patterns of A. ervi, predictions concerning the impact of the parasitoid can be made and possible alterations to the agroecosystem designed. An integrated pest management program favouring natural enemies is the goal; achieving this goal may be expedited with knowledge of the biology and ecology of the natural enemies (Pimental and Goodman, 1978).

Aspects of dispersal investigated include the stage of dispersal, the pattern and extent of dispersal and the stimuli causing dispersal. Members of the Aphidiidae have been recorded dispersing as larvae inside alate aphids or as adults. Alate pea aphids and parasitoids were collected to establish whether A. ervi disperses as a larva or as an adult. The pattern of dispersal from alfalfa to peas was examined in the field during the summers of 1990 and 1991. Pea and alfalfa fields were sampled for pea aphids and parasitoids to survey abundance and percent parasitism. Sticky traps were used to sample parasitoids flying within and out of alfalfa, as well as into a pea plot. The final step involved an examination of possible dispersal stimuli. This behavioural aspect was examined in a laboratory experiment.

2. LITERATURE REVIEW

2.1 Acyrthosiphon pisum, The Pea Aphid

The pea aphid, Acyrthosiphon pisum (Harris), was accidently introduced into North America in the late 1800's. By 1926, the pea aphid was established in Canada, Mexico and from coast to coast in North America (Hagen et al., 1976). Currently, the pea aphid is widely established and commonly found on leguminous plants such as alfalfa, peas and faba beans. In Manitoba, it has become a major pest of field peas (Maiteki and Lamb, 1985). This section will briefly outline the life history and biology of the pea aphid, especially as this relates to its pest status. Finally, the effects of pea aphids on field peas will be discussed.

The pea aphid overwinters in Manitoba as an egg. In the spring, a fundatrix, or stem mother, emerges from the egg. The offspring of the fundatrix, called viviparae, are produced asexually throughout the Manitoban summer. Each aphid passes through four nymphal instars and reaches maturity in 5 to 50 days, depending on the temperature (Philip and Mengersen, 1989). Embryos of the next generation are present inside the aphid when it is born. Between 50 and 150 offspring may be produced by each vivipara (Philip and Mengersen, 1989). In the late summer or fall, photoperiodic changes cue the production of sexuparae (Mackay, 1987). The sexuparae are female aphids that produce both male and egg-laying female aphids. The male and female aphids mate, and the females produce overwintering eggs.

Production of alate viviparae is influenced by maternal effects (Mackay and Wellington, 1977) as well crowding effects and host plant quality (Sutherland, 1969a;

1969b). Alate aphids are able to disperse long distances and infest crops. The population of pea aphids in Manitoba consists of the progeny of the eggs which have overwintered, and alatae which have blown in. Long distance dispersal of pea aphids has been documented (Smith and Mackay, 1989). In Manitoba, the aphid population in peas generally peaks around the end of July or early August. The population generally diminishes rapidly after the peak (Maiteki et al., 1986; Soroka and Mackay, 1990).

The peak aphid population in late July or early August usually corresponds with the most sensitive growth stage of the pea plant, young pod development. The economic threshold, 2-3 aphids per 20 cm tip during flowering, is low because of the extensive damage pea aphids cause during young pod development (Maiteki and Lamb, 1985). Pea aphids cause decrease in dry weight, protein and net primary production (Barlow et al., 1977). As well as directly damaging the plant through feeding, the pea aphid causes economic damage by the excretion of honeydew which promotes fungal growth. The pea aphid can vector several different viruses which cause plant disease (Philip and Mengersen, 1989). The pea aphid, in excessive numbers, can cause severe damage to field peas. The enormous potential for increase, as well as the timing of the population peak contributes greatly to the pea aphid's ability to cause crop damage. Control has involved chemical pesticides, such as malathion and dimethoate. An alternative or supplemental method of control could involve the pea aphid parasitoid, Aphidius ervi Haliday.

2.2 Aphidius ervi, A Pea Aphid Parasitoid

Aphidius ervi Haliday is a member of the family Aphidiidae; aphidiids are solitary parasitoids of aphids. A. ervi has been introduced into North America as a biological control agent, however it may have existed before the introductions, as pre-release studies were not executed. Although Palearctic in origin, A. ervi may have entered North America either via Iceland from Europe or via the Aleutian Islands from the eastern Palearctic, or through accidental introduction (Stary, 1974). The first intentional North American release occurred in 1959 in New Jersey and Delaware. From 1961 to 1963, releases of A. ervi were made in Arizona, Idaho, Maine, Oregon and Washington (Angalet and Fuester, 1977). In the Pacific Northwest, A. ervi as well as Aphidius smithi Sharma and Subba Rao, Aphidius pulcher Baker and Praon pequodorum Viereck were released from 1959 through 1964 (Halfhill et al., 1972; Mackauer and Finlayson, 1967). All parasitoids became established, however A. smithi spread into new areas most successfully. Since that time, the populations of A. smithi have declined and A. ervi is now the dominant pea aphid parasitoid in the Pacific Northwest (Kambhampati and Mackauer, 1989) and the most effective pea aphid parasitoid on alfalfa in Eastern North America (Mertins, 1985). A. ervi and Praon pequodorum Viereck account for 90% of the pea aphid parasitoids in Manitoba (Matheson, 1989). A. ervi is responsible for most of the parasitism of pea aphids in pea and alfalfa crops and in most years, it exists in greater numbers than any other pea aphid parasitoid. Its abundance may make it suitable to be part of a biological control program against the pea aphid in Manitoba.

A. ervi oviposits into an aphid. The egg hatches within the aphid and the larva feeds on its internal organs. Only one egg can develop in each aphid; supernumary eggs or larvae are eliminated through physiological suppression or physical combat (Mackauer, 1990). The first three larval instars have sucking mouthparts, while the fourth and final instar is mandibulate (Stary, 1970). Pupation occurs inside the exoskeleton of the dead aphid. This stage is often referred to as a mummy. The mummy is attached to the substrate with some silk. The adult emerges after chewing a circular hole through the cocoon and aphid exoskeleton in the abdominal area. Adults may mate at this time. Females mate only once, while males may mate several times (Stary, 1970). Once a female has mated or begins ovipositing, she refuses to copulate (Stary, 1970). Reproduction is arrhentokous, which means that unfertilized eggs produce males while fertilized eggs may produce females as well as males. In a mated female, the fertilization of an egg depends on a number of factors, such as temperature, maternal age and host quality (Stary, 1970). Each female can lay between 250 and 600 eggs (Kambhampati and Mackauer, 1989). At 20°C, development from egg to adult takes 10-14 days. Many generations occur over the summer in Manitoba. The parasitoid overwinters as a prepupa, which is a quiescent stage between the larval and pupal periods (Stary, 1970). Diapause is most likely triggered by a number of factors such as short day lengths and low temperatures, as in the case of Aphidius nigripes Ashmead (Brodeur and McNeil, 1989). Adults emerge in the spring.

Host selection in A. ervi is governed by the species and age of an aphid as

well as past ovipositional experience and parental effects. Host range is restricted to the genus Acyrthosiphon according to Mackauer and Finlayson (1967), although other authors have recorded additional hosts. Aphidius ervi will attack Sitobion avenae in addition to Acyrthosiphon pisum after exposure of four or five generations of the parasitoid to the new host although the efficiency of attacking the normal host, Acyrthosiphon pisum is reduced (Cameron et al., 1984). Myzus persicae Sultz. and Macrosiphon euphorbiae Kalt. have also been recorded as hosts (Krombein, 1979). Maternal and paternal background influence host preference (Powell and Wright, 1988). Different populations or biotypes have different host preferences (Pungerl, 1984). Although all aphidiids have an instar preference, they will oviposit in other instars, depending on the abundance of the various instars. Intermediate instars are generally preferred; adults have defensive reactions which make them difficult to handle (Stary, 1970), although the specific preferences of A. ervi have not been investigated.

The consequences of parasitization on the aphid depend on the instar attacked. After parasitization by the aphidiid parasitoid, Praon pequodorum in the third instar, Acyrthosiphon pisum will produce no progeny; if parasitized in the fourth instar, aphids will produce progeny; greater numbers of progeny are produced by aphids parasitized as older fourth instar nymphs (Sequiera and Mackauer, 1988). The size and number of embryos are reduced in Acyrthosiphon pisum parasitized by A. ervi (Polaszek, 1986). After parasitization, in the first, second or third instar wing development of alatiform nymphs is variable, while alatiform aphids parasitized in

the fourth instar complete wing development (Lui and Hughes, 1984). Alatiform nymphs of Acyrthosiphon pisum survive to adulthood if parasitized by Aphidius smithi past the third instar (Campbell and Mackauer, 1975). The change in wing development caused by parasitization affects dispersal of both the aphid and aphid parasitoid, and will be discussed at length in section 2.4. During the egg stage of parasitization, the aphid initially feeds more, but assimilates less efficiently. Aphid feeding drops during the first larval stage, increases during the second larval stage and then is reduced for the remainder of the aphid's life (Stary, 1988).

A. ervi displays qualities important to a biological control agent. Potentially 600 eggs can be produced (Kambhampati and Mackauer, 1989), demonstrating a relatively high reproductive capacity. Synchronization with the host and adaptation to the weather conditions in Manitoba are important aspects of biological control agents. As A. ervi is represented well and overwinters successfully (Matheson, 1989), it appears to be well adapted to the climate of Manitoba. One key quality is its ability to disperse into the annual pea crop. Pea aphid populations usually escalate to damaging levels (Maiteki and Lamb, 1985), which indicates that A. ervi does not disperse into peas sufficiently early enough or in adequate numbers to reduce satisfactorily the pea aphid population. The objective of this study was therefore to examine aspects of A. ervi dispersal ecology to understand why it fails to control pea aphids in annual peas, hopefully enabling the design of manipulations facilitating greater parasitoid populations in pea fields.

2.3 Biological Control

Biological control is "the regulation by natural enemies of another organism's population density at a lower average than would otherwise occur" (Debach, 1974). Classically, natural enemies are introduced with the aim of long term establishment. Three other techniques exist which do not involve the long term establishment of the natural enemies (Waage and Greathead, 1988). Inoculation refers to periodic reintroduction of natural enemies, augmentation refers to introducing more of a naturally occurring population of natural enemies, and inundation refers to the release of many natural enemies for the immediate reduction of one generation of a pest insect. The goal of biological control is the suppression of the pest's population below its economic injury level. This section will explore the theory of biological control, especially as it relates to the Aphidiidae. The mechanism and components which contribute to the success or failure of biological control will be addressed as well as the attributes of the Aphidiidae which contribute to their value as biological control agents.

Although biological control has been successful and economically viable in many instances, 60% of the introductions have been failures (Waage and Greathead, 1988). Both empirical and theoretical studies have been conducted to illuminate patterns which contribute to successful biological control. Practitioners of biological control have attempted to find patterns to establish the causes of success and failure through empirical studies comparing the type of natural enemy, type of host, type of crop, climate, previous association of enemy and pest, and number of natural

enemies used (Greathead, 1986; Ehler and Hall, 1982). The controlling mechanisms involved in predator-prey and host-parasitoid interactions are not fully understood and subject to much controversy. Many theoretical studies involving mathematical modelling have been conducted to examine population dynamics in host-parasitoid systems to elucidate the influence of aggregation and density dependence (eg. Vorley and Wratten, 1985; Lessells, 1985; Comins and Noble, 1986; Reeve, 1988; Chesson and Murdoch, 1986). Patterns in biological control successes are sought through both theoretical and empirical studies.

Most biological control programs have endeavoured to establish stable fluctuations of the natural enemy and pest populations to maintain the pest population below an economic injury level (Horn, 1988). The natural enemy population suppresses the pest population below the level of economic injury, but does not drive the host to extinction. A depression in the natural enemy population will follow the suppression of the pest population. With the depressed natural enemy population, the pest population will rise, however it will be kept in check by the ensuing rise in population of the natural enemies. This stable rise and fall of populations is proposed as the mechanism allowing long term biological control. Parasitoids, which display non-random searching abilities and aggregate in areas of high host density, are likely to establish a stable relationship with their host and thus be effective biological control agents (Beddington et al., 1975). Although parasitoids display aggregative behaviour, density dependent parasitism does not always result (Waage, 1983). Density dependence has been thought to be the mechanism by which

aggregative behaviour promotes stability, however this is clearly not always the case. Aggregation of parasitoids in areas of high host density, as opposed to areas of low density, may result in equal, higher or lower rates of parasitism (Morrison and Strong, 1980). Density dependence does not result from aggregative behaviour; it may not be an important consideration for the success of biological control. The theory that stability is necessary for effective biological control is not accepted by all workers. Murdoch et al. (1985) examine seven successful cases of biological control and conclude that possibly only one of these cases involved establishing a stable system. They argue that local extinctions are more characteristic of successful biological control and suggest that natural enemies with non-aggregative characteristics should be sought, such as predators. However, local extinctions may be part of a stable system, depending on the scale which is considered. Stability, defined as a relatively constant population, could exist over a region, while populations in particular fields or on particular plants might be locally extinct. Waage and Greathead (1988) propose that mechanisms for host and natural enemy stability exist along a continuum dependent on the type of pest and its distribution. Pests with many generations, such as aphids and scales, might be best controlled with predators which would induce local extinctions, while pests with one generation, such as Lepidoptera, might be best controlled with parasitoids which exhibit a non-random search behaviour. This theory suggests predators would be more effective natural enemies for aphids. However, there have been several successful cases of biological control against aphids with parasitoids. The role for stability of the relationship

between the natural enemy and pest in promoting successful biological control is not entirely clear.

The type of control agent is one of the central issues involved with establishing biological control. Characters generally thought to be beneficial include host specificity, high reproductive capacity, dispersal ability greater than the host's, effectiveness at low host density, synchrony with the host, and climatic similarity (Horn, 1988). Parasitoids, including the Aphidiidae, exhibit many of these characters. Perhaps most importantly, aphidiids are generally host specific. Host specificity insures a minimal impact on other elements of the environment. Host specificity has been attributed to coevolution of aphidiids and aphids (Hagen and van den Bosch, 1968) and limited central nervous systems (Greathead, 1986). High reproductive capacity is another advantageous characteristic of most aphidiid parasitoids (Stary, 1970). Effectiveness at low host density is typical of natural enemies which have alternate hosts; predators more often fit this criterion. Synchrony with the host is necessary to all parasitoids for reproduction. The tendency of parasitoids to aggregate in areas of high host density (Waage, 1983; Hagvar and Hofsvang, 1987) is another character regarded as advantageous because a stable system results (Beddington et al., 1978), although the benefits of this character are debatable, as previously discussed. The dispersal ability is an important character that varies a great deal among the Aphidiidae; this will be discussed at length in the section 2.4.

The stability of the agricultural system and the availability of the crop affects the long term survival of the biological control agent. Perennial or semi-perennial

crops, such as orchards and forests provide habitat year round, thus enhancing the persistence of the natural enemy. Agricultural systems can provide refugia through fencerows, fallow or other crops. Diverse agricultural systems, in which two or more plant species are grown simultaneously, generally have reduced herbivore populations, possibly due to increased numbers of natural enemies (Risch et al., 1983; Russell, 1989). Most successful biological control programs with Aphidiidae have been in perennial crops. Successful biological control programs against tree aphids have been reported for the linden (Olkowski et al., 1982), the walnut (van den Bosch et al., 1979) and the black pine aphids (Kfir et al., 1985). Alfalfa is a semi-permanent crop in which the populations of the spotted alfalfa aphid (Hughes et al., 1987; van den Bosch et al., 1959) and pea aphid (Cameron et al., 1981) have been reduced by aphidiid parasitiods. In general, biological control has been more successful in permanent or semi-permanent crops than in temporary or annual systems (Greathead, 1986). A stable relationship between A. ervi and Acyrthosiphon pisum is only likely to develop in semi perennial alfalfa, not in annual field peas. Reducing pea aphid populations in annual peas with biological control presents a greater challenge.

Whether one or several natural enemies provide better control is a hotly debated issue. It can be argued that species competition is reduced if species are introduced singly, and therefore are more likely to become established. However, multiple species introductions may be advantageous if competition is minimal, due to a diverse habitat or use of different life stages of the host. An empirical study

suggests that single species are responsible for successful control in most cases (Ehler and Hall, 1982). However, there are examples of one or several aphidiid parasitoids effecting successful control. Control of the spotted alfalfa aphid in California was achieved with a complex of three parasitoids (van den Bosch et al., 1959). In Australia, three parasitoids were introduced to control the spotted alfalfa aphid, however one parasitoid, Trioxys complanatus Quilis, was responsible for control (Hughes et al., 1987).

Genetic variation is another important consideration for biological control. Evidence for different biotypes and races within species of the Aphidiidae exists. This has tremendous implications for biological control, as genetic differences may affect host finding, host preference and habitat preference. Selection of an appropriate biotype, which is a group with the same genome, is essential to the success of biological control. The colour patterns of A. ervi suggest two different biotypes (Stary, 1983). Parasitoids reared from Acyrthosiphon pisum and Sitobion avenae (F.) exhibit distinctive colour patterns compared to those reared from Microlophium carnosum (Buckt.). Seasonal changes and host plant also affect colouration patterns. A. ervi reared from M. carnosum accept Acyrthosiphon pisum for oviposition but are not able to complete development.

The importance of the selection of an appropriate biotype is demonstrated in the biological control program for the walnut aphid, Chromaphis julandicola Kaltenbach in California. Control was first attempted in 1959, with Trioxys pallidus Haliday. After the failure of the first attempt, an ecotype of this species was

imported in 1968 from Iran (van den Bosch et al., 1979). The hot, arid conditions of California were amenable to the Iranian ecotype of T. pallidus and it spread quickly over California. The second ecotype successfully controlled the walnut aphid.

Appropriate biotypes may be selectively bred. Insecticide resistant parasitoids have been developed for use in an integrated pest management program against the walnut aphid (Hoy et al., 1990). A strain of Trioxys pallidus, selected for resistance to azinphosmethyl, was released into commercial walnut blocks in California. Sampling through the season indicated that T. pallidus survived exposure to azinphosmethyl.

Genetic diversity is an important factor to consider with laboratory experiments involving aphid parasitoids; host selection and preference are altered by genetic factors. Field and laboratory populations of aphidiids sometimes differ in terms of host preference; differences may be the result of the creation of homozygous laboratory populations or altered behaviour caused by the laboratory environment. The use of alternate aphid hosts has been suggested for the maintenance of parasitoid populations during periods when pest aphids are at low numbers. Stinging nettle in fence rows provides habitat for Microlophium carnosum, believed to be an alternate host for A. ervi and Ephedrus lacertosus Haliday (Perrin, 1975). However, another study with A. ervi suggests that it does not respond to M. carnosum (Powell and Zhi-li, 1983). A. ervi was tested with an olfactometer for abilities to respond to different hosts and aphids; it does not respond to M. carnosum or nettle leaves, despite field records of parasitism. Host preference experiments revealed different

results for laboratory and field populations. Host transfer trials conducted with A. ervi and Aphidius rhopalosiphi De Stefani Perez cultured with different hosts revealed differences in host preference (Powell and Wright, 1988). A. ervi cultured on Acyrthosiphon pisum does not transfer to M. carnosum, but those cultured on M. carnosum demonstrate no preference. This population of A. ervi would, therefore, have the potential to be maintained with M. carnosum in fencerows without switching host preference. This is evidence that there are different biotypes or races of A. ervi, perhaps produced through laboratory inbreeding.

Papaj et al. (1987) found differences in host preference and learning between wild and laboratory populations of the Mediterranean fruit fly, Ceratitis capitata (Wiedemann). Naive wild and laboratory flies were exposed to sweet and mock orange for three days and then tested for their propensity to oviposit in mock or sweet orange. Naive wild flies oviposited in sweet and mock oranges with similar frequency, while the naive laboratory flies oviposited in sweet orange significantly more than in mock orange. Wild flies preferred the fruit with which they had previous experience. Laboratory flies previously exposed to mock orange preferred it, however, laboratory flies previously exposed to sweet orange demonstrated no preference. Learning ability was tested by exposing the flies with previous ovipositional experience to another host fruit for days and testing their preference. Fruit acceptance was different for the wild and laboratory flies; laboratory flies significantly altered their preferences after exposure to sweet orange while the host preference of wild flies was affected more by exposure to mock orange. The authors

suggest that the differences are based on genetic variations caused by selection in artificial culture.

Testing both field and laboratory populations is an important step in identifying potential problems. Undoubtedly characters, such as larval competition and instar preference, are affected by genetics and could be incorrectly assessed with a homozygous population. The relevance of laboratory experiments investigating the physiology and biology of parasitoids depends on an adequate representation of the natural population.

In summary, aphidiid parasitoids have many qualities sought in biological control agents such as host specificity and high reproductive capacity. Perennial crops are more conducive to their success as biological control agents. Questions remain concerning the number of natural enemies best suited for biological control and whether stability is necessary. Genetic and behaviourial variability of the parasitoids must be considered when extrapolating to the natural population from laboratory experiments, when selecting an appropriate biotype for release and when selectively breeding superior biological control agents. An understanding of the potential biological control agent's ecology and biology will be useful to the implementation of a biological control program in most cases (Pimental and Goodman, 1978). One important quality of a biological control agent, which has not been examined in Aphidius ervi, is the ability to disperse. The dispersal abilities of A. ervi were therefore investigated.

2.4 Dispersal, an important character of a biological control agent

An important aspect of a biological control program involves the dispersal and host finding ability of the natural enemy used. Knowledge of the dispersal abilities of a natural enemy is an important consideration in order to manage the biological control agent productively. Although release experiments have not been monitored for the Aphidiidae, other hymenopterous parasitoids display limited dispersal abilities. An egg parasitoid of the spruce budworm, Trichogramma minutum Riley, was introduced inundatively and its movement from the central point monitored (Smith, 1988). The average distance travelled in 5 days was 18.5 m. The furthest movement of Muscidifurax zaptor Kogan and Legner (Pteromalidae), a pupal parasitoid of house and stable flies, was 8 m (Pawson and Peterson, 1988). Dispersal of over one km has been recorded for the egg parasitoid of plant hoppers, Anagrus delicatus (Mymaridae) (Antolin and Strong, 1987). Glyptapantales flavicoxis Marsh (Braconidae), a parasitoid of the gypsy moth, does not disperse more than 150 m from the point of release (Krause et al., 1991). Dispersal abilities of aphidiid parasitoids can be inferred from records of movement after introductions; the mechanism of dispersal and distances travelled varies.

The Aphidiidae may disperse as a larva inside an alate aphid or as an adult. Dispersal as a larva only occurs with species which have an ovipositional preference for aphid instars in the third or fourth stage. If an alatiform nymph is parasitized in the first or second instar, wing development is disrupted (Lui and Hughes, 1984). Parasitoids which have ovipositional preferences for older instars have the potential

to travel further because alate aphids can be carried great distances by winds. The potential to arrive simultaneously with the founders of new aphid populations exists for dispersing parasitoid larvae. Dispersal as a larva is significant for some species of Aphidiidae, such as Praon volucre Haliday (Stary, 1970). If dispersal as a larva is an important mechanism for a particular species, it must parasitize older instars and therefore ovipositional preference is an important clue. The mechanism of dispersal can be deduced by examining ovipositional preferences directly and by collecting alate aphids to check for parasitization. In addition, monitoring the spread of newly released parasitoids as some biological control release programs have done, allows inferences as to dispersal mechanism to be made.

Dispersal distances have been monitored in many biological control programs. In California, three parasitoids were introduced to control the spotted alfalfa aphid in alfalfa from 1955 to 1957 (van den Bosch et al., 1959). The spread of these parasitoids, Trioxys utilis Muesebeck, Praon palitans Muesebeck, Aphelinus semiflavus Howard, varied because of their differing abilities to disperse. P. palitans has an ovipositional preference for third instars; parasitized alate aphids carry the parasitoid larvae up to 30 km (Schlinger and Hall, 1959). This dispersal advantage led to the greater spread of P. palitans initially. T. utilis oviposits preferentially in first, second or third instars. The parasitized nymph dies before reaching maturity, precluding the possibility of developing functional wings. First and second instars are preferred by A. semiflavus disallowing dispersal of the host aphid as well (Schlinger and Hall, 1959). By 1962, T. utilis became established widely due to its greater

climatic tolerances (van den Bosch et al., 1964). Dispersal as an adult resulted in its slower spread into new areas.

In Australia, three parasitoids, Trioxys complanatus, Praon exsoletum (Nees), and Aphelinus asyschis Walker, were introduced to control the spotted alfalfa aphid (Hughes et al., 1987). All three became established, but only T. complanatus maintained a high population over the following three years. T. complanatus spread throughout the alfalfa growing areas of Australia, which are extensive in temperate areas from southern Queensland to south-west Western Australia. Parasitoids were established on nursery alfalfa crops, and farmers introduced parasitoid-infested hay into their alfalfa fields. Between-field parasitoid movement was, therefore, largely anthropogenic, although T. complanatus apparently moved within fields and controlled the spotted alfalfa aphid.

Strip cutting maintained the parasitoid, Aphidius smithi, and increased its control of spotted alfalfa aphids in California (van den Bosch et al., 1967) Parasitoids, primarily females, were detected in the uncut strips. However, the authors suggest that movement of the parasitoids is due to habitat change, rather than an active phase of dispersal. In other words, the parasitoids would not move unless their habitat became inhospitable.

In contrast, grain aphid parasitoids do not move within fields very effectively (Carter, 1987). A winter wheat field was sprayed for all insects in alternate strips; the unsprayed strips were left as reservoirs for parasitoids. The amount of parasitism in the sprayed strips remained minimal throughout the season despite the burgeoning

aphid population, indicating that the parasitoids did not move from the unsprayed strips.

Knowledge of A. ervi dispersal will help predict its potential value as a control agent. Knowledge of stimuli, as well mechanisms of dispersal, will allow the manipulation of parasitoids. Different species within the Aphidiidae have varying capabilities for flight or utilization of aphids as dispersive vehicles. Considering the details of the biology of the potential biological control agent may increase the probability of success.

3. MATERIALS AND METHODS

The investigation of the dispersal of Aphidius ervi focused on three major themes. First, the life stage or mechanism responsible for dispersal was investigated. Second, the amount and pattern of movement of the parasitoid in alfalfa and into field peas was documented and an attempt was made to increase the number of A. ervi in two pea fields in 1991. Third, the behaviour of the parasitoids which might affect their dispersal from alfalfa was examined in the laboratory.

3.1 Life Stage of Dispersal

The dispersing stage was investigated by collecting airborne insects with two four foot suction traps at the Agriculture Canada Research Station in Glenlea, Mb. The traps were located 10 m apart on a small hill between a wheat field and some oak trees.

One suction trap collected insects onto a faba bean plant (Vicia faba minor (L.) cv. Diana). Plants were changed three times a week in 1990 and two times per week in 1991 from mid June until the end of August. Use of a leguminous plant allowed for the selection of the pea aphid, which feeds on legumes. No other aphid which resembles the pea aphid feeds on leguminous plants. Pea aphids were removed from the trap plant with a small paintbrush and reared on excised faba bean leaves. Mummy formation was used as an indicator of parasitization after one week of incubation at 20°C, 20hL:4hD.

The second suction trap collected insects into Weaver's solution (100 ml 40%

formaldehyde, 5 ml glacial acetic acid, 400 g chloral hydrate made up to 2 litres with water). Aphids were preserved in Weaver's solution as it does not contain alcohol which dehydrates aphids making them too brittle for dissection. Weekly samples were sorted to remove Acyrthosiphon pisum and A. ervi. Acyrthosiphon pisum were dissected and examined for the presence of parasitoid larvae.

3.2 Pattern and Extent of Dispersal

Sampling schemes were designed to examine the abundance and pattern of A. ervi in perennial alfalfa and annual field peas. Population density and distribution within an alfalfa plot were examined and compared to those in commercial pea fields. Population densities of A. ervi were estimated with sweep net sampling, and the percent parasitism of pea aphids in both alfalfa and pea fields was calculated. Sticky traps were used to monitor A. ervi movement in and above the alfalfa canopy. Movement from alfalfa to peas within the canopy was also monitored with sticky traps.

The alfalfa plot sampled was located at the University of Manitoba Research Station at Glenlea, Mb. The arrangement of crops within the plot varied between years (Figures 1 and 2). The alfalfa plot used in 1990 was planted 4 years previously. Half of the 1990 alfalfa plot was planted in peas in 1991, while half of the previous pea plot was planted to alfalfa. The plots were surrounded on three sides by wheat fields and the fourth side was edged by a ditch.

3.2.1 Sweep Samples in Alfalfa

In 1991, sweep net samples were collected in an alfalfa plot at Glenlea. Although direct comparisons cannot be made, because of differences in sampling efficiency, the numbers and seasonal patterns of Aphidius ervi could be roughly compared to those found in peas. Ten samples of 25, 180° sweeps were collected each week from June 5 to August 21. Samples were taken along a transect approximately 2-3 m from the edge of the plot. Five steps (approximately 5 m) separated the collection of each sample. The sweep samples were put into small plastic bags and stored in a freezer until they were sorted. Numbers of A. ervi were recorded.

3.2.2 Sweep Samples in Peas

Four commercial pea fields around Morris, Manitoba were sampled for A. ervi in 1990 and 1991. The fields were in different locations in each year. In 1990, a pea plot at Glenlea Research Station was also sampled. The abundance of the parasitoids in field peas over the summer was estimated from the sweep net samples. Ten samples of 25 (1990) or 30 (1991) 180° sweeps were collected each week from two parallel transects in the middle and edge of each field. Edge samples were taken within 2 m of the crop margin. Middle samples were taken from the approximate middle of the field, which was at least 20 m from the edge of the crop; the first sample was collected 10 steps (approximately 10 m) into the field. Sweep sampling was conducted along two parallel transects, 10 steps (approx. 10 m) were taken

between samples. The samples were stored in a freezer until they were sorted and numbers of A. ervi counted. Numbers of A. ervi were compared between the edge and middle of each field and between fields using analysis of variance, after using Bartlett's Test to confirm homogenity of the variance (Snedecor and Cochran, 1980).

3.2.3 Pea Aphid Populations and Levels of Parasitism in Peas and Alfalfa

Pea aphid populations and the numbers of parasitized pea aphids were assessed as an indicator of the relative abundance of A. ervi and its impact on the pea aphid population.

From four commercial pea fields around Morris, Manitoba the pea aphids on 50 20 cm stem samples from both the edge and middle of each field were counted each week in 1990 from July 5 to August 2. As well, 100 aphids, 5 aphids from every fifth stem sample counted, were collected each week. These were reared on excised faba beans at 20°C 20hL: 4hD in the laboratory to check for parasitism.

Larger numbers of aphids were collected in 1991, as the aphid samples collected in 1990 were too small to detect parasitism. Fifty 20 cm stem samples were collected from both the edge and middle of each of the four fields every week from June 28 to July 30. Each sample was placed in an individual bag and returned to the laboratory in a cooler. In the laboratory, all the aphids were counted and all but first instar aphids were reared on excised faba bean leaves with the same conditions as in 1990. One week later, the aphids were examined for mummy formation as an indicator of parasitization.

In 1991, the percent parasitism in the alfalfa plot at Glenlea Research Station was estimated weekly from June 10 to August 27. Ten samples of 10 third or fourth instar aphids each were collected and reared on excised faba bean leaves. One week later they were checked for mummy formation and percent parasitism was calculated for each sample.

3.2.4 Sticky traps in Alfalfa

Sticky traps were placed in alfalfa above and in the plant canopy once a week during the growing season of 1990 and 1991. The traps were constructed of a 21.5 by 28 cm colourless transparent plastic sheet supported by a cardboard frame stapled to a wooden stake. Sticky stuff^{tm} was applied to the sheets with a paintbrush. The traps were colourless in order to be as non-attractive as possible and therefore sample by interception only. In 1990, trapping started on June 25 and finished on August 20, and in 1991 it began on June 26 and finished on August 19. Traps were placed in the middle of an 100 X 100 m alfalfa plot at Glenlea Research Station approximately 10 metres from each other. Four traps were left in the field for approximately 48 hours after which the sticky sheets were covered with plastic wrap to facilitate handling and removed from the wooden stake. Examination of the traps revealed the numbers of A. ervi on each trap. Bartlett's test was used to insure that the variances were homogeneous (Snedecor and Cochran, 1980) and then analysis of variance was used to test for significant differences between the numbers in the canopy and above the canopy.

In 1990, the entire alfalfa plot at Glenlea was cut on July 7. Comparisons between above and below the canopy were not possible for several weeks following. In 1991, cutting of the alfalfa plot was staggered, so that one half of the plot was suitable for sampling at all times. The same plot at Glenlea Research Station was used in both years.

3.2.5 Sticky Traps in Peas

The movement of parasitoids from an alfalfa plot to a pea plot was monitored in an attempt to determine how well parasitoids disperse through a canopy of suitable habitat. A plot of peas cv. Trapper was planted adjacent to the alfalfa plot at Glenlea Research Station. In 1990, the peas were planted on May 25 and in 1991 they were planted on June 4. Sampling began when the crop was about 0.5 m high. The arrangement of the plots in 1990 (Figure 1) differed from the arrangement in 1991 (Figure 2). Sticky traps, similar to those used in alfalfa, were placed in the pea plot adjacent to the alfalfa plot. The traps were equal distances apart, starting and ending 1 metre from the field margin. Traps were placed in the canopy only. Every week during the growing season, from early June to mid August, the sticky traps were placed in the pea plots for approximately 48 hours. After this time, the sticky plastic sheets were covered with plastic wrap to facilitate handling and removal to the laboratory. The traps were examined in the laboratory, and the numbers of A. ervi recorded. Differences in A. ervi numbers in relation to distance from the alfalfa plot were analyzed using analysis of variance and linear contrast on the effect of distance.

3.3 Augmentation

Preliminary results from 1990 suggested that Aphidius ervi disperse in small numbers and too late in the summer to affect pea aphid populations in annual peas. Therefore, introductions of A. ervi were attempted into two pea fields in 1991 using a modified method of Stary (1968). Numbers of parasitized aphids were monitored before and after the introductions.

Faba beans were planted in 16 52 by 26 cm propagation trays containing a 75:25 vermiculite:perlite mixture on June 6. One and a half weeks later 50 - 60 adult laboratory reared pea aphids were added to each propagation tray. One week later, on June 24, when the aphid population was approximately 300 aphids/tray, approximately 20 parasitoid mummies from the laboratory colony were added to each propagation tray.

Two large commercial fields planted with Titan (site 1) and Trapper (site 2) peas near Morris, Manitoba were chosen as release sites. Two one square metre field cages were placed near the centre of each field on June 28. At the same time, two propagation trays of unparasitized pea aphids were introduced into each of the four cages.

The propagation trays with mummified aphids were introduced into the field cages on July 5. On July 14, the field cages were removed, releasing the parasitoids into the field.

To monitor the number of parasitized aphids, the field was sampled before and after the release. Sampling occurred on: June 17(only site one because of rain),

June 28, July 12, July 19, July 25 and August 1. Sampling involved collecting 50 20 cm stem samples from both the edge of the field and from the middle, close to the field cages. Each sample was placed in a small plastic bag and returned to the laboratory in a cooler. In the laboratory, each sample was counted and all the aphids reared for one week to check for mummy formation. Pea aphids from each stem sample were reared in separate petri dishes at 20°C 20hL: 4hD. Percent parasitism was calculated.

3.4 Stimuli Affecting Dispersal

3.4.1 Colony Maintenance

Aphidius ervi used in the behaviour experiment were taken from a colony established with A. ervi collected from alfalfa at Glenlea Research Station. The colony was maintained in a growth room at 20°C and 18hL: 6hD. Parasitoids were reared on Acyrthosiphon pisum, which were in turn reared on faba bean plants. Propagation trays of faba beans were used as the base for a cage. When the plants were two weeks old, approximately 600 second instar aphid nymphs were put in the cage. Two days later, after the aphids had established themselves on the plants, 25 to 30 mummies were added to the cage. Aphids of a similar age were used in order to produce parasitoids of a uniform size. Three cages were maintained. Some mummies from the each of the three cages were distributed into each of the three cages in order to maintain genetic diversity. Each cage yielded approximately 200 parasitoids; and 10 were put in each of the next three cages. Colonies of 30

Aphidius ervi individuals maintain 86% of measured heterozygosity after 14 generations (Unruh et al., 1983). Similar levels of heterozygosity should have been retained in this colony system, as three cages with 30 founding individuals were maintained.

3.4.2 Stimulus Experiment

A stimulus affecting dispersal was investigated in laboratory. Five plexiglass cages (3 000 cm^3) were used as observation arenas. The cages had screened holes along the top of all four sides. Three faba bean plants in 10 cm diameter styrofoam containers were placed in each cage. Faba bean plants were chosen because they are easy to grow in the laboratory and are suitable hosts for pea aphids. The plants were approximately 20 cm high and bent over naturally to form a canopy of sorts in each cage. Either two or three of the cages also had pea aphids; ten second or third instar nymphs were placed on each plant. The aphids were placed on the plants the day before observations began. Two or three newly emerged male parasitoids were placed in every cage in order to eliminate the possibility that lack of males or mating would alter female behaviour. Ventilation and thus humidity control was maintained with small fans, which blew air through the small holes in the cages. The experimental group was maintained with the same photoperiod as the colony.

To begin the observations, a large number of mummies from which adults were soon to emerge were placed in a small petri dish inside a cage. As soon as one female parasitoid emerged, the rest of the mummies were removed and put into the

next cage. If a male emerged, it was left in the cage; if more than one male emerged, the extra males were removed with an aspirator. This procedure was repeated until all five cages had newly emerged female parasitoids. Unnatural disturbance of emerging females was reduced by not handling the adult parasitoids directly.

Observations were conducted three or four times a day, at approximately 9:00, 12:00, 15:00 and sometimes 17:00. Each observation period consisted of watching and recording the behaviour of each parasitoid for two 10 minute bouts. Each parasitoid was observed for at least an hour every day for three or four days. The order in which the cages were observed was randomly assigned for each set of observations. The behaviour of the parasitoid was separated into eight classifications, namely: being out of the canopy, searching, preening, antennal waving, flying, ovipositing and mating. Out of the canopy describes any activity that took place on the top of the cage. Searching was defined as walking on the plant or containers while moving antennae back and forth, presumably to detect host aphids. Preening involved either cleaning antennae by drawing them through the mouth or cleaning the wings by brushing the hind legs over them while standing still. Antennal waving was defined as standing still while waving the antennae back and forth. Flying involved flying between plants. Ovipositing involved inserting the ovipositor into an aphid, although the aphids were not dissected to check for eggs. Mating was only observed once. Each behaviour was mutually exclusive. These observations were recorded on a standard data sheet (appendix 1). For each 10 minute period the

amount of time involved in each activity was calculated as a percentage.

Seven replicates of this experiment were conducted between August and November 1991. Analysis of variance was employed to determine if there were significant differences in behaviour between parasitoids with and without access to aphids, between days and between replicates.

4. RESULTS

4.1 Life Stage of Dispersal

The two potential life stages in which A. ervi could disperse were collected, namely alate pea aphids, which could contain parasitoid larvae, and adult parasitoids. None of the pea aphids collected in preservative or in the plant trap were parasitized, although numerous aphids were collected in July and August (Figures 3, 4, 5 and 6). Very small numbers of parasitoids were collected into preservative. In 1990, two parasitoids were caught during each of the sampling periods of July 18 to 25 and August 1 to 8. In 1991, only one parasitoid was caught in the week of July 24 to 31. The parasitoids caught were female.

To compare resident and dispersing populations, A. ervi populations and the amount of pea aphid parasitization in alfalfa and annual peas were surveyed.

4.2 Pattern and Extent of Dispersal

4.2.1 Aphidius ervi in Alfalfa

Numbers of A. ervi in the alfalfa plot were low throughout June and peaked at the end of July (Figure 7). The peak occurs at a similar time to that in the pea crop (see below), although the numbers were greater in alfalfa.

4.2.2 Aphidius ervi in Commercial Pea Fields

In contrast to alfalfa, relatively few parasitoids were caught in five pea fields sampled in 1990 (Table 1) and four fields sampled in 1991 (Table 2). The numbers

collected in the edge and middle of each field were not significantly different in 1990 ($F=0.03$, $df=1,47$, $P> 0.05$) or 1991 ($F=0.01$, $df=1,11$, $P> 0.05$). The peak in numbers occurred at in the beginning of August, which is similar to the alfalfa plot. The other measure of the presence of the parasitoid was its impact on the pea aphid population.

4.2.3 Pea Aphid Populations and Percent Parasitism in Peas and Alfalfa

Overall, the pea aphid populations in the commercial field peas were high in 1990, peaking at an average of 55 aphids per 20 cm stem sample (Figure 8). There was no overall significant difference between numbers in the edge and middle of the fields ($F=0.02$, $df=1,392$, $P> 0.05$). The peak population occurred at the beginning of August. In 1991, the pea aphid populations were lower and peaked in mid July (Figure 9-12). In fields 1 and 2, the peak population was 30 aphids per 20 cm stem sample; fields 3 and 4 were sprayed, and had minimal numbers of aphids. Differences between pea aphid numbers in the middle and edge of the four fields were not significant in 1991.

In 1990, accurate estimates of parasitism were not obtained. 100 aphids were collected from every field, however on collecting dates August 2 and 7th, which were very hot, high mortality of the aphids ensued. None of the aphids collected during July were parasitized. Many aphids were infected with fungus, which contributed approximately one third of the mortality of all the samples over the summer. The parasitism rate for July was probably low, but the rate of parasitism for August is

unknown. The parasitism of pea aphids in all four commercial pea fields was low in 1991 (Figures 9-12), never rising above 6%. The total number of aphids per individual stem sample varied from 1 to 80. Parasitism of pea aphids was much higher in the alfalfa plot (Figure 13). Peak parasitism of 23% occurred in late July.

Populations of A. ervi and the amount of parasitism were both lower in annual peas than in alfalfa. This suggests that A. ervi remains in its overwintering site in alfalfa. The next experiment was designed to examine dispersal out of alfalfa in more detail.

4.2.4 Sticky Traps in Alfalfa

In both 1990 and 1991, more parasitoids were caught in the canopy than above the canopy (Tables 3 and 4). In 1990, several traps were blown down by strong winds and data from these traps were discarded from analysis; the numbers of samples were further reduced by the discontinuous sampling period. Average catches per sticky trap were 3.0± 0.7(ave.± S.E.) in the canopy and 2.0± 0.9 above the canopy in 1990. Although there was not a significant difference in the numbers of A. ervi caught above and in the canopy ($F=0.27$, $df=1,24$, $P> 0.05$), a trend for more A. ervi to remain in the canopy is apparent.

In 1991, the average catches per sticky trap were 0.3± 0.1 above the canopy and 1.6± 0.5 in the canopy. These differences were significant ($F=17$, $df=1,70$ $P< 0.05$ for July). In June and August the numbers of parasitoids caught were very low and no significantly differences between numbers in and above the canopy were found.

These results suggest that A. ervi, when present, remains primarily in the canopy. If this is the case, dispersal would not result to any great extent from parasitoids flying out of the canopy. The possibility of dispersal throughout a canopy was examined in the next experiment.

4.2.5 Sticky Traps in Peas

In 1990, more parasitoids were caught in the row of traps near the alfalfa (2.0± 0.4) in comparison to the middle (1.2± 0.3) and far (1.1± 0.3) sites. Analysis of variance among the three showed differences were not significant ($F=2.8$, $df=2,40$, $P> 0.05$), however a linear contrast on distance revealed significant differences ($F=4.7$, $df=1,40$, $P< 0.05$). In contrast, in 1991, the parasitoids were spread throughout the pea plot. Average catches per sticky trap for the five sites were, in order of increasing distance from alfalfa, 0.9± 0.5, 0.6± 0.3, 0.9± 0.4, 0.8± 0.3 and 1.1± 0.5. No significant difference between the numbers caught at various distances from the alfalfa were shown by analysis of variance ($F=0.39$, $df=4,67$, $P> 0.05$) or linear contrast on distance ($F=0.56$, $df=1,67$, $P> 0.05$). However only small numbers of parasitoids were caught in both years (Tables 5 and 6).

These results indicate that there is some potential for the parasitoid to disperse within a crop or into an adjacent crop. The next experiment involved an attempt to introduce A. ervi into pea fields in order to control the pea aphid population.

4.3 Augmentation

In both sites, percent parasitism was very low before the parasitoids were released. After the release, parasitism was still very low. Various mortality factors adversely affected the pea aphid population in both sites. Just after the pea aphids were released, the Red River Valley region of Manitoba experienced heavy rainfall. The rain may have adversely affected the establishment of the aphids in the field cages, which in turn would adversely affect the establishment of the parasitoids. In addition, field 1 was sprayed for aphid control around the time of the removal of the field cages. The spraying decimated the aphid population, and the parasitoid population. Also, the aphids in field 2 experienced a great deal of fungal mortality. The aphid population crashed in early August, and any effect of the released parasitoids was not apparent. No parasitism was detected in the release sites, however, this may be on account of the minimal aphid population.

The last experiment examined possible behavioural reasons for the lack of dispersal performance of A. ervi.

4.4 Stimuli Causing Dispersal

This experiment compared the behaviour of Aphidius ervi with and without access to pea aphids (Figure 14). Parasitoids without access to aphids spent, on average, 50% of their time above the canopy. This was interpreted as an attempt to disperse to a new area. In the presence of aphids, parasitoids spent, on average, 32% of their time out of the canopy. These differences were significant ($F=6.7$, $df=1,30$,

P< 0.05). Parasitoids in cages with aphids spent 43% of their time searching, as opposed to 25% for parasitoids in cages with no aphids (F=9.2 df=1,30, P< 0.01). Parasitoids in cages with aphids also spent more time flying than those with no aphids (F=4.4, df=1,30, P< 0.05). The increased amount of flying, 2% versus 0.7%, probably relates to increased searching behaviour. The time spent flying was low in both groups. There were no significant differences in the time spent preening (F=1.8, df=1,30, P> 0.05) or antennal waving (F=1.5, df=1,30, P> 0.05).

Activity patterns over the four days of each experiment differed significantly in terms of amount of time spent in the canopy (F=3.3, df=3,536, P< 0.05). On days 1 and 4, parasitoids without access to aphids spent more time out of the canopy as compared to the parasitoids with access to aphids. This could be interpreted to mean that the parasitoids without aphids remain in their environment for a day before moving on. The amount of time spent searching did not vary significantly over the course of the experiment (F=0.65, df=3,536, P> 0.05).

The difference between replicates is not significant, in terms of time spent out of the canopy (F=1.7, df=6,487, P> 0.05), if the fourth day is excluded from analysis. Including data from the fourth day, results in significant differences between the replicates in terms of time spent out of the canopy (F=2.2, df=6,536, P=0.05). The amount of time searching does not vary significantly between replicates (F=1.9, df=6,536, P> 0.05).

5. DISCUSSION

This investigation centred on the dispersal abilities of Aphidius ervi, a potential biological control agent for the pea aphid. The mechanism, pattern, extent and behaviourial aspects of dispersal were investigated to gain information about the movement of A. ervi from its overwintering sites in alfalfa to annual field peas.

All factors investigated suggest that A. ervi disperses less readily than its host. Because the predominant life stage to disperse is the adult, which is relatively poor disperser, A. ervi would not be prone to move long distances. Sampling both alfalfa and pea fields corroborated the prediction that parasitoid density and percent parasitism are higher in alfalfa than in annual peas. An attempt to increase the A. ervi population was not successful, however the technique may have potential to reduce pea aphid populations in pea fields. Laboratory experiments suggested that A. ervi displays a greater dispersal response when hosts are not available.

5.1 Mechanism of Dispersal

Aerial insect populations may be effectively sampled with suction traps. Suction traps neither attract or repel insects but their efficiency decreases with increasing winds and with larger insects (Southwood, 1978). In this study they were used to catch alate pea aphids and the aphid parasitoid, Aphidius ervi, which are both relatively small insects. Adult female parasitiods were caught in the suction traps, and no parasitized aphids were ever caught in the suction traps, suggesting that the primary dispersal mechanism of A. ervi is the flight of the female adult.

Aphidiid parasitoids have been recorded dispersing as adults (Carter, 1987; Schlinger and Hall, 1959) and as larvae (Cameron et al., 1981; Bahana and Karuhize, 1986); the distance travelled by larvae greatly exceeds that of adult parasitoids. Alate aphids, potentially containing parasitoid larvae, can migrate long distances on the wind, while there is little evidence that adult parasitoids disperse far. Possibly adult aphidiid parasitoids are unable to move into or be carried into winds which would carry them long distances. Aphids are not strong fliers, but have developed a set of behaviours which allows them to use the wind to disperse (Johnson, 1969). No evidence for such behaviour exists within the Aphidiidae.

All the parasitoids caught were female. Other workers have also detected female parasitoids dispersing disproportionately to males. In collections made in strips of cut alfalfa between strips of uncut alfalfa, female Aphidius smithi were much more common than males (van den Bosch et al., 1967). Aphidius spp. immigrants found in late-sown winter wheat in England are primarily female (Vorley and Wratten, 1987). Aphidiids were collected over the East China Sea from a ship with an aerial plankton net; all specimens were female (Mochida and Takada, 1977). These authors suggest that females are more likely to be caught because they live longer. Female dispersal likely involves the location of suitable egg laying habitat; female dispersal is important to the continuation of the species and therefore might be expected to be more predominant (Johnson, 1969).

Newly colonized areas tend to have parasitoid populations with a skewed sex ratio because primarily unmated females disperse (Stary, 1970). In a new area, the

first generation would be primarily male as the females would all be unmated. For example, in late-sown wheat fields in England, spring populations of female Aphidius spp. were followed by a generation with a male biased sex ratio (Vorley and Wratten, 1987). A population with a large number of males would not have as big an effect on the aphid population as a population with a higher proportion of females.

As the adult parasitoid is the dominant dispersal stage of Aphidius ervi, its potential to disperse into new territory annually may be somewhat limited. If the parasitoids cannot disperse very far during each growing season, parasitoid numbers must be artificially increased for use in a biological control program against the pea aphid in annual peas. The parasitoids that arrive in the annual crop naturally may be primarily unmated females which produce a generation with a large number of males, which do not reduce the aphid population.

5.2 Pattern and Extent of Dispersal

As predicted, more Aphidius ervi were found in alfalfa, their overwintering site as opposed to annual field peas, to which A. ervi must disperse. A. ervi is found in alfalfa fields early in the year, that is, in May and is found in diapause in alfalfa in August and September, it is believed to overwinter in alfalfa on dessicated leaves (Matheson, 1989). Two measures, parasitoid adult numbers and percent parasitism of pea aphids, were examined in alfalfa and peas. Although direct comparisons cannot be made, because of differences in sampling efficiency, the numbers and seasonal patterns of Aphidius ervi in alfalfa can be roughly compared to those found

in peas. Relatively low parasitoid populations characterized the pea fields sampled in 1990 and 1991. At least twice as many parasitoids were caught in the alfalfa plot. Highly variable parasitism rates which never exceeded 6% were evident in pea fields sampled in 1991, while parasitism peaked at 23% in alfalfa. Field 4 in 1991 had higher parasitism rates and larger populations of A. ervi than any other field. An alfalfa field was one quarter section away from field 4, and this may account for the higher populations of A. ervi. In 1983 and 1984, Matheson (1989) also found lower levels of parasitism in peas (< 1% until mid August) than in alfalfa where percent parasitism peaked in early August at 11% in 1983 and 29% in 1984. In 1985, percent parasitism was also measured, but it was insignificant due to high fungal mortality of pea aphids.

Abundant populations of pea aphids were present in the pea fields sampled in 1990 and 1991 and thus the lack of parasitoids is not due to a lack of available hosts. In 1990, the aphid population grew steadily over July, peaked in late July and declined rapidly in early August. Other workers have described similar seasonal patterns for pea aphids (Maiteki et al., 1986; Soroka and Mackay, 1990). The very wet weather in the spring of 1991 probably caused the reduction in aphid numbers in comparison to 1990. To limit the pea aphid population, parasitoids would have to be in the pea crop before the peak aphid population in late July or early August. Because the pea aphid has a high reproductive rate, the parasitoids would have to be introduced in early July, to have any chance of moderating the aphid population.

A closer look at parasitoid movement from alfalfa, and into peas was

conducted with sticky traps. Fewer parasitoids were caught above the alfalfa canopy suggesting dispersal out of the canopy does not to occur to a large extent. Parasitoid numbers in the canopy were greater than numbers caught above the canopy, although the aerial volume sampled above the canopy was proportionally smaller above the canopy as opposed to in the canopy. Dispersal through a canopy of suitable habitat was also examined by placing sticky traps in a pea plot next to an alfalfa plot. Few parasitoids were caught in both 1990 and 1991, however the spread of the parasitoids varied between years. In 1990, significantly more parasitoids were caught closer to the alfalfa plot while in 1991 the parasitoids spread evenly throughout the field. The arrangement of traps in 1991 was altered to determine more precisely the movement of the parasitoids. The indication from the 1991 data that some parasitoids disperse throughout a canopy may have more weight than the 1990 data which suggests the opposite. The numbers of parasitoids caught in the canopy of alfalfa was slightly more than the numbers caught in the pea canopy in both years, indicating that some dispersal within the canopy does occur. Although parasitoids did not leave alfalfa in large numbers either out of or through the canopy, the potential to disperse through a canopy was present, for the 200 m distance measured.

The pattern of dispersal within the commercial pea fields also indicates that A. ervi dispersed throughout a canopy of suitable habitat. No difference was found between the numbers of parasitoids in the edge and middle of each field, suggesting that the parasitoids actively disperse throughout the fields. Cameron et al. (1983) observed dispersal throughout a canopy by another aphidiid parasitoid. Early season

releases of Aphidius eadyi Stary, Gonzales and Hall in alfalfa fields in New Zealand led to the presence of the parasitoid throughout the field within one week. Multiple introduction sites might compensate for the slow rate of dispersal.

Providing alfalfa refugia closer to peas might allow A. ervi to enter the pea crop from alfalfa earlier and in larger numbers. A. ervi would have a reduced distance to disperse in that case. Alteration of the arrangement or composition of the agroecosystem to enhance natural enemy populations has been advanced as an approach to reduce pest populations. Thomas et al. (1991) successfully increased the number of predators by incorporating grass refugia in wheat fields. Diverse multicropping systems have generally supported larger numbers of natural enemies and fewer pests (Risch et al., 1983; Russell, 1989). As well as providing refugia and alternate hosts for predators and parasites, multicropping systems may disrupt the pest's habitat (Russell, 1989). However, diverse multicropping systems do not always harbour fewer pests. In some cases, pests are able to exploit all the resources offered in a diverse system and increase to damaging levels (Way, 1977). Refugia and alternate hosts can be utilized by pest species as well as natural enemies. On the other hand, monocultures may reduce the effect of pests. Dilution of pest attack by abundance of the plant host, concentration of pest attack in field edges, deprivation of alternate hosts and refugia or a sowing date which puts the pest out of phase with the crop may reduce the pest's impact on the crop (Way, 1977). Although alfalfa provides an overwintering site for A. ervi, reservoirs of parasitoids in alfalfa strips beside pea fields would not likely be successful in providing sufficient parasitoids to

reduce pea aphid populations. Pea aphids, which are also present in the alfalfa, disperse much more readily and reproduce rapidly. It is difficult to exactly compare the reproductive rates, as they vary with temperature and individual. A method of introducing parasitoids without aphids may be necessary.

Annual introductions to enhance the parasitoid population in the annual crop before the aphid population peaks would be necessary for a biological control program against the pea aphid. Some evidence suggests dispersal within the canopy occurs. In large commercial fields, multiple introduction sites might be necessary to insure all the aphids will be reached by parasitoids.

5.3 Augmentation

Attempts at augmentation of the pea aphid parasitoid population in two pea fields in 1991 were unsuccessful. No increase in parasitism of pea aphids was detected. Other workers have attempted to increase the number of aphid parasitoids in crops thorough localized introductions with varying success. Shands et al. (1975) attempted to introduce two parasitoids of aphids infesting potatoes, using three systems: field cages, small plots and small fields. None of these systems displayed an increase of aphid parasitism despite the introduction of tens of thousands of parasitoids. Because negligible aphid parasitism resulted in the field cages and small fields, it is assumed that the parasitoids flew away. In the field cages, unusual behaviour of the parasitoids was observed; congregations were seen on the top and sides of the cages. In the small plots and fields, parasitoids were released directly

into the fields from mesh cages, and such behaviour could not be observed although it may have occurred. The cause of this behaviour is unknown although it may be associated with meterological factors as parasitoids in the laboratory cultures parasitized aphids efficiently. As the parasitoids in the field situations flew away instead of searching the vegetation for hosts, no increase in parasitism resulted. Ankersmit (1982) attempted to increase the amount of aphid parasitism before the peak aphid population, in hopes of lowering the peak. For three years, trials were conducted in wheat fields in the Netherlands using Aphidius rhopalosiphi and Praon volucre to control Sitobion avenae and Metapolophium dirhodum (Walker). In mid May parasitoids and some aphid hosts, S. avenae, were introduced into wheat fields. No increase in parasitism was noted. The author suggested that either the parasitoids dispersed due to lack of hosts or that the original aphid hosts did not become established and therefore only a few parasitoids were produced. Hughes et al. (1987) directed the placement of hay infested with parasitoid mummies into alfalfa fields throughout Australia. Trioxys complanatus became established and decreased the numbers of Therioaphis trifoli Monell, the spotted alfalfa aphid. Alfalfa, which is semi perennial, may be more conducive to the establishment of parasitoids than annual crops. Another successful introduction involved Stary's use of boxes infested with aphids and parasitoid mummies. These boxes are called artificial foci units and led to the establishment of Aphidius transcapicus Telenga to control Hylopterus pruni Geoffr. in Czechoslovakia (Stary, 1968).

For large scale introductions, the addition of alfalfa hay, containing parasitoid

mummies, to the pea crop early in the growing season might allow the introduction of parasitoids without aphids. Hay with an increased number of parasitoid mummies could be produced in field cages or small portable greenhouses in alfalfa fields (Halfhill and Featherstone, 1967). Enhanced aphid populations result from field cages, as the aphids are protected. Field collected or insectary reared parasitoids added to the field cages could parasitize large numbers of aphids. The alfalfa inside the cage, once dried and relatively aphid-free, could be added to the pea field. Aphids do not survive after alfalfa is cut (Harper et al., 1990). This system of annual parasitoid introductions might be successful in reducing pea aphid populations to below the economic threshold. For commercial use of this introduction system, further trials and cost benefit analysis are necessary.

Although the introduction attempts in 1991 were unsuccessful, there is reason to believe the system could be workable. More releases under more controlled circumstances are necessary to determine the possible usefulness of establishing artificial foci of parasitoids in annual peas.

5.4 Stimuli Causing Dispersal

Factors which affect behaviour are important to consider in biological control because they radically affect the actions of the parasitoids and subsequent regulation of the target pest population. Every individual insect has the potential to behave differently depending on its genetic make-up, physiological state and environmental influences (Lewis et al., 1990). Investigations into the mechanism and extent of

dispersal indicated that Aphidius ervi disperses primarily as an adult but usually does not disperse far from its overwintering site, alfalfa. Examination of the possible stimuli inducing dispersal was the next question investigated. Availability of hosts was one environmental factor investigated in terms of its influence on A. ervi dispersal behaviour.

Aphids were used as a stimulus to investigate the dispersal responses of newly emerged A. ervi. Because A. ervi does not display very good dispersal abilities in the field, it was hypothesized that it does not have a discrete dispersal phase, but rather moves only when the habitat is unsuitable. The parasitoids without access to aphid hosts spent significantly more time out of the canopy, which was interpreted as dispersal behaviour. A. ervi with access to hosts exhibited less dispersal behaviour, conforming to the prediction of the hypothesis. To adequately test the hypothesis, more investigations are necessary.

Parasitoids with available aphid hosts spent significantly more time searching than parasitoids without access to aphid hosts. It is not surprising that the parasitoids with access to aphids spent more time searching. After oviposition, which frequently occurred in cages with aphids, searching is intensified (personal observation; Cloutier and Bauduin, 1990).

The dispersal response of A. ervi varied over the four day observation period. Parasitoids without access to aphids did not spent more time out of the canopy than those with access to aphids on the first and third day. On the second and fourth day, parasitoids without access to aphids spent more time out of the canopy. One

interpretation of the results could be that the parasitoids investigate the suitability of their environment before attempting to move on. On the second day, the majority of parasitoids attempt to leave their environment which is devoid of hosts. On the third day, they descend into the canopy, perhaps searching for hosts. On the fourth day, the parasitoids disperse out of the canopy, presumably because they did not find hosts.

Other workers have investigated factors which influence dispersal into new habitat. Giving up time (GUT) is a term referring to the length of time a parasitoid will search until it moves on to new habitat. The apple maggot fly, Rhagoletis pomonella (Walsh), has been the model for many investigations concerning foraging behaviour. Although it is a phytophagous insect, behaviourially and functionally it is similar to an endoparasitic insect. Factors affecting the GUT of the apple maggot fly include host density, host quality (ie. number unparasitized), the visual appearance of fruit and the sequence of successful versus unsuccessful searches (Roitberg and Prokopy, 1983). The structural complexity of the plant affects the foraging and GUT of Trichogramma nubilale Ertle and Davis (Andow and Prokrym, 1990). Simple surfaces were searched for a longer period of time and more efficiently than complex surfaces. Similarly, A. rhopalosiphi prefers searching the leaves rather than the complex surface of the wheat ear (Gardner and Dixon, 1985). Patch size influences the leaving rate of Diaeretiella rapae (M'Intosh), but not finding rates (Sheehan and Sheldon, 1989). Vinson (1976) reviews the factors affecting host selection. This investigation, which involved only host availability as a stimulus, clearly does not

reveal the entire picture of the factors controlling A. ervi dispersal. However it is clear that the dispersal response in a favourable environment was less than in an unfavourable environment.

In terms of annual releases for biological control, reduced dispersal behaviour could be very beneficial. After the parasitoids are released into a pea field, they will likely stay in that area. If the parasitoids initially dispersed after eclosion, many of them would leave the pea field and the pea aphid population would remain intact. Because they disperse less readily if hosts are present, they could be suitable candidates for annual introductions.

6. CONCLUSION

Examination of the dispersal abilities of Aphidius ervi was undertaken to evaluate, in part, its potential for use in a biological control program against the pea aphid in annual field peas. The life stage, pattern, and a stimulus involved with dispersal were investigated. A. ervi overwinters primarily in perennial alfalfa (Matheson, 1989) and must disperse annually into the pea crop. All factors investigated suggest that A.ervi disperses less readily than its host and might require annual introductions into the pea crop for biological control.

To the extent which A. ervi disperses, the life stage involved is the adult, which is apparently a relatively poor disperser. Trapping of dispersing pea aphids was unsuccessful in discovering any parasitized alatae, indicating that dispersal as a larva is not common. Adult parasitoids were caught in small numbers, 4 in 1990 and 1 in 1991. The number of parasitoids caught dispersing would suggest a low level of movement out of alfalfa compared to their host.

Sampling both alfalfa and pea fields corroborated the prediction that most parasitoids remain in alfalfa and few disperse to annual peas. More A. ervi were caught in alfalfa than in peas with sweep net sampling. Their effect on the pea aphid population was correspondingly greater in alfalfa where parasitism peaked at 24%, while parasitism never exceeded 6% in the commercial pea fields sampled. Little dispersal out of the alfalfa canopy was detected with sticky traps; some movement through the canopy of a pea plot proximal to alfalfa was detected. A. ervi seems to have some ability to disperse within a canopy. Ability to disperse within a canopy

throughout a crop would be an essential characteristic for annual introductions for biological control.

Control of the pea aphid with A. ervi was not successful with this author's release effort. Further research is necessary to establish an efficient and effective A. ervi release procedure.

A lack of host aphids promoted greater dispersal response than was noted in the presence of aphids. This evidence suggests that A. ervi might have a tendency to remain in alfalfa, if there are pea aphids present. If introduced into an area with hosts, A. ervi might have a tendency to remain in the new area.

Further research should be directed at refining methods of introducing A. ervi and combining its use with other methods of reducing the damage caused by pea aphids. Some cultivars of field peas are less susceptible to pea aphid attack. A lesser degree of pea aphid control, such as that provided by A. ervi, might be sufficient. Conjunctive use with other aphid enemies, such as lacewings, might have possibilities. A combination of biological techniques could reduce or eliminate the need for chemical pesticides, which would be of great economic benefit.

TABLE 1: Total numbers of Aphidius ervi collected in 10 sweep net samples of 25 180° sweeps from commercial pea fields around Morris and Glenlea, Manitoba 1990

DATE	PF1*		PF2		PF3		PF4		PF5**	
	E***	M***	E	M	E	M	E	M	E	M
JUL 5	1	0	0	0	0	0	1	0	0	0
JUL12	1	2	0	0	0	0	0	0	4	0
JUL19	2	0	0	2	0	3	1	3	0	0
JUL25	12	2	6	16	1	5	15	8	7	2
AUG 2	7	4	11	3	3	11	3	5	9	3
AUG 7	7	5	0	11	10	8	-	-	21	11

*PF= pea field
**PF5= Glenlea Research Station
***E=edge, M=middle

TABLE 2: Total numbers of Aphidius ervi collected in 10 sweep net samples of 30 180° sweeps from commercial pea fields around Morris, Manitoba 1991

DATE	PF1*		PF2		PF3		PF4	
	E**	M**	E	M	E	M	E	M
JUNE 27	0	0	0	0	0	0	0	0
JULY 9	0	0	0	0	0	0	0	0
JULY 16	1	0	0	1	0	0	9	3
JULY 25	10	***	9	8	2	4	16	20
AUG 1	2	***	***		***		4	6

* PF= pea field
** E= edge, M= middle
*** the pea plants in these areas were dead due to flooding

TABLE 3: Numbers of Aphidius ervi caught on sticky traps in an alfalfa plot at Glenlea Research Station 1990

	NO. APHIDIUS ERVI/TRAP							
POSITION OF TRAP	1		2		3		4	
	ABOVE	IN	ABOVE	IN	ABOVE	IN	ABOVE	IN
DATE								
JUNE 25	3	0	0	0				
JULY 6	2	2	0	0	0	0		
JULY 31	6	6	*	3	*	4		
AUG 7	1	1	1	5	3	7	1	7
AUG 12	6	5	0	*	6	*	5	*
AUG 20	0	0	0	2	0	0	1	0

* TRAPS BLOWN DOWN

TABLE 4: Numbers of Aphidius ervi caught on sticky traps in an alfalfa plot at Glenlea Research Station 1991

	NO. APHIDIUS ERVI/TRAP							
POSITION OF TRAP	1		2		3		4	
	ABOVE	IN	ABOVE	IN	ABOVE	IN	ABOVE	IN
DATE								
JUNE 26	0	2	0	0	0	1	0	0
JULY 3	0	0	0	0	0	0	0	0
JULY 8	0	0	0	0	0	0	0	1
JULY 15	1	2	0	6	0	4	0	0
JULY 22	1	4	0	9	0	*	0	4
JULY 29	2	8	4	14	0	12	2	3
AUG 7	0	1	1	2	0	2	1	0
AUG12	0	0	0	0	0	1	0	0
AUG 19	0	2	0	0	0	0	2	0

*TRAP BLOWN DOWN

TABLE 5: Numbers of Aphidius ervi caught on sticky traps in a pea plot next to an alfalfa plot at Glenlea Research Station 1990

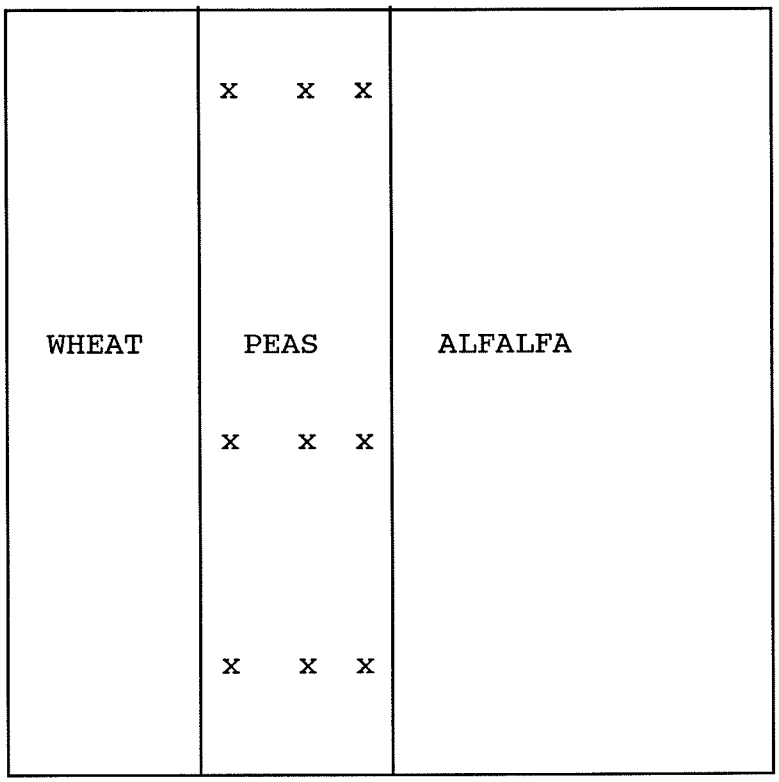
	NO. APHIDIUS ERVI/TRAP											
	FAR TRAPS				MIDDLE TRAPS				CLOSE TRAPS			
DATE	1	2	3	4	1	2	3	4	1	2	3	4
JUNE 25	0	0	-	-	-	-	-	-	0	0	-	-
JULY 6	0	0	0	-	0	0	0	-	0	0	0	-
JULY 9	0	0	0	0	0	0	0	0	0	1	0	0
JULY 14	1	3	1	0	1	0	3	0	3	1	0	1
JULY 23	0	0	3	2	1	2	0	0	0	1	1	5
JULY 31	3	1	1	1	4	2	4	2	2	5	2	6
AUG. 7	0	0	2	0	0	0	0	0	3	0	3	1
AUG. 12	1	1	-	-	0	0	1	1	0	0	0	0

TABLE 6: Numbers of Aphidius ervi caught on sticky traps in a pea plot next to an alfalfa plot at Glenlea Research Station 1991

	NO. APHIDIUS ERVI/TRAP									
DATE	TRAP NO.									
	A*		B		C		D		E**	
	1	2	1	2	1	2	1	2	1	2
JULY 10	0	0	0	0	1	0	0	0	0	0
JULY 15	0	0	0	1	0	0	0	0	0	0
JULY 22	2	7	3	1	0	1	0	3	1	0
JULY 29	3	4	4	1	6	2	2	4	8	2
AUG 7	2	0	2	1	2	2	0	0	2	1
AUG 12	0	0	0	0	1	0	0	0	0	0
AUG 19	0	0	0	0	0	0	1	0	0	0

* FURTHEST FROM ALFALFA PLOT
** CLOSEST TO ALFALFA PLOT

FIGURE 1: LAYOUT OF STICKY TRAPS IN PEA PLOT AT GLENLEA RESEARCH STATION 1990 (trap placement not to scale)



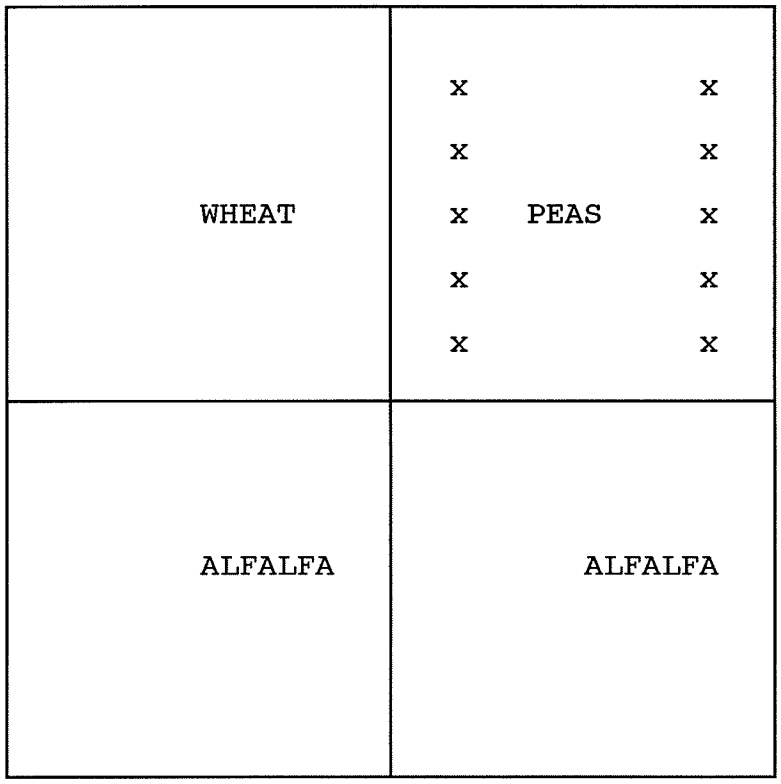
N↑

200 M

200 M

x - sticky trap

FIGURE 2: LAYOUT OF STICKY TRAPS IN PEA PLOT AT GLENLEA RESEARCH STATION 1991 (trap placement to scale)



N↑

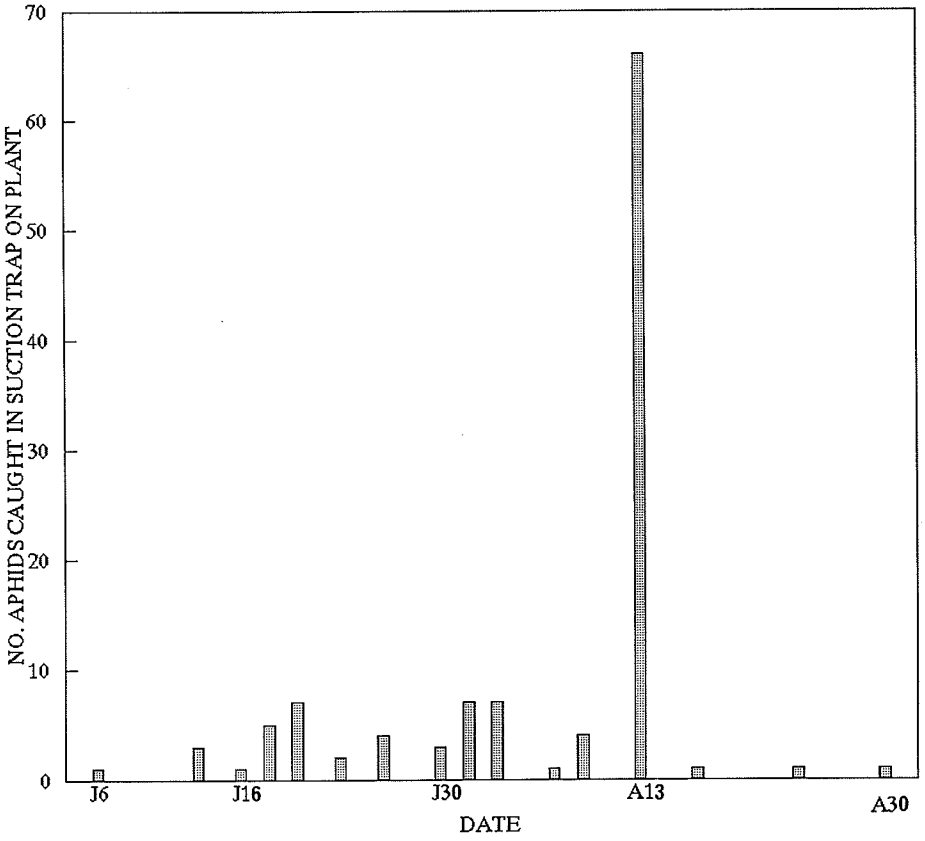
200 M

200 M

x - sticky trap

FIGURE 3: NUMBERS OF PEA APHIDS CAUGHT BY A SUCTION TRAP WITH PLANTS IN 2 TO 3 DAY INTERVALS AT GLENLEA RESEARCH STATION FROM JUNE 13 TO SEPTEMBER 7 1990

FIGURE 4: NUMBERS OF PEA APHIDS CAUGHT WEEKLY BY A SUCTION TRAP IN PRESERVATIVE AT GLENLEA RESEARCH STATION FROM JUNE 27 TO AUGUST 22 1990 (DATE INDICATES FIRST DAY OF WEEKLY SAMPLING PERIOD)


70
60
50
40
30
20
10
0
NO. APHIDS CAUGHT IN SUCTION TRAP ON PLANT
J6
J16
J30
A13
A30
DATE

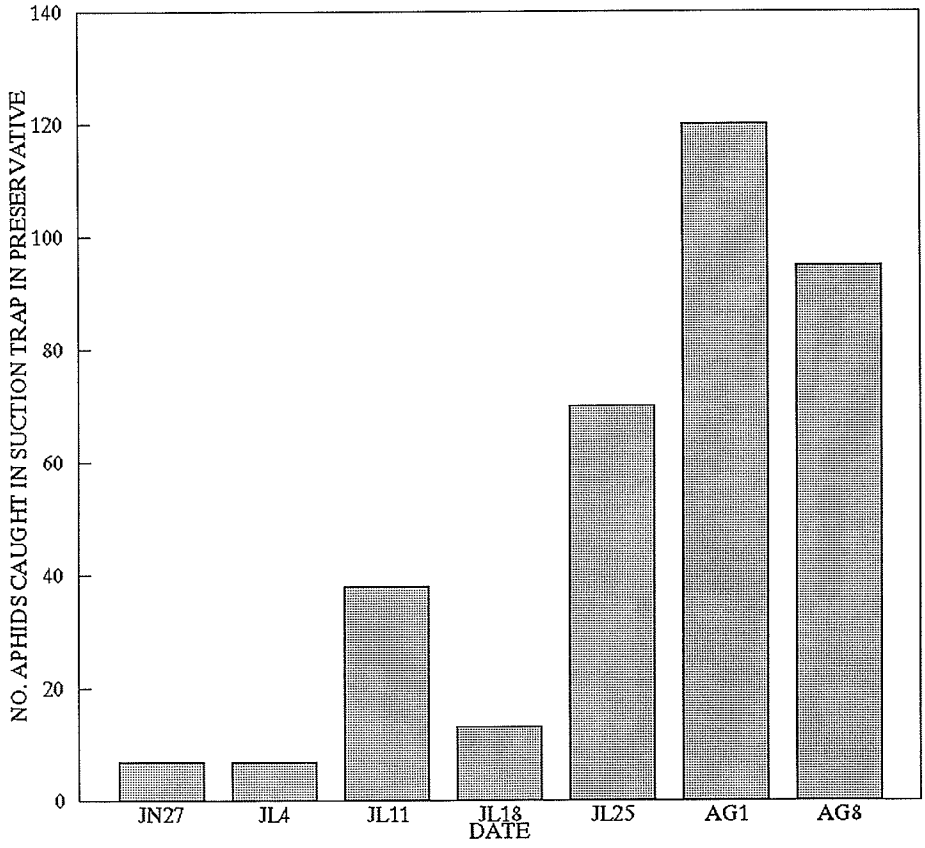
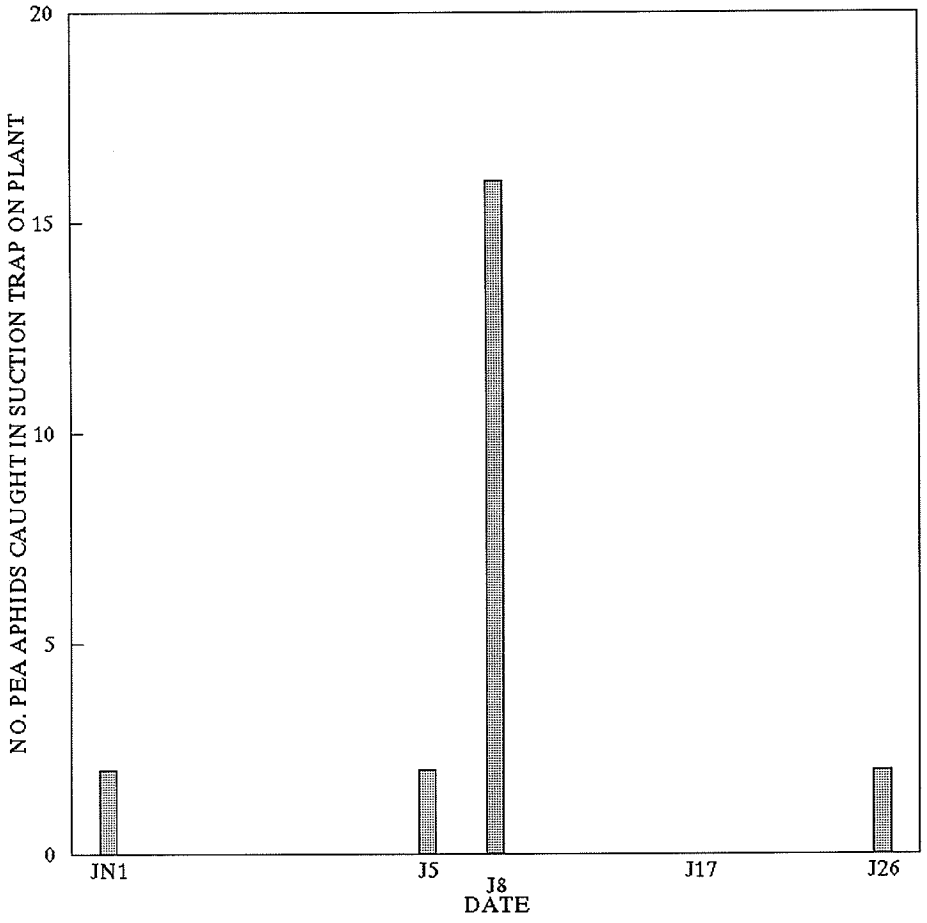

140
120
100
80
60
40
20
0
NO. APHIDS CAUGHT IN SUCTION TRAP IN PRESERVATIVE
JN27
JL4
JL11
JL18
JL25
AG1
AG8
DATE

FIGURE 5: NUMBERS OF PEA APHIDS CAUGHT BY A SUCTION TRAP WITH PLANTS IN 3 TO 5 DAY INTERVALS AT GLENLEA RESEARCH STATION FROM JUNE 17 TO SEPTEMBER 4 1991

FIGURE 6: NUMBERS OF PEA APHIDS CAUGHT WEEKLY BY A SUCTION TRAP IN PRESERVATIVE AT GLENLEA RESEARCH STATION FROM MAY 29 TO AUGUST 21 1991 (DATE INDICATES FIRST DAY OF SAMPING PERIOD)


20
15
10
5
0
NO. PEA APHIDS CAUGHT IN SUCTION TRAP ON PLANT
JN1
J5
J8
J17
J26
DATE

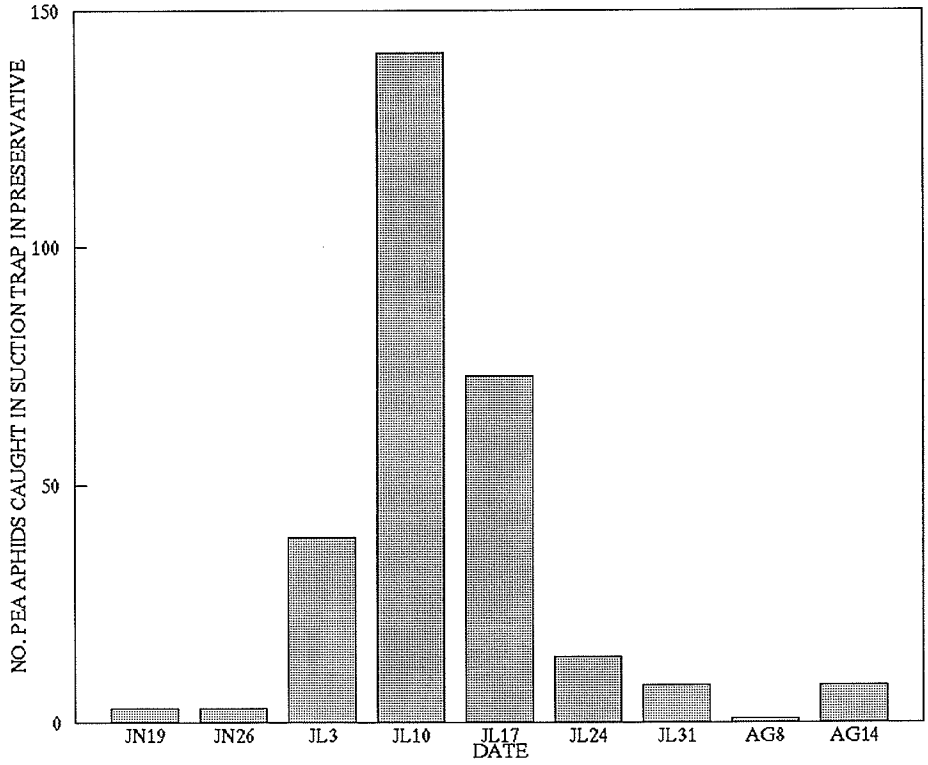

150
100
50
0
NO. PEA APHIDS CAUGHT IN SUCTION TRAP IN PRESERVATIVE
JN19
JN26
JL3
JL10
JL17
JL24
JL31
AG8
AG14
DATE

FIGURE 7: TOTAL NUMBER OF APHIDIUS ERVI CAUGHT IN 10 SWEEP SAMPLES OF 25 180° SWEEPS IN AN ALFALFA PLOT AT GLENLEA RESEARCH STATION 1991

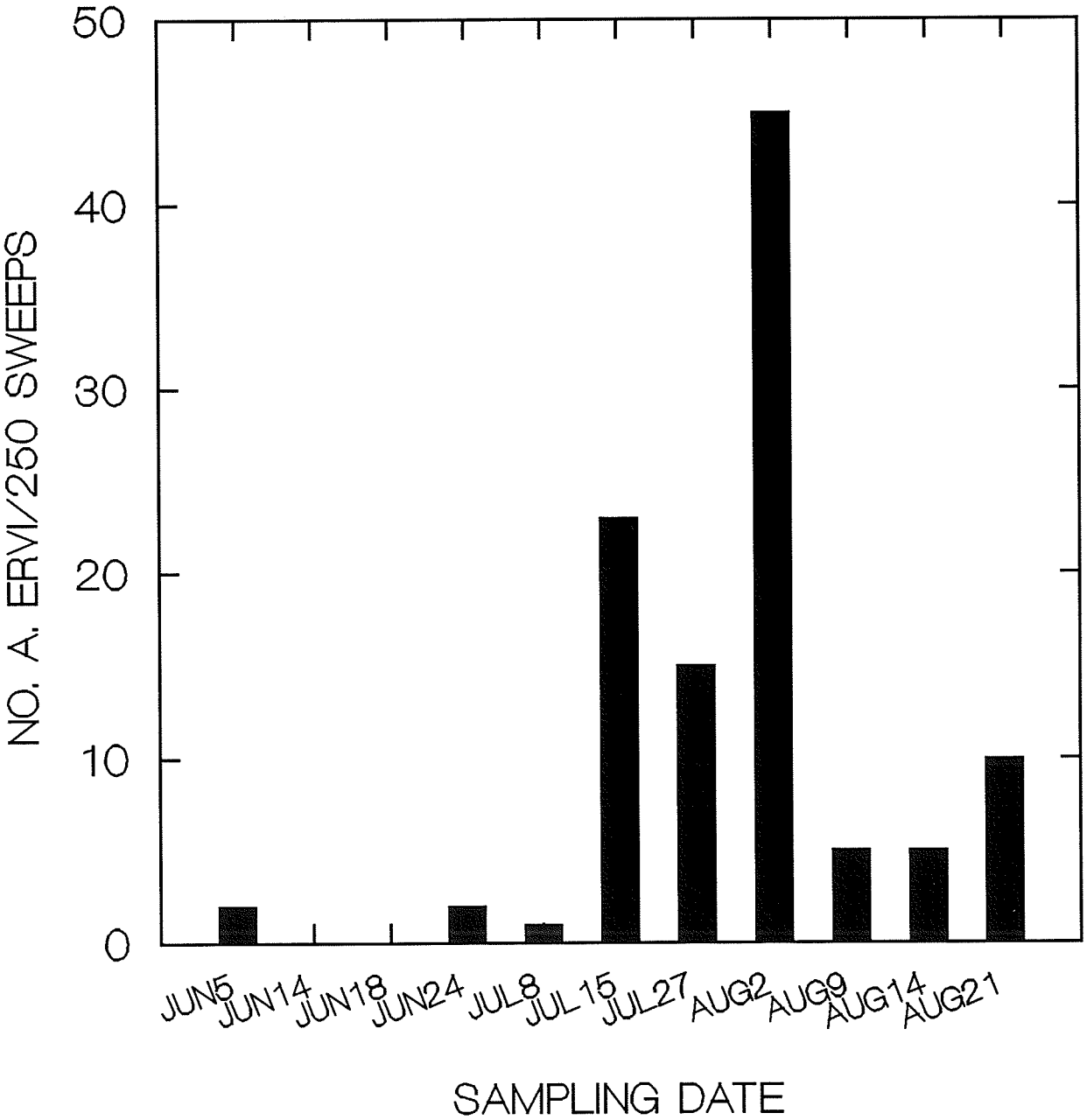

50
40
30
20
10
0
NO. A. ERVI/250 SWEEPS
JUN5
JUN14
JUN18
JUN24
JUL8
JUL15
JUL27
AUG2
AUG9
AUG14
AUG21
SAMPLING DATE

FIGURE 8: AVERAGE NUMBER OF PEA APHIDS PER 20 CM STEM SAMPLE FOR FOUR COMMERCIAL PEA FIELDS MEAR MORRIS, MANITOBA 1991

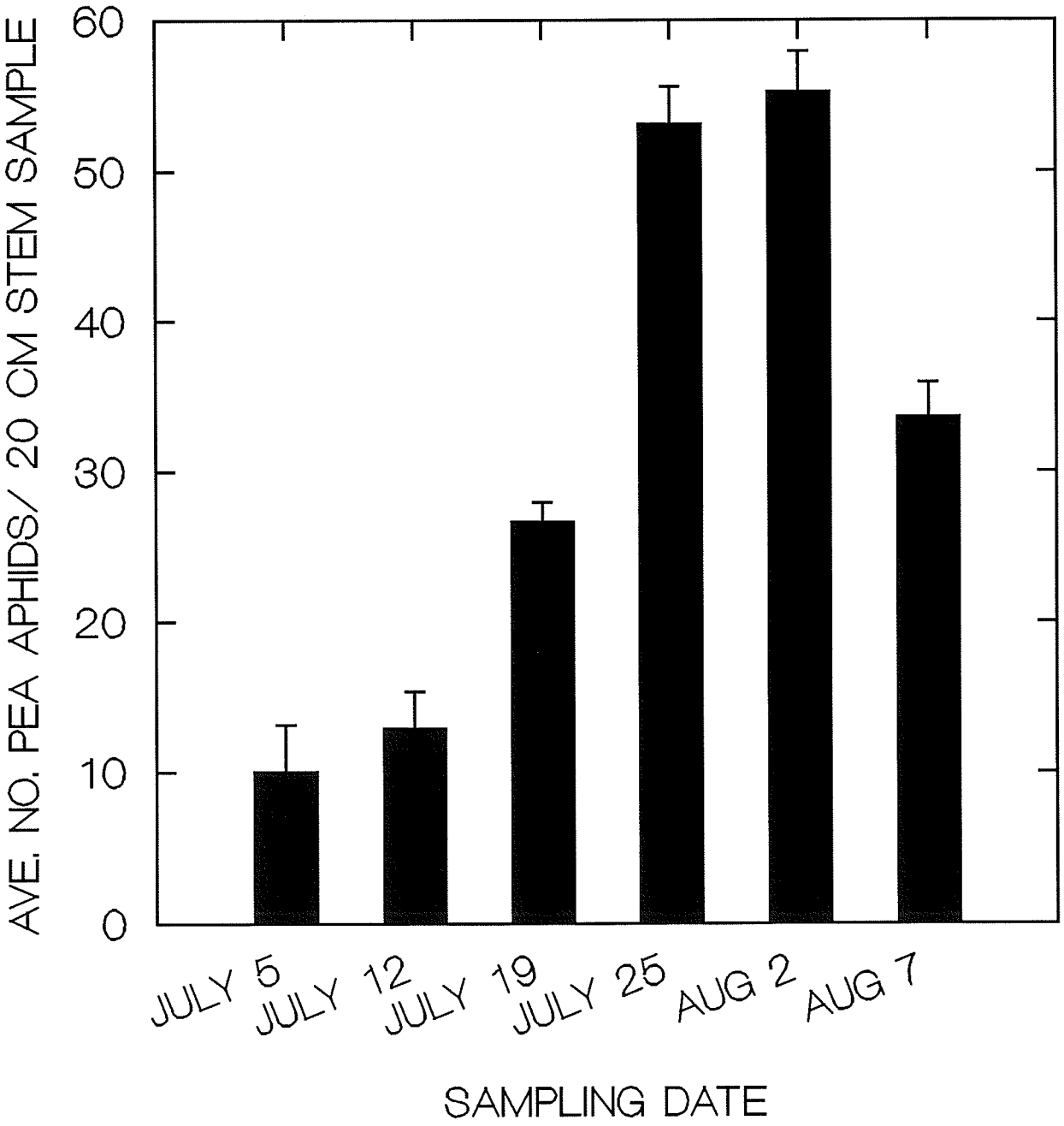

AVE. NO. PEA APHIDS/ 20 CM STEM SAMPLE
60
50
40
30
20
10
0
JULY 5
JULY 12
JULY 19
JULY 25
AUG 2
AUG 7
SAMPLING DATE

FIGURE 9: PERCENT PARASITISM AND AVERAGE NUMBER OF PEA APHIDS PER 20 CM STEM SAMPLE IN PEA FIELD 1, MORRIS MANITOBA 1991

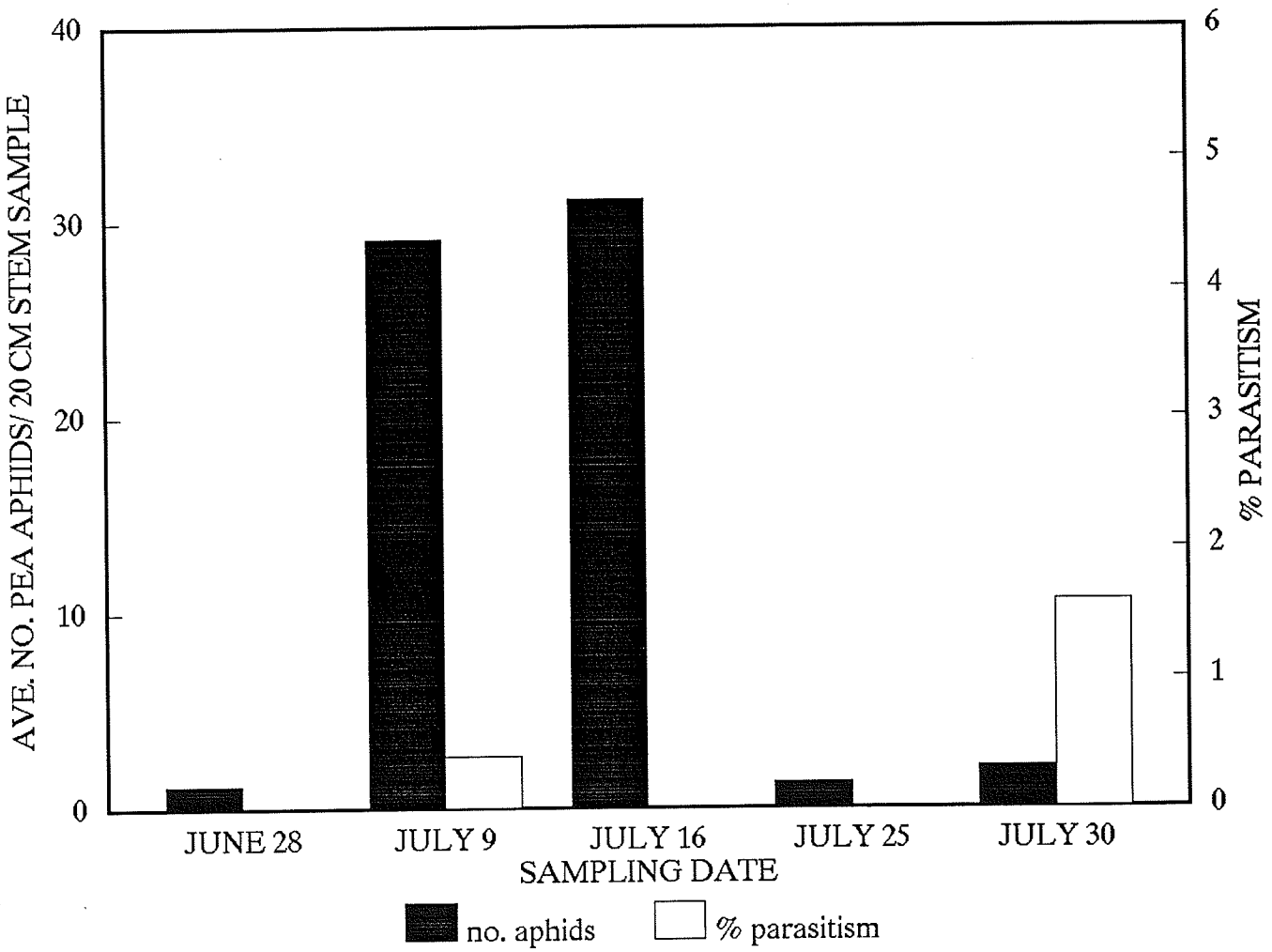

AVE. NO. PEA APHIDS/ 20 CM STEM SAMPLE
% PARASITISM
40
30
20
10
0
6
5
4
3
2
1
0
JUNE 28
JULY 9
JULY 16
JULY 25
JULY 30
SAMPLING DATE
no. aphids
% parasitism

FIGURE 10: PERCENT PARASITISM AND AVERAGE NUMBER OF PEA APHIDS PER 20 CM STEM SAMPLE IN PEA FIELD 2, MORRIS MANITOBA 1991

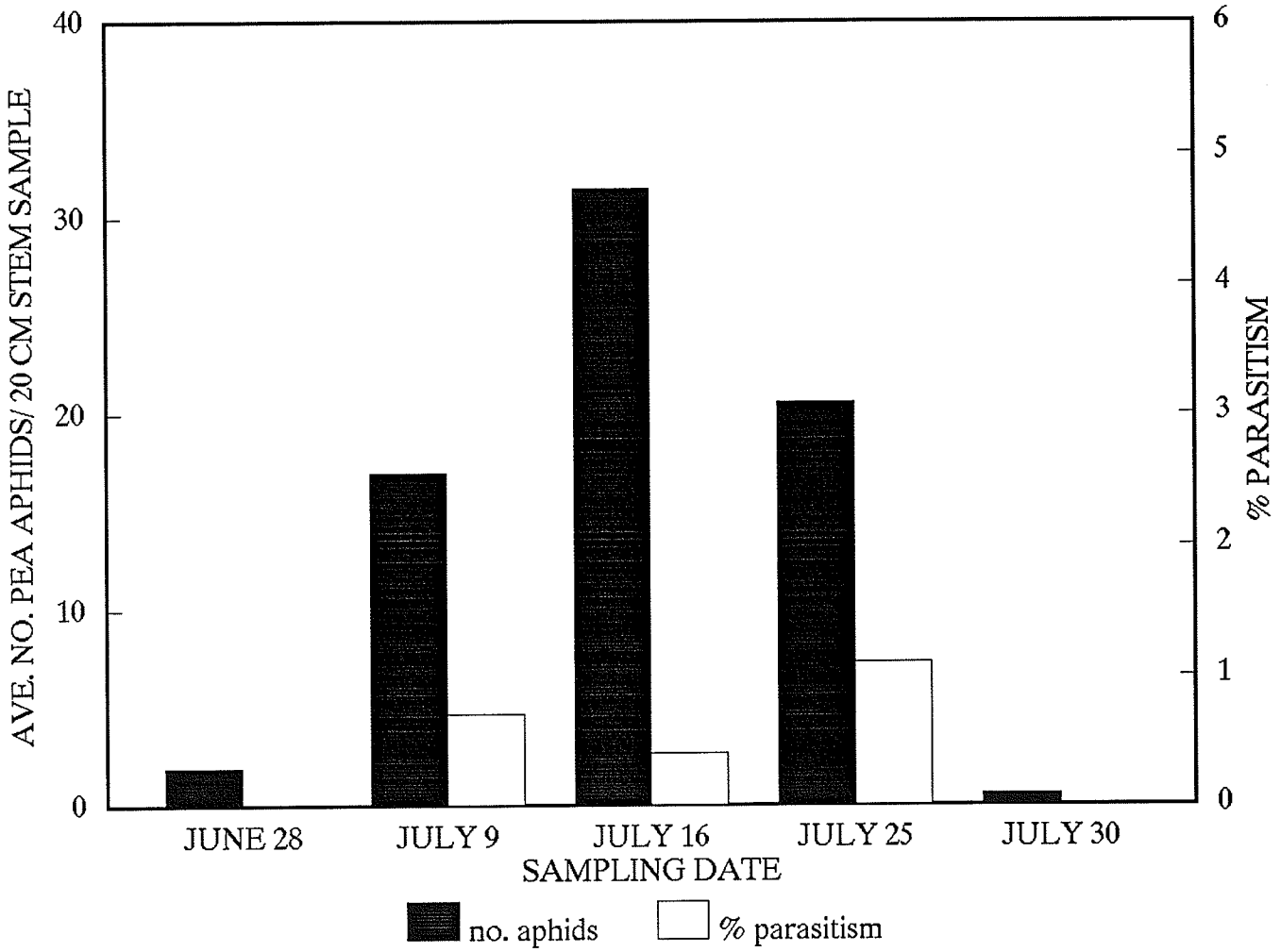

AVE. NO. PEA APHIDS/ 20 CM STEM SAMPLE
% PARASITISM
40
30
20
10
0
6
5
4
3
2
1
0
JUNE 28
JULY 9
JULY 16
JULY 25
JULY 30
SAMPLING DATE
no. aphids
% parasitism

FIGURE 11: PERCENT PARASITISM AND AVERAGE NUMBER OF PEA APHIDS PER 20 CM STEM SAMPLE IN PEA FIELD 3, MORRIS MANITOBA 1991

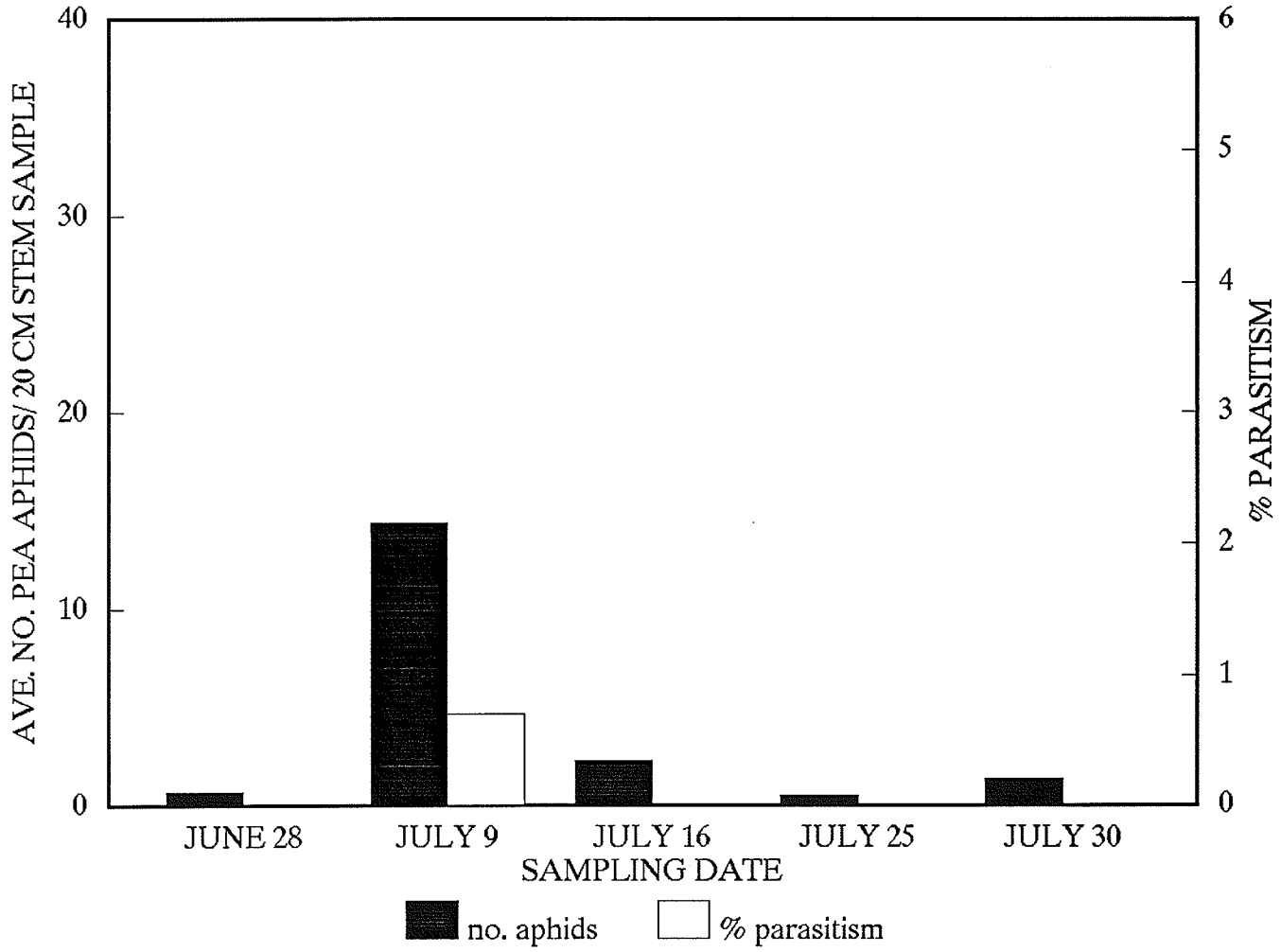

40
30
20
10
0
AVE. NO. PEA APHIDS/ 20 CM STEM SAMPLE
6
5
4
3
2
1
0
% PARASITISM
JUNE 28
JULY 9
JULY 16
JULY 25
JULY 30
SAMPLING DATE
no. aphids
% parasitism

FIGURE 12: PERCENT PARASITISM AND AVERAGE NUMBER OF PEA APHIDS PER 20 CM STEM SAMPLE IN PEA FIELD 4, MORRIS MANITOBA 1991

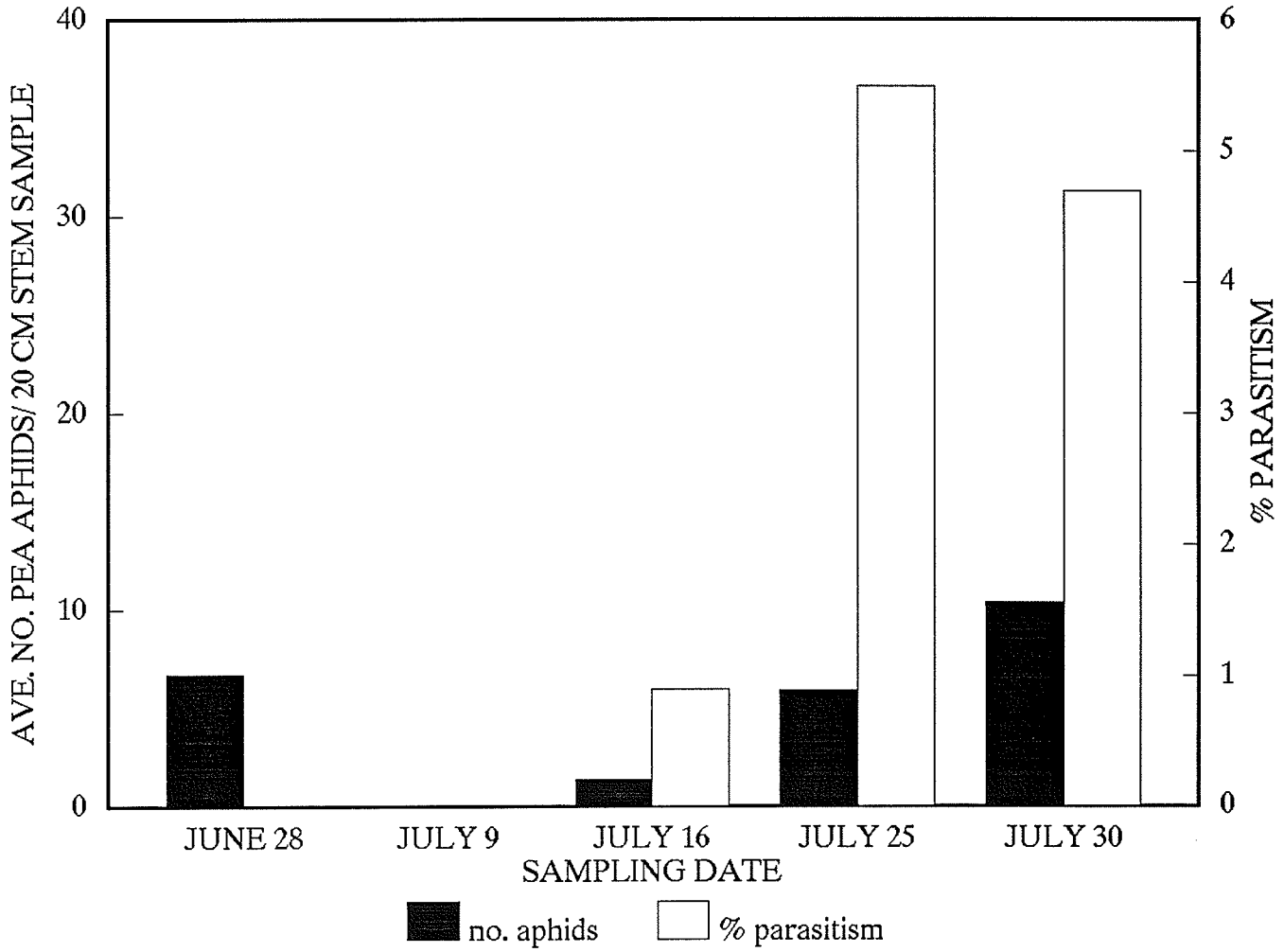

AVE. NO. PEA APHIDS/ 20 CM STEM SAMPLE
% PARASITISM
40
30
20
10
0
6
5
4
3
2
1
0
JUNE 28
JULY 9
JULY 16
JULY 25
JULY 30
SAMPLING DATE
no. aphids
% parasitism

FIGURE 13: PERCENT PARASITISM OF PEA APHIDS IN AN ALFALFA PLOT AT GLENLEA RESEARCH STATION 1991

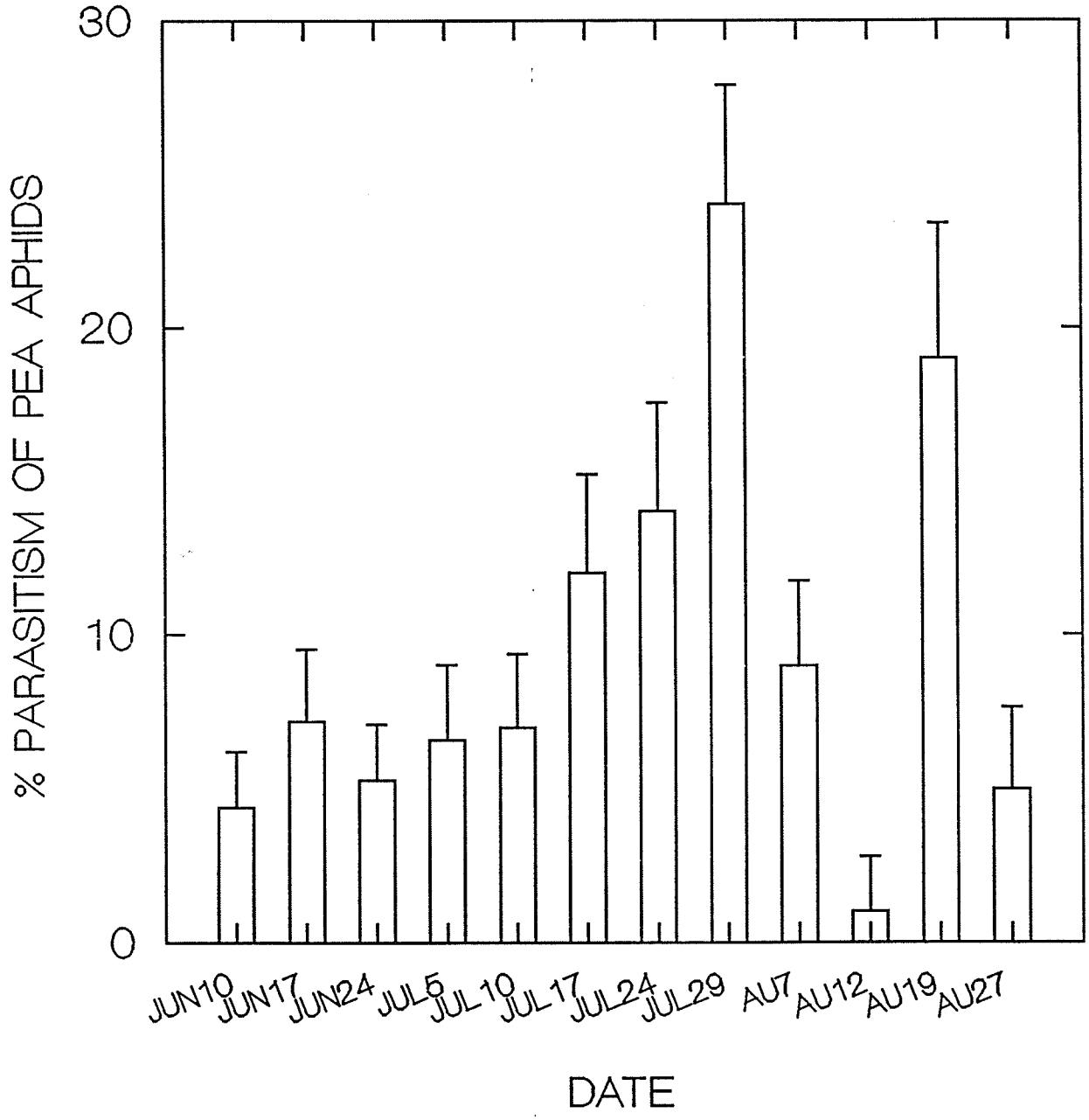
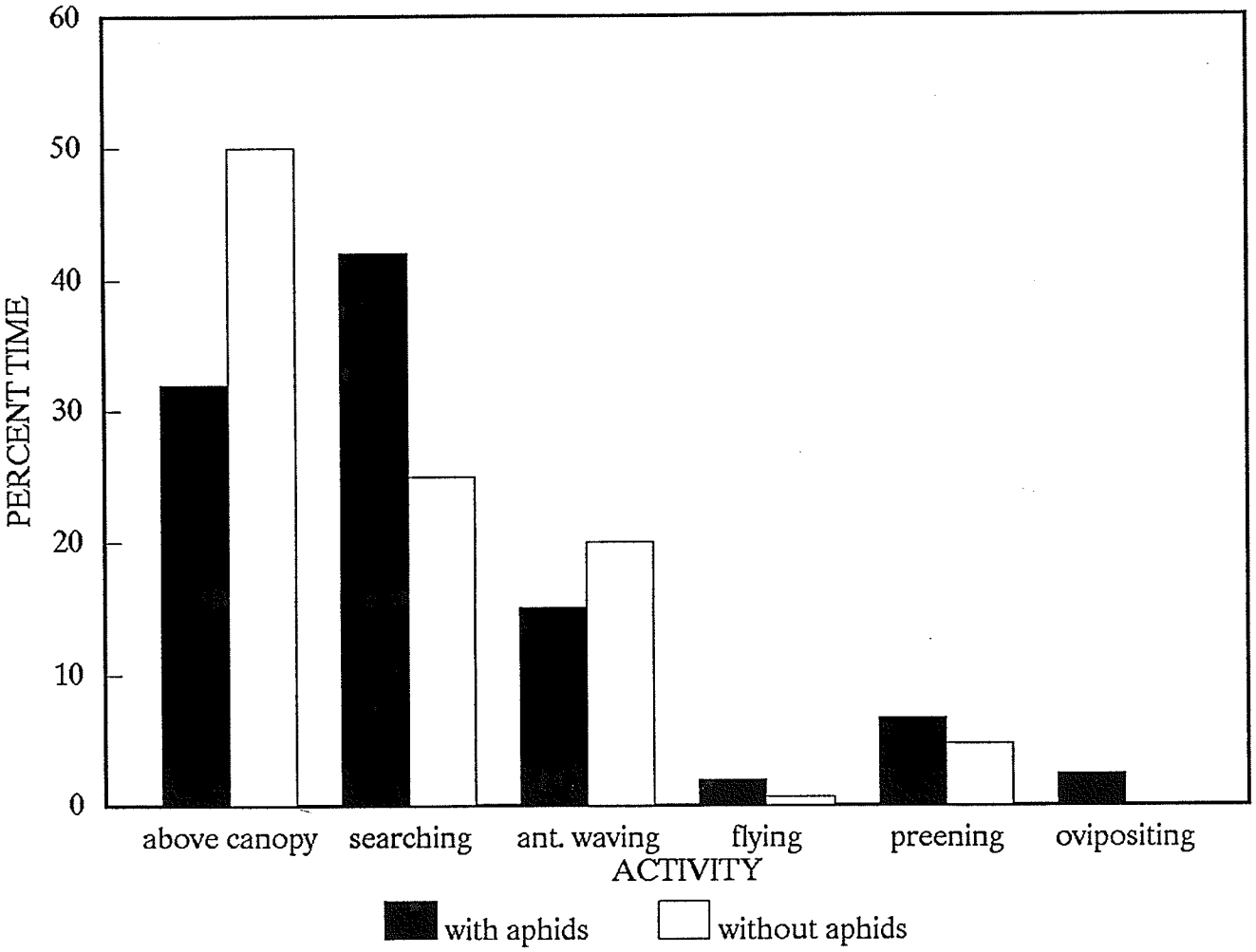

30
20
10
0
% PARASITISM OF PEA APHIDS
JUN10
JUN17
JUN24
JUL5
JUL10
JUL17
JUL24
JUL29
AU7
AU12
AU19
AU27
DATE

FIGURE 14: COMPARISON OF PARASITOID BEHAVIOUR WITH AND WITHOUT APHIDS


60
50
40
30
20
10
0
PERCENT TIME
above canopy
searching
ant. waving
flying
preening
ovipositing
ACTIVITY
with aphids
without aphids

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APPENDIX 1: Data Sheet for Behaviour Experiment

OBSERVATIONS OF APHIDIUS ERVI

CODES:
- **A - antennal waving, standing still**
- **S - searching, walking and waving antennae**
- **P - preening**
- **M - mating**
- **O - oviposition**
- **F - flying**
- **H - high, out of canopy**

CAGE NO.: **REPLICATE NO.:** **DATE:**

CONDITIONS:

TIME:

TIME:

TIME:

TIME:

TIME:

TIME:

TIME:

TIME:

OBS.#1	%P	%S	%A	%H	%F	%0	%M
OBS.#2	%P	%S	%A	%H	%F	%0	%M
OBS.#3	%P	%S	%A	%H	%F	%0	%M
OBS.#4	%P	%S	%A	%H	%F	%0	%M
OBS.#5	%P	%S	%A	%H	%F	%0	%M
OBS.#6	%P	%S	%A	%H	%F	%0	%M
OBS.#7	%P	%S	%A	%H	%F	%0	%M
OBS.#8	%P	%S	%A	%H	%F	%0	%M
TOTAL:	%P	%S	%A	%H	%F	%O	%M