THE PARASITOIDS OF SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* LEDERER (LEPIDOPTERA:TORTRICIDAE), IN MANITOBA

A Thesis

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by

Deirdre A. Zebrowski

In Partial Fulfilment of the

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Abstract

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The Parasitoids of Spruce Budworm, *Choristoneura fumiferana* Lederer (Lepidoptera:Tortricidae), in Manitoba.

Major Professor: N.J. Holliday

The parasitoids of epidemic and endemic spruce budworm populations were studied in eastern Manitoba in the summers of 1994 and 1995. Three sites were established, two in epidemic budworm populations, and one in an endemic budworm population. Sampling of the sites occurred from early May and continued until viable egg masses were no longer found in the collections. Budworm were reared on artificial diet until either a parasitoid or moth emerged. In 1995, a second site was established in the endemic population into which approximately 3000 budworm larvae were released. This site was established in order to collect parasitoids that are present but may not be collected through regular sampling of endemic populations.

There were 16 parasitoid species collected from Manitoba. The parasitoid species collected from the epidemic budworm populations were similar to the species collected from epidemic populations in other locations. Several species found to be of importance in endemic budworm populations in localities other than Manitoba were not collected in this study. *Lypha setifacies* (West), which was collected in the endemic site in Manitoba, has not been previously recorded

from an endemic budworm population.

The parasitoid guilds in the epidemic and endemic budworm populations were found to differ from each other. The difference in the two parasitoid guilds centres around the relative abundance of three parasitoid species: *L. setifacies*, *Meteorus trachynotus* Vier., and *Enytus montanus* (Ashmead). Although all three of these species were collected in both epidemic and endemic populations, each had a higher relative abundance within the endemic parasitoid guild than within the epidemic guild.

The parasitoid guild attacking budworm feeding on spruce differed from the parasitoid guild attacking budworm feeding on fir. This difference arose from decreased host availability on spruce for late larval and pupal parasitoids due to a higher rate of mortality on spruce than on fir. This resulted in early larval parasitoids comprising a much higher proportion of the parasitoid guild attacking spruce than of the guild attacking fir.

Earlier studies have suggested that delaying spraying for the spruce budworm until fourth instar can help conserve the parasitoid *Apanteles fumiferanae* Vier. Examination of day degree accumulation and the related timing of budworm instars in this study suggests that delaying spraying for spruce budworm until early June will help conserve *Apanteles fumiferanae* Vier. in the study area.

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The spruce budworm

Taxonomy and distribution

The eastern spruce budworm, *Choristoneura fumiferana* (Clem.), is a forest pest native to North America and does not occur elsewhere (Miller, 1963a). The first recorded specimen of the spruce budworm was collected in 1865 in Virginia. These specimens were identified as *Tortrix fumiferana* Clemens. Since that time, the species has been moved by various investigators to the genus *Harmologa* Meyr., then to the genus *Cacoecia* Hbn., and then to the genus *Archips* Hbn. In 1947, the species was placed in the genus currently used, *Choristoneura* Lederer (Freeman, 1953). The nomenclature of the genus *Choristoneura* was clarified by Powell (1980), who determined that there are two series of *Choristoneura* in North America which feed on the trees of the family Pinaceae. The two series are called the Lambertiana series and the Fumiferana series. Members of the Lambertiana series feed exclusively on trees of the genus *Pinus*. Members of the Fumiferana series feed primarily on spruces and firs of the genera *Picea*, *Abies*, and *Pseudotsuga*.

The eastern spruce budworm (from here on referred to as the spruce budworm or budworm) is recognized as a distinct species from the other four components of the Fumiferana complex. While the other components of the Fumiferana complex occur in the northwestern United States and parts of southern British

Columbia, the spruce budworm is most commonly associated with the boreal forest and occasionally the Great Lakes - St. Lawrence and Acadian forest region. Its distribution spans the eastern states from Virginia to Minnesota and all the forested regions of Canada from Newfoundland to Alberta, northeastern British Columbia, northward to the Arctic circle in the Mackenzie River Valley and the Yukon (Harvey, 1984). Although distribution in the eastern and central parts of the continent is well documented, that in some of the more remote and mountainous parts of the western and northwestern limits is less substantiated (Harvey, 1984).

Biology

Two main host plants are associated with the spruce budworm, balsam fir, *Abies balsamea* (L.) Mill., and white spruce, *Picea glauca* (Moench) Voss (Harvey, 1984). Although the spruce budworm does most of its feeding on fir and white spruce, it is also known to feed on black spruce, *Picea mariana* (Mill.) B.S.P., and red spruce, *Picea rubens* Serg. (Harvey, 1984).

The spruce budworm has a one year life cycle. Moths emerge from pupae and mate in late June to late July. Oviposition takes place in late July and early August. The eggs are laid in masses on the needles of host trees. The number of eggs in a mass varies, with the average number being 20 eggs per mass (Miller, 1963a). The photopositive first-instar larvae move towards the branch

tips after emergence. At this time, larvae may be dispersed by wind, or forced by crowded conditions to drop off the branches on silken threads (Wellington and Henson, 1947). The first-instar larvae do not feed, but rather spins a cocoon-like structure called a hibernaculum in which it moults to the second-instar (Wellington, 1950). The second instar-larvae remain in the hibernacula where they overwinter in diapause. Larvae usually spin their hibernacula in locations that offer some shelter, such as between bark scales, in bark fissures, between staminate flower bracts or in lichens (Miller, 1958).

The second-instar larvae emerge from their hibernacula in late April to mid-May. The larvae find old needles, unopened vegetative buds or staminate flowers which they mine and eat. As new foliage emerges, the larvae begin to feed on the new growth (McGugan, 1954). The third-instar to sixth-instar larval period takes place from early June to early July. The late instar larvae often pull two or more shoots together with webbing to form a feeding tunnel. The current year's foliage is preferred by larvae of all stages, but they will feed on old foliage if young foliage is unavailable. Feeding on old foliage can result in reduction in the size of the pupa and in the fecundity of the adult (Blais, 1952). Pupation occurs during mid-June to early July within the feeding shelter or in other protected sites, and moths emerge after 8-12 days (Miller, 1963a).

Population dynamics

Budworm populations fluctuate between extreme levels. When a population is at very low or endemic levels, it can be very difficult to find larvae, even with intensive sampling (Greenbank, 1963). At the other extreme, when a population is at very high levels, it is termed an outbreak or epidemic population. At epidemic levels, extensive damage can occur to the budworm host trees, sometimes resulting in tree death if the outbreak lasts over a period of years. Extent of tree mortality during an outbreak is often related to host tree species that are present in the stand. Balsam fir is less resistant to budworm than the three spruce species. This is attributed to the phenologies and foliage qualities of the different host trees (Greenbank, 1963). Balsam fir buds burst prior to those of white, black and red spruce. Overwintering larvae usually emerge only a few days prior to fir bud burst and therefore the larvae only have to feed on old needles and vegetative buds for a short period (Greenbank, 1963). White spruce suffers less damage than fir as, on average, its buds burst four days later and its shoots grow significantly longer than those of fir. Therefore, the new foliage of white spruce suffers proportionately less damage than fir at similar population levels (Greenbank, 1963). Black spruce and red spruce buds open approximately 13 days after those of fir. The old foliage and vegetative buds on these two species do not provide the budworm larvae with adequate food. This often results in larvae starving or abandoning the tree. Therefore, populations on black and red spruce are depleted before shoot growth commences and as a

result, damage to these species is limited (Greenbank, 1963).

Due to the economic costs caused by the budworm during outbreaks, many studies have been undertaken to examine how to control the population levels of the budworm. In particular, several studies have looked at the parasitoids of the spruce budworm as potential control measures. Although not viewed as effective regulating agents on their own during budworm outbreaks (Blais, 1960; Miller 1963b), it is still felt that parasitoids have a role to play in the population dynamics of the spruce budworm (Royama, 1993). The development of new insecticides which are effective against lepidopterous larvae, (Klein and Lewis, 1966; Smirnoff, 1963; and Smirnoff, 1973), but which have a high degree of host selectivity (Niwa et al., 1987), has renewed interest in using parasitoids as part of a budworm control strategy. Selective insecticides are not as damaging to non-target species such as parasitoids, and the timing of applications can be adjusted to conserve certain parasitoid species (Nealis and van Frankenhuyzen, 1990). This type of strategy would give the benefit of both budworm mortality from the insecticide and additional budworm mortality due to conservation of the parasitoid population.

Spruce budworm in Manitoba

Surveys of spruce budworm defoliation began in Manitoba in 1938 and outbreaks have been recorded every year since that time (K. Knowles, Manitoba

Natural Resources - Forestry Branch, Pers. comm.). The longest outbreak in the recorded history of the province is the current infestation in the Whiteshell area which has been ongoing from 1975 to the present (Knowles and Matwee, 1996).

Although Manitoba has a history of budworm outbreaks, there has been very little research done on the parasitoids of the budworm in Manitoba. Manitoba recently used Mimic® (tebufenozide) and previously *Bacillus thuringiensis* var. *kurstaki* Berliner as part of the budworm control program (Knowles and Matwee, 1995), and both have a high degree of host selectivity. Therefore, there is the potential to include parasitoids as a part of an integrated control program in Manitoba. Before this can be done however, information is required about the parasitoids that occur in Manitoba. The overall aim of this study is to begin the collection of information needed to investigate integrated control for the spruce budworm in Manitoba. The specific objectives of this study represent a first step in that direction. The specific objectives of this study were:

1. Identify the naturally occurring parasitoids, and their rates of parasitism in epidemic spruce budworm populations in Manitoba;
2. Compile a list of naturally occurring parasitoids of endemic spruce budworm populations in Manitoba, with information on relative importance of each parasitoid species.

3. Compare parasitoid guilds in epidemic budworm populations and in endemic budworm populations in Manitoba.

Literature Review

Introduction

The spruce budworm has been extensively studied throughout its range in North America. This literature review will not cover this entire wealth of information, but rather will focus on studies which have examined parasitoids of the spruce budworm. In addition to reviewing the literature on parasitoids, this section of the thesis will also briefly address the population dynamics of the budworm and the appropriate sampling techniques for the budworm. Terms often used when discussing parasitoids, but which may be interpreted differently in other disciplines, will also be clarified.

Definitions

There are several terms used in the following sections regarding parasitoids. These terms are used in the majority of the literature on this subject, and will be used here as defined by Miller (1963b). Alternate host(s) refers to the host(s) required by a parasitoid, with more than one generation per year, in addition to the budworm. An alternative host(s) refers to a host(s) susceptible to attack at the same time as the spruce budworm.

Population dynamics

Although there are several hypotheses regarding the population dynamics of the spruce budworm (Wellington et al., 1950; Greenbank, 1956; Greenbank, 1957;

Morris, 1963a; Stehr, 1968; Blais, 1981; Lucuik, 1984), Royama's theory, first expressed in 1984 and later revisited in 1993, is currently considered the most comprehensive model to date. Royama, unable to fully accept any of the existing theories, reanalysed the Green River Project data (Morris, 1963b) and produced his own theory, the continuous oscillation theory. This theory proposes that within a particular stand, the spruce budworm population fluctuations are governed by a cyclical oscillation and a random fluctuation around this oscillation. This is based on the assumption that the most important processes in the spruce budworm population dynamics are feeding larval stages, pupal stages and the year to year rate of change in population density or net reproductive rate. The net reproductive rate is determined by both generation survival, and recruitment rate (ratio of the number of eggs to the number of locally emerged moths [both sexes]; it is often expressed as the "E/M ratio"). Deposition of eggs by both local moths and immigrant moths at a given forest stand depends primarily on the level of defoliation, not on the local population density. Therefore, in stands where defoliation is heavy, the E\M ratio would be low in comparison to stands where there was little defoliation. For this resaon the recruitment rate can be said to be defoliation dependent (Royama, 1993).

The major source of mortality of the feeding and pupal stages of the spruce budworm is a complex of natural enemies (Royama, 1993). The members of this complex are also attacked however, by their own natural enemies. Based on

this, the continuous oscillation theory postulates the existence of a food web (Figure 1) that includes spruce budworm and other forest defoliators feeding on spruce and fir foliage. There is spruce budworm mortality due to three types of natural enemies (Figure 1): those parasitoids which may complete their life cycle entirely on the spruce budworm (although they may also have many other alternative hosts); those parasitoids or predators which cannot complete their life cycle on the spruce budworm, but must have alternate hosts or prey to complete their life cycle; and pathogenic microbes including viruses, fungi, bacteria and yeasts (Royama, 1993). In turn, the first two types of natural enemies mentioned above would be parasitized and preyed upon by their own natural enemies. The spruce budworm can tolerate extremely crowded conditions and therefore, in the absence of any natural enemies, its defoliation-dependent recruitment rate would be the only self-imposed regulation of the budworm population (Royama, 1993). This regulation would not be able to prevent defoliation. If natural enemies of the sort that can complete their annual life cycle in the spruce budworm are introduced to the model, then the picture changes (Royama, 1993). Parasitoids of this sort (the microsporidia in the genus *Nosema* are also included here) are capable of increasing their numbers reproductively in response to an increase in budworm numbers. Therefore, these parasitoids are theoretically capable of controlling the spruce budworm populations (Royama, 1993). The efficacy of these parasitoids is reduced however, by the attack of their own natural enemies (Royama, 1993). Therefore, it will take years in many cases for the parasitoids

Figure 1. Stratified food web formed around the budworm and upon the infrastructure of a forest. (Royama, 1993)

I. Fir and spruce foliage

II. Defoliators:

    a. Spruce budworm

    b. Other

III. Primary natural enemies of budworm:

    a. Univoltine parasitoids and *Nosema* (microsporidia)

    b. Multivoltine parasitoids and omnivorous predators

    c. Pathogenic microbes (viruses, fungi, bacteria and yeasts)

IV. Secondary natural enemies:

    Hyperparasitoids and predators of IIIa. and b.

(Royama, 1993)

to build up to the point where they can have a significant effect on budworm survival. This will result in the forest-budworm-natural enemy system oscillating slowly with a high amplitude. If local systems are synchronized, a widespread outbreak may occur at almost regular intervals (Royama, 1993). The spruce budworm recruitment rate may drop when defoliation becomes severe. This will stop spruce budworm population increase, but will not substantially reduce the number of progeny. The budworm population, as a result, will stay at a plateau for several years, fluctuating as the E/M ratio fluctuates (Royama, 1993). The spruce budworm population will decline if the natural enemy complex catches up with it (Royama, 1993).

The system described above will also be affected by the natural enemies which rely on hosts or prey other than the spruce budworm to complete their life cycles (Royama, 1993). These species are only able to respond reproductively to changes in the budworm density if their alternate hosts are abundant. If their alternate hosts are much less abundant than the budworm, these natural enemies are not able to respond reproductively to changes in the budworm density. Thus, the alternate hosts and prey will control the ability of these multivoltine parasitoids and omnivorous predators to have a significant effect on the numbers of spruce budworm (Royama, 1993).

Sampling spruce budworm

Assessing mortality

Thompson (1928) distinguishes between real and apparent mortality, indicating that the difference between the two is that apparent mortality is estimated from samples of a population, whereas real mortality is the true level of mortality occurring in the population. Apparent mortality, as it is only an estimate of what is occurring in the population, may not reflect what is happening in terms of real mortality. Studies of parasitism generally use samples from the host population to determine mortality caused by parasitoids (Miller, 1954). Apparent parasitism, or apparent mortality, reflects the proportion of hosts attacked by parasitoids and is expressed as a percentage of the number examined (Miller, 1963b). The ratio of the parasitized hosts to all the hosts in the sample is commonly reported as the "percent parasitism" (Van Driesche, 1983). The number examined should only include susceptible hosts for that generation, not all hosts examined (Van Driesche, 1983). Errors in using the term percent parasitism are less important in faunistic studies which seek to identify species of parasitoids present in particular times, hosts or locations, or those which seek to rank the relative commonness of the species observed (Van Driesche, 1983).

Branch samples

The use of 45 cm branch samples originated in Ontario for insect survey purposes (Atwood, 1944). Apical branch samples are sufficiently small to

provide flexibility of sampling design and are easily collected (Morris, 1955). Morris (1955) suggests that there are two limitations of this type of sampling. The first limitation is that when branches are defoliated, the tips are the first to be defoliated. Therefore as an outbreak progresses, the budworm population may progress towards the centre of the tree and away from the branch tips (Morris, 1955). Secondly, depending on the time that samples are collected, the apical portion of the branches may support different proportions of the larval population. However, Régnière et al. (1989) found that for all stages of the spruce budworm, with the exception of the overwintering stage, greater than 50% of the budworm on a branch were present in the 45 cm apical portion of balsam fir and white spruce branches. During fourth and fifth instars, greater than 80% of the population on a branch were within 45 cm of the tip. Although fewer than 50% of overwintering budworm were found within 45 cm of the tip, by the peak of the second instar, over 50% of the population was within 45 cm of the branch tip (Régnière et al., 1989). The vertical distribution of budworm larvae in the crowns of host trees has been found to be of little consequence (Régnière et al., 1989; Piene, 1996).

Parasitoids of the spruce budworm

Parasitoids in epidemic populations

There have been numerous studies looking at the parasitoids present in epidemic spruce budworm populations. Approximately 90 parasitoid species

have been recovered from the spruce budworm (McGugan and Blais, 1959). Egg, larval and pupal stages are all affected by parasitoids. The same 12-15 parasitoid species (Table 1) seem to make up the important elements of all parasitoid complexes studied in epidemic budworm populations, regardless of location (Wilkes et al., 1948). The less common and occasional species vary from location to location (McGugan and Blais, 1959). Blais (1960) observed some differences between parasitoid complexes among different outbreaks of the spruce budworm. The parasitoid species present during the beginnings of outbreaks, and those present during the later years differed. Blais (1960) suggests that the differences are due to the availability of alternate hosts.

Parasitoids attacking small larvae

Glypta fumiferanae (Vier.) (Hymenoptera: Ichneumonidae), and *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae) are common parasitoids of the spruce budworm. Both of these species have been collected from most places where parasitoids of spruce budworm have been studied including: British Columbia (Coppel, 1946; Wilkes et al., 1948), Ontario (McGugan and Blais, 1959), Quebec (Blais, 1960; Blais, 1965), New Brunswick (MacDonald, 1959; Miller, 1963b), Colorado (Dowden et al., 1948), New York (Dowden et al., 1948; Dowden and Carolin, 1950), Maine (Jaynes and Drooz, 1952; Tilles and Woodley, 1984), and Oregon (Carolin and Coulter, 1959).

Table 1. **Parasitoid species considered to be important elements in the parasitoid complex attacking outbreak populations of the spruce budworm. (Wilkes et al., 1948)**

Parasitoid species
Hymenoptera
Braconidae:
Apanteles fumiferanae Vier.
Ichneumonidae:
Glypta fumiferanae (Vier.)
Phaeogenes maculicornis hariolus (Cress.)
Phytodietus fumiferanae Rohw.
Itoplectis quadricingulata (Provancher)
Ephialtes ontario (Cress.)
Trichogrammatidae:
Trichogramma minutum Riley
Diptera
Tachinidae:
Phyrxe pecosensis (Tns.)
Lypha setifacies (West)
*Winthemia fumiferanae*Tothill
Cyzenis incrassata (Smith)
Nilea erecta (Coquillet)
Madremyia saundersii (Will.)
Ceromasia auricaudata Tns.
Sarcophagidae:
Agria affinis (Fall.)

There are five other species of *Apanteles* that also attack early instars of the spruce budworm: *A. morrisi* Mason, *A. renaulti* Mason, *A. milleri* Mason, *A. absonus* Mues., and *A. petrovae* Walley (Mason, 1974). These five species were not clearly distinguished from each other until 1974 (Mason, 1974) and therefore many of the above records may have included *Apanteles* species other than *A. fumiferanae*. Mason (1974) cautions that although there are published statements that *Apanteles* species attack first or second instar larvae of the budworm, both *A. fumiferanae* and *A. absonus* have been reared from *Acleris variana* (Fernald), a species that overwinters in the egg stage. If these host records are correct, they would imply that these two parasitoids may oviposit in the eggs of their hosts in some circumstances (Mason, 1974). Despite Mason's views, the majority of other authors assume that *A. fumiferanae* attacks first or second instar budworm larvae. This assumption appears to be based on the evidence that *A. fumiferanae* can be reared from overwintering budworm larvae (Mason, 1974). Aside from the statements made by Mason (1974), there is no documentation in the literature of *A. fumiferanae* attacking budworm eggs. Therefore, although Mason's statements are presented here as a cautionary note, the remainder of this section and all other sections will treat *A. fumiferanae* in the same manner as the majority of the literature - as attacking first and second instar larvae.

Apanteles fumiferanae and *G. fumiferanae* are both univoltine species. They

attack budworm larvae in July or August and overwinter in the budworm. The following summer, the mature parasitoids emerge from the host, and spin cocoons in the foliage. The adults emerge from the cocoons in time to attack the subsequent generation of budworm (Miller, 1963b). The stages of both parasitoid species have been described by Brown (1946a, 1946b) with details on the external morphology at each stage.

Hosts parasitized by *A. fumiferanae* and *G. fumiferanae* emerge from their hibernacula in the spring 7 to 10 days later than non-parasitized larvae (Lewis, 1960). These parasitoids also retard later larval growth and inhibit gonadal development (McGugan, 1955). A third effect of these parasitoids on their hosts is that parasitized hosts respond negatively or not at all to light. Non-parasitized larvae are positively phototactic. This behaviour together with the late emergence may cause parasitized hosts to disperse less (Lewis, 1960).

Although *A. fumiferanae* is one of the most common parasitoid species of the budworm, its recorded apparent rate of parasitism ranges from as low as 1% to as high as 66% (Miller 1963b, McGugan and Blais, 1959). Miller (1963b) suggests that in a severe outbreak, with a high rate of host increase followed by an equally high rate of decline, parasitism by *A. fumiferanae* will remain relatively low without any significant increases until the budworm population begins to collapse. Where the outbreak is less severe, apparent parasitism of *A.*

fumiferanae will be higher during the outbreak, but again, will not increase significantly until the budworm population begins to decline (Miller, 1963b). The apparent rate of parasitism of *G. fumiferanae* was observed by Miller (1963b) to peak with or slightly after the peak density of the budworm population. The apparent parasitism of *G. fumiferanae* then declined as the budworm population declined.

There is a third parasitoid which attacks and overwinters in the spruce budworm early instars, *Horogenes cacoeciae* (Vier.). This parasitoid is rare in both eastern and western North America (Miller, 1963b). Few specimens have been collected in New Brunswick during budworm outbreaks. When budworm populations decline, *H. cacoeciae* increases in numbers, but the reported apparent rate of parasitism has never exceeded 5% (Miller, 1963b). Miller (1963b) concluded that as this species shows no numerical response to budworm density, it may prefer a host other than the spruce budworm.

Parasitoids attacking third and fourth instars

There are only two important parasitoids that attack third and fourth instars of the budworm: *Synetaeris tenuifemur* (Wly.)(Hymenoptera: Ichneumonidae) and *Enytus montanus* (Ashmead) (Hymenoptera: Ichneumonidae). The life history and description of immature stages of *S. tenuifemur* are given by Miller and Renault (1963). This species is univoltine (Miller and Renault, 1963), and was

first recorded in Ontario (McGugan and Blais, 1959) in areas with declining budworm infestations. It was also collected from budworm in declining populations in New Brunswick (Miller, 1963b). The species' association with declining budworm populations led Miller and Renault (1963) to suggest that it is associated with endemic budworm populations. *Synetaeris tenuifemur* attacks third instar larvae, emerges as a larva from fifth instar budworm larvae and overwinters in a cocoon (Miller and Renault, 1963).

Enytus montanus has been collected from budworm in Ontario (McGugan and Blais, 1959; Fye 1963; Fye 1965), New Brunswick (Miller, 1963b, Miller and Renault, 1976) and from Maine (Tilles and Woodley, 1984). It was relatively rare in all above locations and is suspected to overwinter in an alternate host (Miller, 1963b). In New Brunswick, *E. montanus* was consistently recovered from *Acleris variana* Fern., the blackheaded budworm, which feeds on the same host trees as the spruce budworm. *Enytus montanus* has also been recovered from other lepidopterous hosts, including several that feed on deciduous trees (Krombein et al., 1979).

Parasitoids attacking large larvae

There are several parasitoid species which attack the fifth and sixth larval instars of the spruce budworm. One of these species, *Meteorus trachynotus* Vier. (Braconidae), attacks fifth or early sixth instar larvae and emerges from sixth

instar larvae (Miller, 1963b). A cocoon is formed by mid July and an adult emerges from the cocoon by late July or early August. *Meteorus trachynotus* has been recovered from spruce budworm in British Columbia (Wilkes et al., 1948), Ontario (McGugan and Blais, 1959), Quebec (Blais, 1960; Blais, 1965), New Brunswick (MacDonald, 1959; Miller, 1963b), New York (Dowden and Carolin, 1950), Maine (Jaynes and Drooz, 1952; Tilles and Woodley, 1984), and Oregon (Carolin and Coulter, 1959). In many of these places, *M. trachynotus* has been collected in the last years of an outbreak, but is fairly rare during the peak years of an outbreak (Dowden and Carolin, 1950; Blais, 1960; Miller, 1963b; Miller and Renault, 1976). Maltais et al. (1989) found evidence that *M. trachynotus* overwinters in *Choristoneura rosaceana* (Harr.). Closer examination of the adequacy of synchrony in the development of *C. fumiferana*, *C. rosaceana* and *M. trachynotus* may help explain the changes in rate of parasitism by *M. trachynotus* at different stages of budworm outbreaks (Maltais et al., 1989).

The tachinid (Diptera) species *Lypha setifacies* (West), *Actia interrupta* Curr., *Madremyia saundersii* (Will.), *Winthemia fumiferanae* Toth., *Eumea caesar* (Aldr.) and *Phryxe pecosensis* (Tns.) also attack the late larval stages. *Actia interrupta* and *L. setifacies* attack fifth or sixth instar budworm and emerge from sixth instar budworm (Brooks, 1945). *Lypha setifacies* overwinters as a puparium and has been observed to increase in rate of parasitism as budworm density decreases (Miller, 1963b). *Actia interrupta* requires an alternate host to

complete its development (Blais, 1965). Although this species is rare or uncommon in many areas, it has been shown to be abundant in some areas of northeast North America (Tilles and Woodley, 1984). It has also been associated with light budworm infestations which is thought to be due to restrictions caused by the availability of its alternate hosts (Blais, 1965).

Madremyia saundersii appears to be confined to the temperate areas of North America. It is a native parasitoid that attacks a wide range of lepidopterous hosts (Coppel and Maw, 1954). This parasitoid attacks fifth or sixth instar budworm and emerges from sixth instar larvae or pupae of the host (Coppel and Maw, 1954; Miller, 1963b). It is not known in what stage the parasitoid overwinters, but it is suspected that it remains as a larva in diapause in one of its alternate hosts (Coppel and Maw, 1954). Immature and mature stages of *M. saundersii* have been described by Coppel and Maw (1954).

Winthemia fumiferanae is a univoltine parasitoid that overwinters in a puparium on the forest floor. Females lay macrotype eggs directly on late instars of the budworm (Hébert et al., 1989). The eggs hatch at the time of host pupation and therefore *W. fumiferanae* larvae develop entirely in host pupae (Coppel and Smith, 1957; Hébert and Cloutier, 1990). *Winthemia fumiferanae* has been found in most locations where parasitoids of budworm have been studied with the exception of New Brunswick (Wilkes et al, 1948; McGugan and Blais, 1959;

Blais, 1960; Blais, 1965; MacDonald, 1959; Miller, 1963b; Dowden and Carolin, 1950; Jaynes and Drooz, 1952; Tilles and Woodley, 1984; Carolin and Coulter, 1959; Dowden et al. 1948).

Eumea caesar and *P. pecosensis* both attack fifth and sixth instar budworm larvae, but may emerge either from sixth instar budworm or from budworm pupae. Both of these parasitoids require alternate hosts to complete their life cycle (Dowden and Carolin, 1950). This limits their effectiveness as control agents of the budworm and accounts for the variation in their rates of parasitism observed in different budworm outbreaks (Miller, 1963b). *Eumea caesar* is more efficient in light infestations than *P. pecosensis*. The rate of parasitism of *P. pecosensis* was observed to decline as a budworm population collapsed, whereas the rate of parasitism of *E. caesar* increased under these conditions (Dowden and Carolin, 1950). The immature stages of *P. pecosensis* are described by Maw and Coppel (1953). The immature stages of *E. caesar* are described by Wishart (1945).

Parasitoids attacking pupae

Ephialtes ontario (Cress.), *Itoplectis conquisitor* (Say), *Phaeogenes maculicornis hariolus* (Cress.) (Hymenoptera: Ichneumonidae), *Mesopolobus tortricis* (Brues.), *Mesopolobus verditer* (Norton) (Hymenoptera: Pteromalidae) and *Sarcophaga aldrichi* Park. (Diptera: Sarcophagidae) are all parasitoids found attacking the

pupal stage of the spruce budworm. *Ephialtes ontario*, *I. conquisitor* and *P. maculicornis hariolus* attack a large number of hosts in addition to the spruce budworm (Krombein et al., 1979). Both *E. ontario* and *I. conquisitor* require alternate hosts in order to complete their life cycles. *Phaeogenes maculicornis hariolus* is suspected to overwinter as an adult (Miller, 1963b; Miller and Renault, 1976). These parasitoids have been collected in almost all studies of parasitism of the spruce budworm and in most locations were common or abundant (Wilkes et al, 1948; McGugan and Blais, 1959; Blais, 1960; Blais, 1965; MacDonald, 1959; Miller, 1963b; Dowden and Carolin, 1950; Jaynes and Drooz, 1952; Tilles and Woodley, 1984; Carolin and Coulter, 1959; Dowden et al., 1948). Although all three species have been collected during budworm outbreaks, *E. ontario* is more abundant during the collapse phase of an outbreak (McGugan and Blais, 1959; Blais, 1965), whereas *I. conquisitor* and *P. maculicornis hariolus* both decrease in the final years of an outbreak or when budworm density is low (McGugan and Blais, 1959; Dowden and Carolin, 1950).

Mesopolobus tortricis was a common parasitoid of budworm in studies in Ontario (McGugan and Blais, 1959) and New Brunswick (Miller, 1963b). *Mesopolobus verditer* was also common in these two locations as well as in New York (Dowden et al., 1948; Dowden and Carolin, 1950) and Oregon (Carolin and Coulter, 1959). *Mesopolobus verditer* has also been observed in low numbers in British Columbia (Coppel, 1946; Wilkes et al., 1948) and Quebec (Blais 1960;

Blais, 1965). Both of these species require alternate hosts in which to overwinter. *Mesopolobus tortricis* is usually a primary parasitoid of Lepidoptera, although it has been recorded as a secondary parasitoid of Ichneumonidae (Huber et al., 1996). *Mesopolobus verditer* is both a primary parasitoid and a hyperparasitoid of Lepidoptera and sawflies and their parasitoids. It has been commonly reared in New Brunswick as a hyperparasitoid of budworm pupae through attacks on Tachinidae and Ichneumonidae (Huber et al., 1996).

Sarcophaga aldrichi is a pupal parasitoid of the spruce budworm. It has only been recorded as abundant in budworm populations in Quebec (Blais, 1960; Blais, 1965). It has been observed attacking budworm in small numbers in British Columbia (Arthur and Coppel, 1953) and Ontario (McGugan and Blais, 1959). *Sarcophaga aldrichi* is limited to lepidopterous hosts and has been collected in the largest numbers from the forest tent caterpillar, *Malacosoma disstria* Hbn. (Hodson, 1939; Arthur and Coppel, 1953). This species attacks its hosts as they begin to pupate. It only completes one generation per year as it has a long period of dormancy after emerging from its hosts (Hodson, 1939). For this reason it does not require an alternate host. *Sarcophaga aldrichi* competes with other parasitoids and kills them when they occur in the same host (Hodson, 1939). This species will develop in carrion, mashed caterpillars, and other organic material and therefore has been classified as a facultative parasitoid that bridges the gap between a specialized parasite and an exclusive

scavenger (Hodson, 1939).

Parasitoids in endemic populations

Although many studies of parasitoids of spruce budworm have followed budworm populations from peak epidemic stages through to the collapse of the population, very few have looked at the endemic population stage that follows. The endemic populations are difficult to study due to the intensive effort required to find sufficient numbers of spruce budworm (Miller and Renault, 1976). There are only three studies in the literature which look at true endemic populations as opposed to collapsing populations. These studies took place in Vermont (Hanson, 1982), Ontario (Fye, 1963, 1965) and New Brunswick (Miller and Renault, 1976). Although the studies in both New Brunswick and Ontario examined endemic populations, both of these endemic populations occurred after the collapse of an outbreak population (Miller and Renault, 1976; Fye, 1963, 1965). Only the study in Vermont looked at a stable endemic population - a population that had been at low levels for some time and was not immediately following an outbreak (Hanson, 1982).

Miller and Renault (1976) concluded that much of the difference found between parasitoids attacking epidemic versus endemic populations in New Brunswick could be traced to three species: *Apanteles fumiferanae* Vier., *Meteorus trachynotus* Vier., and *Synetaeris tenuifemur* (Wly.) (Ichneumonidae). Both *A.*

fumiferanae and *M. trachynotus* were common during the collapse phase of an outbreak, but declined as the budworm density reached the endemic phase. *Synetaerius tenuifemur* was common during the endemic phase but did not respond to budworm density increases (Miller and Renault, 1976). In the Ontario study, *A. fumiferanae* and *G. fumiferanae*, both common during the outbreak phase, were not recorded in the endemic phase. Several parasitoids considered of minor importance during the outbreak were collected in the endemic population. These parasitoids included: *Horogenes cacoeciae* (Vier.) (Ichneumonidae), *Enytus montanus* (Ashmead) *(=H. conodor* (Vier.)) (Ichneumonidae), *Exochus nigripalpis tectulum* Tow. and Tow. (Ichneumonidae), and *S. tenuifemur* (Fye, 1963). The Vermont study found that *A. fumiferanae* constituted the highest percentage of parasitoids reared from the endemic populations. *Glypta fumiferanae* and *M. trachynotus* were also found to be abundant in Vermont. Although *S. tenuifemur, E. montanus,* and *H. cacoeciae* were not collected, the Vermont study did record *E. nigripalpis tectulum.* The species *Charmon gracilis* (Prov.) (Braconidae) and *Tranosema rostrale rostrale* Brischke (Ichneumonidae) were also collected from Vermont. This is the first record of these species from an endemic budworm population (Hanson, 1982). Some of the overall differences in species collected between these three studies may be explained by the Ontario and New Brunswick studies being done in endemic populations which occurred after an outbreak, versus the Vermont study which took place in a stable endemic population. A forest after an

outbreak is very different from one in which the budworm population has been at low stable numbers for many years. In addition, the study in New Brunswick looked largely at overwintering and young larvae in the spring; sixth instar larvae and pupae were collected but in limited numbers and only when circumstances allowed (Miller and Renault, 1976). This may also have affected the findings.

Factors affecting parasitoids

There are many factors which can potentially affect the parasitoids of the spruce budworm. One such factor is weather. Rainfall impedes activity of *G. fumiferanae* and so excessive rainfall may prevent this parasitoid from attaining high rates of parasitism (Nyrop and Simmons, 1986). A decrease in temperature may reduce the capacity of this species to oviposit. Nyrop and Simmons (1986) also suggest that extremes in temperature may create a shift in female ovipositional activity relative to other activities, which could reduce the proportion of successful attacks by this parasitoid. Temperature also affects *Winthemia fumiferanae* Toth. survival; mortality was evident at 15° C or higher, but was insignificant at lower temperatures. Therefore, high temperatures may negatively affect the reproduction of this parasitoid (Hébert and Cloutier, 1990).

Stand characteristics also affect parasitoids of the spruce budworm. One study has shown that as stand density decreases, parasitism of the spruce budworm increases (Simmons et al., 1975). This relationship was observed regardless of

stand composition (Simmons et al., 1975). Stand characteristics have been found to influence *Trichogramma minutum*, the only recorded egg parasitoid of the spruce budworm (Kemp and Simmons, 1979). It was observed that parasitism rates of *T. minutum* increased as the density of non-host trees for the spruce budworm increased. This is probably because *T. minutum* requires alternate hosts that utilize tree species that are not hosts for the spruce budworm (Kemp and Simmons, 1979). Similar results have been found for other parasitoid species. Significant associations were found between densities of balsam fir and white spruce and pupal parasitoids including *Actia interrupta* Curran, *Eumea caesar* (Aldrich), *Phyrxe pecosensis* (Townsend) and *Itoplectis conquisitor* (Say) (Simmons et al., 1975). These four species also require alternate hosts in order to complete their life cycle, or to overwinter in (Dowden and Carolin, 1950; Maw and Coppel, 1953; Miller, 1963b). A forest with lower densities of fir and spruce would provide a greater variety and abundance of alternate host insects for these species (Simmons et al., 1975). In addition, as the density of budworm host trees increases, the area to be searched by the parasitoids also increases, which may result in lower rates of parasitism. When tree density increases, regardless of tree species, parasitism rates decrease (Simmons et al., 1975). Although this may be due in part to searching behaviour, it can also be traced to other effects of increased tree density such as reduced light. Reduced light intensities in cages have been shown to inhibit activity of *E. ontario* (Ryan and Medley, 1972). It has been suggested that the

many conflicting reports on the importance of parasitoids in the population dynamics of the spruce budworm may be a result of a failure to consider the effects of stand characteristics on parasitoids (Kemp and Simmons, 1979).

Only one study has examined whether parasitoids of the spruce budworm prefer to attack budworm feeding on one host tree species over another. Miller (1959), in olfactometer experiments, found that female *A. fumiferanae* prefer white spruce foliage over severely defoliated balsam fir. This lead Miller (1959) to believe that A. fumiferanae may therefore spend more time searching spruce than fir under some circumstances.

Previous studies in Manitoba

In 1937-38, a study of the naturally occurring parasitoids of *Choristoneura* in Manitoba were surveyed in a thesis entitled "Studies on the biological control of the spruce budworm, *Cacoecia fumiferana* Clemens, in southeastern Manitoba and northwestern Ontario" (Lejeune, 1939). However, the majority of budworm collected in this study were taken from jack pine, *Pinus banksiana* Lamb., and therefore it is most likely that it was jack pine budworm (*Choristoneura pinus* Free.) observed in Lejeune's study (1939), and not spruce budworm. These two species were considered to be the same species until Freeman (1953) designated the form attacking jack pine to be a separate species.

In 1946, releases were done in Manitoba in an attempt to establish parasitoids from British Columbia (Coppel et al., 1959). However, there are no published records of the results of these releases in Manitoba, nor any information on other parasitoids that may have been observed in Manitoba during this release experiment.

Materials and Methods

Study design

The following study design was used to address the three objectives listed in the Introduction. Three forest stands were chosen: two with epidemic budworm populations, and one with an endemic budworm population. One site was established in each stand. Each site was sampled twice weekly in 1994 and 1995. The budworm larvae collected on each sampling occasion were brought to the laboratory, where they were reared on an artificial diet. Parasitoids that emerged were preserved and identified.

A fourth site was established adjacent to the endemic site, in the same forest stand, in 1995. Previous unpublished studies have suggested that releasing large numbers of budworm in endemic budworm populations will allow the collection of parasitoids, which are present in the population, but which may not be collected through regular sampling of the endemic population (V. Nealis, Canadian Forest Service, pers. comm.). The fourth site was used to release budworm larvae in an attempt to collect these additional parasitoid species. Spruce budworm larvae were released in this site in the spring of 1995. This site was sampled in the same manner and with the same intensity as the other three sites.

Stand selection

Stands were chosen using maps provided by the Manitoba Forestry Branch and the Canadian Forest Service which showed location and severity of spruce budworm outbreaks. The map information was used to select potential stands to visit for ground-truthing, as a result of which three stands were selected. Criteria for the stands with epidemic populations were that there was clear evidence of a moderate to severe budworm outbreak, but also that trees in the stand were likely to survive for the two year duration of the study. The endemic stand had to have budworm present, but no obvious signs of a budworm outbreak in the recent past. All three stands were also chosen to be in areas where they would not be affected by spruce budworm spray operations. In addition, all three stands were chosen to be as similar as possible to each other in general topography, tree species composition, age and density of stand, degree of pre-outbreak canopy closure, dominant ground vegetation, and drainage characteristics.

All stands used in this study were located in the Whiteshell Provincial Park in eastern Manitoba, and were selected in late April of 1994. The soils in the locations used belonged predominantly to the Lettonia Series with the dominant texture being clay. The parent material of this soil type is moderately calcareous, saline lacustrine clay. This type of soil is generally stone free with good drainage (Smith et al., 1967). The three stands were dominated by balsam fir.

Site set-up

Within each stand, one site was established. The sites were named epidemic 1, epidemic 2, and endemic. The epidemic 1 site was located on Highway 307, approximately 50 m south of the road, at the junction of Highways 307 and 309. The epidemic 2 site was located on Highway 309, approximately 9.1 km east of the Highway 307 - Highway 309 junction. The site was located approximately 500 m north of the road. The endemic site was located on the south side of Highway 44, approximately 19.4 km east of the Highway 44 - Highway 307 junction. The site was placed approximately 50m south of the road. Additional information regarding the location of each site is presented in Table 2. All sites were square, 1 ha in area, and at least 50 m from any roads or trails. Each site was divided into 100 10 m x 10 m subplots, the corners of which were marked by metal stakes.

Sampling procedures

Site characterization

To document environmental characteristics of sites, five 10 m x 10 m subplots were randomly selected within each site in August 1994.

Table 2. **Site Locations**

Site	Section Township Range	Latitude	Longitude	Topographic Map (1:50 000)	
				Map Index #	Grid Reference (to the nearest 100m)
Epidemic 1	SW 33-12-15E	50° 02' 08" N	95° 29' 10" W	52L/3	211454
Epidemic 2	NW 12-13-15E	50° 04' 51" N	95° 23' 42" W	52L/3	285504
Endemic	NW 5-10-17E	49° 48' 47" N	95° 16' 28" W	52E/14	364203

In each subplot observations were made as follows. The tree species and number of each within the subplot were recorded. An increment borer was used to take cores from two randomly selected trees from each tree species present within the subplot. Cores were taken at breast height, stored in plastic straws, and returned to the laboratory where they were used to determine tree age. The number of rings from the centre to the bark of the core was counted, to estimate tree age. The estimates were averaged for each tree species within each site. The standard error of the mean (SEM) was also calculated for each tree species age.

The ground cover in each subplot was sampled using two 2 m x 2 m quadrats for shrubs and two 1 m x 1 m quadrats for herbs. Species and their percent cover were recorded for each quadrat. In addition, a visual description of each site was recorded. This description included records of overall wetness, direction of any water flow, and amount of rock outcropping.

Insect sampling

Field procedures

Field sampling for spruce budworm took place in the summers of 1994 and 1995. Sampling began in early May and continued until August, when there were no longer viable egg masses in samples. Each site was sampled twice weekly throughout this period. On each sampling occasion, ten trees were sampled in

each site. The trees to be sampled were determined using random numbers. One set of random numbers was used to determine which ten 10 m x10 m subplots were to be sampled; a second set of random numbers was used to select one tree within each subplot. From each selected tree, one branch was removed using pole pruners (Figure 2). Branches were removed from the upper third of the crown, cut to approximately 45 cm in length x 45 cm in width, placed individually in plastic bags, and removed to the laboratory. Trees less than 2m in height were not sampled. Branches that were severely defoliated were also not sampled. This sampling procedure was used in all sites in both years with the exception of the endemic site in 1995, when two branches were removed from each sampled tree. The increase in sampling intensity was an effort to increase the numbers of budworm collected from the endemic site.

Laboratory procedures

In the laboratory, the branches were examined one at a time. An attempt was made to recover 11 larvae, pupae or egg masses, depending on the stage of life cycle present at the time, from each branch. When achieved, the result was 110 budworm collected from each site on each sampling occasion; of these 100 were reared and 10 were preserved. The first 11 budworm to be found on a branch were the eleven that were collected. Ten of these budworm would be reared and one budworm would be preserved. This collection of 11 specimens did not differentiate between life cycle stages. The 11 specimens collected from each

Figure 2. Branch removal using pole pruners.

branch could consist entirely of larvae, entirely of pupae, entirely of egg masses or a mixture of any of these stages. Therefore, on sampling occasions where more than one life cycle stage was present, the 110 budworm reared/preserved consisted of a mixture of the life cycle stages present.

Larvae to be reared were placed individually in plastic vials which contained artificial diet. The diet was prepared according to Lyon's (Lyon et al., 1972) modification of McMorran's (1965) artificial diet for spruce budworm with the exception that formaldehyde was added. As the larvae reared were collected from the field, they could not be sterilized effectively. The addition of 0.05 ml of 37 % formaldehyde per 100 g of diet helped to reduce the risk of microbial growth. The collection site, date, and tree species of each larva collected were recorded. The vials were placed in an incubator at 20 °C, 60% relative humidity and with a light : dark regime of 18hrs : 6hrs. Rearing continued either until a moth emerged, a parasitoid emerged or the larvae died for some other reason. Pupae and egg masses were also reared in vials, but without diet. After all 10 branches had been examined from a site, if the target 110 larvae, pupae or egg masses was not achieved, the deficit was made up, if possible, from branches with more than 11 larvae, pupae or egg masses.

Larvae for preservation were placed in 70% ethanol as a record of the instars present on that particular date. Larval head capsules were measured

(McGugan, 1954) to determine which instars were present on each collecting occasion from each site. In 1995, the vegetative buds on the sampled branches were examined. Based on these observations, the buds on each branch were recorded as one of five developmental stages as described by Osawa et al. (1983). These bud classes were used to determine stage of bud development throughout the sampling period.

Identification

Parasitoids that emerged were identified and pinned, or else identified and preserved in 70% ethanol. All identifications, with the exception of the pentatomid bugs, were done by D. Zebrowski. Identifications were made using type specimens and keys provided through Vince Nealis at the Great Lakes Forestry Centre (Natural Resources Canada). Further assistance and confirmation of the identifications were provided by Dr. Vince Nealis and by Dr. Eldon Eveleigh and Steve Pollack of the Canadian Forest Service - Fredericton (Natural Resources Canada). Identification of the pentatomid bugs was done by Dr. Dave Rider of North Dakota State University. Confirmation of identification of spruce budworm was provided by Richard Westwood (Manitoba Natural Resources - Forestry Branch). Voucher specimens of each parasitoid species collected in this study have been deposited in the J.B. Wallis Museum in the Department of Entomology, University of Manitoba.

Release site

The release site, established in the spring of 1995, was used to release budworm larvae into an endemic population in order to collect parasitoid species not collected through regular sampling of endemic populations. The release site was established in the same forest stand as the endemic site, and approximately 50m east of that site. This site was 10 m x 10 m and was used only in 1995. On May 18, 1995, approximately 3000 second instar budworm larvae were released on the mid crowns of two balsam fir trees, in the centre of the site. The budworm were on cheesecloth which was attached to the trees using flagging tape. The release trees were monitored for larval emergence, which began between May 25th and May 29th. Sampling in the release site began on May 29th. The trees in the release site were sampled in the same manner and with the same frequency as the other sites. Due to the dispersal of young larvae (Wellington and Henson, 1947), sampling in the release site included all host trees in the release site, not just the release trees. Sampling continued in this site until viable egg masses were no longer found in any of the samples from any of the sites.

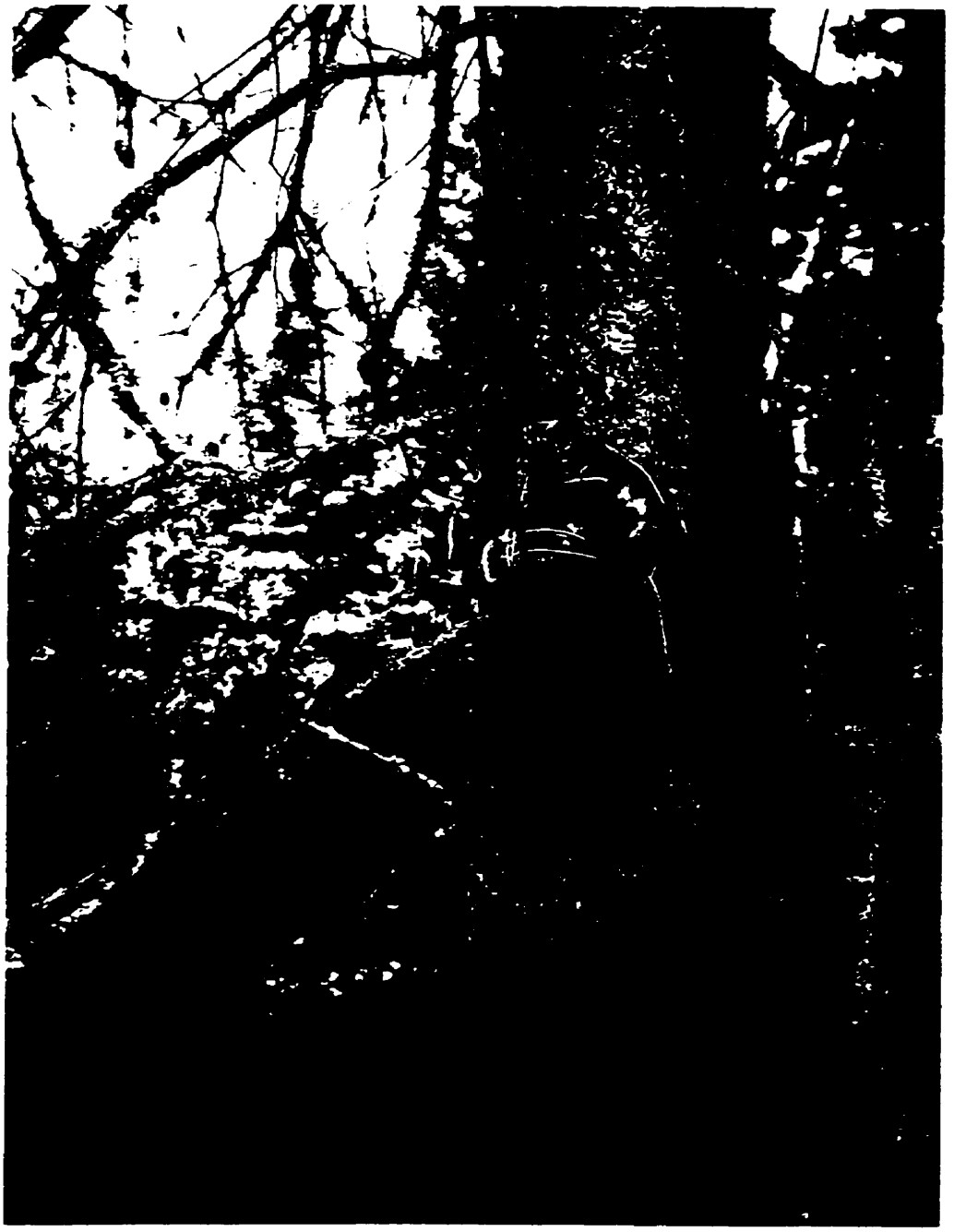
Environmental data collection

Temperature

In 1995, air temperature was recorded using Hobo XT Temperature Loggers (Onset Instruments Corp. ®). The temperature loggers were placed in plastic

containers with the probes extending from one end of the container. The containers were attached to the north side of trees with duct tape. The probes extended downwards about 2.5 cm from the bottom of the containers which resulted in the probes being approximately 2 m above the ground. Moss from the surrounding area was tied with string over the containers to prevent squirrels from chewing on data loggers and probes (Figure 3). The measurement end of the probe extended slightly from under the moss. Two data loggers were put in the centre of each site. The temperatures recorded from both data loggers were used to determine an average temperature for each site. One of the data loggers in the epidemic 2 site was damaged by squirrels. Therefore for this site, data from only one data logger was used. The data loggers were placed in each site on March 19, 1995 and were removed from the sites on August 1, 1995. The temperature was recorded by the data loggers every 2.4 hours.

Figure 3. Data logger on tree



Light intensity

In both 1994 and 1995, light intensity was recorded in the endemic and two epidemic sites. Due to time constraints in 1994, the light intensity was measured in September. The light intensity was measured in the endemic site on September 19. Light intensity data were measured from the epidemic sites on September 22. In 1995, light intensity was measured in all three sites on July 31. Random numbers were used to determine 25 locations in each site, and light readings were taken at each of these points. In addition, two readings were taken on the road, one before and one after taking the readings in each site. The readings from the road were used to standardize the readings from the sites. All measurements were taken at 2 m above the ground. The light intensity measurements were taken on cloudless days using a Li-Cor 185 Quantum/Photometer with a photometer probe.

Data analysis

Temperature calculations

The temperature data was converted to day degrees using the formula:

Day degrees = $[(T_{max} + T_{min})/2] - Z$

where: T_{max} = daily maximum

T_{min} = daily minimum

z = developmental threshold

The above formula was used when T_{min} is greater than Z. On days when the T_{min}

was below Z, the Lindsey Neuman Table (Lindsay and Neuman, 1956) was used so that the number of day degrees was not underestimated. The developmental threshold (Z) used in this study was 4.5 °C. This developmental threshold has been determined by the Manitoba Forestry Branch to be the most accurate developmental threshold for eastern Manitoba based on field data (K. Knowles, Manitoba Natural Resources, Forestry Branch, Pers. Comm.).

Determination of apparent rate of parasitism

The apparent rate of parasitism was determined based on the number of hosts at risk. Each parasitoid species attacks a certain stage of the spruce budworm and emerges from or kills another stage. Any budworm larva falling within the "attack/kill" range of a specific parasitoid was said to be "at risk" from that particular parasitoid. Therefore, for each parasitoid collected, an at risk period for the spruce budworm was determined from the literature. Then it was determined on a per site basis how many budworm collected during the study in each year were at risk of being parasitized by each parasitoid species. The apparent rate of parasitism was then determined to be the percentage of collected budworm at risk that were in fact parasitized.

Log linear models

Log linear models were used to investigate the relationships between occurrence of each parasitoid species and host tree species, site, and year. The

likelihood ratio chi-square was the test statistic used to determine the fit of the models (Bishop et al., 1975). This method compares observed and expected values in contingency tables to assess the statistical significance of differences between proportions based on samples from different populations (Mead et al., 1993). This approach can also be extended to test hypotheses about the proportions of individuals occurring in different categories when several classification factors are involved in the definition of categories (Mead et al., 1993). This analysis was performed using SYSTAT (Wilkinson, 1992).

Correspondence analysis

The pattern of relationships among objects (eg. individuals, sampling units, taxa etc.) can be described using ordination analysis (James and McCulloch, 1990). Ordination analysis is a multivariate technique that allows the representation of multi-dimensional data in a low dimensional space (Gauch, 1982; Greenacre, 1984; ter Braak, 1985; James and McCulloch, 1990). This technique results in an ordination diagram in which the arrangement of objects around the axes is such that similar entities are close to each other and dissimilar entities are far apart (Gauch, 1982; Greenacre, 1984). The axes are arranged in an orthogonal manner. Each axis is orthogonal to preceding axes and is placed in the direction which will account for the maximal possible variance remaining in the data after variation attributable to all previous axes has been removed (Gauch, 1982). The eigenvalue associated with each axis describes the amount of variation in the

data explained by that axis (ter Braak, 1987-1992). The signs on the axes in ordination diagrams are arbitrarily assigned and are for orientation purposes only (ter Braak, 1987-1992). The axes are considered to be latent variables associated with the data and are interpreted on the basis of what is known about the species in the data set and the environment in which they exist (Gauch, 1982; ter Braak, 1985). Objects near the centre of the diagram may be ubiquitous and unrelated to the ordination axes (ter Braak and Prentice, 1988).

Correspondence analysis (CA), also referred to as reciprocal analysis, is a non-linear ordination technique which is commonly used to analyze data on the incidence or abundance of species in samples (ter Braak, 1985; ter Braak and Prentice, 1988). The CA method is the ordination technique most suitable for data consisting of counts. It may be used for presence-absence data as well as abundance data (James and McCulloch, 1990). In the ordination diagrams produced by CA, sites are generally placed close to the species which are most prominent in those sites. The CA methodology is a compromise between putting emphasis on samples and on species (Noy-Meir, 1975). This results in species that are both low in abundance, and rare, as being treated as extremely distinctive. CA places species that fall into this category at the extreme ends of the ordination axes (Gauch, 1982). This sensitivity may be useful in some applications, but can cause problems when the goal is to detect major trends (ter Braak and Prentice, 1988). In situations where this becomes a problem, the rare

species should be removed from the data set before performing the analysis (Gauch, 1982; ter Braak and Prentice, 1988).

CA was used to examine whether the parasitoid guild collected from the epidemic spruce budworm populations differed from the parasitoid guild collected in the endemic spruce budworm population. Ordination diagrams produced using this analysis were also used to determine the differences between the parasitoid guilds on a species level. The CA ordinations were produced using CANOCO (ter Braak, 1987 - 1992). All CA ordinations were produced using the default settings of CANOCO. No transformations were used. The relationship of vegetation and sites was also examined with CA ordinations.

Linear Regression

Linear regression was used to examine budworm mortality on spruce. This was done by performing a linear regression on the percentage of budworm in the pooled epidemic sites collected from spruce on each sampling occasion. This regression analysis was done for both 1994 and 1995. A linear regression was also performed on the percentage of spruce branches collected in the pooled epidemic sites on each sampling occasion. This regression was only done for 1995 as the number of fir versus spruce branches collected on each sampling occasion were not recorded in 1994. The linear regressions were performed using SYSTAT (Wilkinson, 1992). Analysis of variance was used to test the

hypothesis that the slope is = 0. A large F-ratio occurs when the independent variable helps to explain the variation in the dependent variable (Mead et al., 1993).

Although the linear regression is not shown graphically, the same data was graphed using the LOWESS graphing technique to show the non linear trends emanating empirically from the data. LOWESS is a smoothing method that uses an iterative, locally weighted, least-squares method to fit a curve to a set of points. The tension for the LOWESS smoothing was set at 0.9. The tension determines the stiffness of the curve and can vary between 0 and 1. The SYSTAT default setting for tension is 0.5 (Wilkinson, 1992). The data used in these graphs and in the linear regressions were weighted based on the total number of budworm collected on each sampling occasion. This was done so that undue importance would not be attributed to the sampling occasions when only a few budworm were collected.

Results

Site characteristics

Vegetation

Five tree species were found in all of the 1 ha sites : balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Table 3 shows the mean density ± SEM and average age ± SEM of each tree species in each site. All three stands were dominated by balsam fir with small amounts of white spruce, jack pine, trembling aspen, and white birch. The epidemic 1 site contained more aspen than the other three sites (Table 3). Based on the average tree ages, the stand age (defined as the time since the last disturbance) is estimated to be approximately 80 to 90 years. This stand age was based primarily on the ages of the white spruce trees. The release site was not core sampled to determine age, but was in the same stand as the endemic site and therefore tree ages are expected to be similar to those found in the endemic site. The release site, due to its small size did not contain any spruce trees. This smaller site contained a few trembling aspen but was dominated by balsam fir.

In all three sites there was some understorey vegetation, but there was also large amounts of bare ground. Table 4 shows the estimated percent cover for bare ground and each herbaceous and shrub species in each site. Understorey

herbaceous vegetation, where present, was dominated in all three sites by bunchberry (*Cornus canadensis* L.) (Table 4). Other herbaceous species found commonly in at least one site (estimated percent cover = or > 5%) were blueberry (*Vaccinium angustifolium* Ait.), labrador tea (*Ledum groenlandicum* Oeder), and smooth wild strawberry (*Fragaria virginiana* Dcne.). The most abundant shrub was alder, *Alnus crispa* (Ait.) Pursh., which occurred in patches in all three sites, often covering several square metres in area. The release site was in the same forest stand as the endemic site and therefore had the same type and composition of understory vegetation as the endemic site.

Topography

The epidemic 1 site was higher at the east edge and gradually sloped downhill from east to west until almost at the western edge of the site. At the western edge, there was an area of standing water, which stretched over the entire 100 m of the site in a north-south direction. This standing water was approximately 2 - 5 m wide. The entire western edge of the site was dominated by a large rock outcrop.

The epidemic 2 site had a large rock outcrop along the northern edge of the site. The rock outcrop was approximately 7 m in an east-west direction and approximately 2 m in a north-south direction. There was no standing water in this site and aside from the rock outcrop, the site was level.

The endemic and release sites were fairly level with no major changes in elevation, and no rock outcrops. The release site had no wet areas. Along the southern edge of the endemic site there were some wet areas with standing water. Most of these areas were a few m^2 or smaller in size. The rest of the site was fairly dry.

Light intensity

Mean light intensities and coefficient of variation ($CV_{(x)}$) values are shown in Table 5 for all three sites in both years. The light intensity measurements for each year were standardized to the maximum light intensity value measured in that year. Mean light intensities were calculated from the standardized measurements. This was done to allow for comparison of measurements and mean light intensities between sites in each year. Due to time constraints during the sampling years, the light measurements in 1994 were taken in September and the light measurements in 1995 were taken in July. For this reason the mean light intensities cannot be compared between years. The endemic site was the darkest of the three sites in both years (Table 5). The epidemic sites were similar to each other with regards to mean light intensity in both years (Table 5). Coefficients of variation were calculated for each site in each year to indicate the relative patchiness of each site. The $CV_{(x)}$ is a dimensionless quantity which puts the expression of variability on a relative basis (Mead et al., 1993; Freese, 1962) and therefore the $CV_{(x)}$ values for each site can be

compared between the two years. Based on the $CV_{(x)}$ calculations, all three sites had a similarly high degree of patchiness in both years (Table 5).

Spruce budworm collections

The numbers of spruce budworm collected from balsam fir and white spruce in each site in each year are shown in Table 6. In all sites and in all years, there were more budworm collected from balsam fir than from white spruce. More egg masses were collected from fir than from spruce in all sites and in all years as well (Table 6). There were no egg masses collected from the endemic or release sites in either year.

Parasitoid species

There were 16 parasitoid species collected in total (Table 7). All but four species were collected in both years. *Apanteles morrisi* Mason and *Mesopolobus tortricis* (Brues.) were collected in 1994 only, and *Sarcophaga aldrichi* Park. and *Enytus montanus* (Ashmead) were collected only in 1995. The five parasitoid species collected from the endemic site during the two year collecting period were all collected in the epidemic sites as well.

Although approximately 3000 budworm larvae were released in the release site, only 135 were recovered. This low recovery rate is most likely due to the presence of many pentatomid bugs of the genus *Podisus*. These pentatomids

were observed on several branches collected from the release site and may have been preying on the budworm larvae. The six parasitoids collected in the release site are listed in Table 8; all of these were collected in one or more of the other sites. All parasitoids collected in this site were collected from fir. There were some parasitoid species collected from the release site that were not collected from the endemic site and were therefore most likely present in the endemic site as well. The release of the budworm in early May meant that species such as *A. fumiferanae*, *G. fumiferanae*, and *A. morrisi*, which attack the budworm in June and then overwinter in the budworm, could not be collected here.

Out of the 16 parasitoid species collected, 11 were hymenopteran parasitoids and five were dipteran parasitoids (Table 9). The majority of the parasitoids collected were species that attack the late larval and pupal stages of the spruce budworm (Table 9).

The apparent rate of parasitism for each parasitoid species in 1994 is listed in Table 10. Table 11 shows the apparent rate of parasitism for each parasitoid species collected in 1995. The importance of each parasitoid species on each host tree in each site is shown in Table 12 and Table 13. The parasitoid species in these tables are listed in approximate descending order of most abundant to least abundant. *Apanteles fumiferanae* is notable due to its ubiquitous nature

regardless of host tree. Even in the very small spruce samples, where only a few parasitoid species were collected, *A. fumiferanae* was found in all but one site in one year. Although not listed in these tables, one hyperparasitoid, the chalcid *Baryscapus sp.*, was collected on one occasion from the epidemic 2 site in 1994. One *M. verditer* was also collected from the same pupa.

Interactions of parasitism rate with host location

Each parasitoid species was tested using log linear analysis to determine whether its apparent rate of parasitism interacted significantly with the site, and tree species, from which the host budworm larvae were collected. It should be noted that in small samples, such as those collected from spruce, the apparent rate of parasitism is highly affected by a single parasitoid and therefore all results should be interpreted cautiously. In 1994, there were only two significant effects observed from the log linear model analysis. The apparent rate of parasitism of *A. morrisi* was significantly affected by tree species ($G = 8.16$, $df = 1$, $p < 0.01$); the apparent rate of parasitism being 0.10% of hosts at risk on balsam fir and 4.17% of hosts at risk on white spruce. These results apply to the epidemic 1 site only. This interaction was not examined for the epidemic 2 and endemic sites as there were no *A. morrisi* collected from these sites in 1994. No *A. morrisi* were collected in 1995 and therefore this interaction was not examined for *A. morrisi* in 1995.

In 1994, the apparent rate of parasitism of *A. fumiferanae* was also significantly affected by tree species ($G = 5.31$, $df = 1$, $p < 0.025$); the apparent rate of parasitism was 7.73% of hosts at risk on balsam fir and 10.80% of hosts at risk on white spruce. This interaction was not significant for *A. fumiferanae* in 1995. These results include all three sites as *A. fumiferanae* was collected from all three sites in both years.

In 1995, several significant interactions occurred. There were six parasitoid species in which the apparent rate of parasitism was significantly affected by site (Table 14) and three parasitoid species in which the apparent rate of parasitism was significantly affected by tree species (Table 15). Two of the three significant interactions with tree species (Table 15), those involving *M. verditer* and *I. conquisitor*, were not reflected in trends seen in 1994. The apparent rate of parasitism of *W. fumiferanae* was not significantly affected by tree species in 1994, but did show a similar trend to what was seen in 1995 (Table 10, Table 11). Three of the species showing significant interactions with site, *G. fumiferanae, P. maculicornis hariolus* and *M. verditer*, had their highest apparent rates of parasitism in the epidemic 1 site and were not collected in the endemic site at all (Table 14). *Meteorus trachynotus* and *E. montanus* both had lower rates of parasitism in the epidemic 1 site and their highest rates of parasitism in the endemic site (Table 14).

Comparisons between the two sampling years showed a number of different significant interactions. The apparent rate of parasitism for five species was significantly different between 1994 and 1995 (Table 16). For nine parasitoid species, the interaction between tree species, and site that they were collected from, were significantly different in the two sampling years (Table 17). For two parasitoid species, *I. conquisitor* and *E. caesar*, the apparent rates of parasitism in the different sites were significantly different in the two sampling years (Table 18).

Ordination analysis of sites and vegetation

Correspondence analysis

The 1994 site and vegetation data were used in a correspondence analysis to compare the similarity of the sites to each other. This analysis included percentage cover for herbaceous plants, including shrubs and estimates of bare ground (Table 4). For use in this analysis, the tree data shown in Table 3 were converted to percentages. This information was collected in 1994 and therefore only 1994 sites were used in this analysis (Figure 4). The first two axes combined have an eigenvalue of 0.315. The first axis represents 65.7% of the variation in the data and the second axis represents 34.3% of the variation in the data. Although the three sites are all separated from each other, they are all similar to each other with respect to dominant tree species. This is evident as the dominant tree species are all located near the centre of the diagram.

The endemic site and the epidemic 2 site are not too far apart along axis one, however they are well separated along axis two. The epidemic 1 site is separated from the other two along both axes. These separations occur as each site has at least one species that was only collected in that site. *Cornus alba, F. virginiana*, and *J. communis* were only found in the endemic site. *Ledum groenlandicum*, *R. idaeus* var. *aculeatissimus* and *M. canadense* were only found in the epidemic 2 site. *Amelanchier alnifolia* was only found in the epidemic 1 site.

Ordination analysis of parasitoid species

Correspondence analysis

A correspondence analysis was done on the 1994 and 1995 site and parasitoid species data shown in Tables 7 and 8. The resulting ordination diagram is shown in Figure 5. The first axis represents 52.3% of the variation and the second axis represents 22.9% of the variation within the data, respectively. Together the first two axes combined have an eigenvalue of 0.273 and represent 75.2% of the variation within the data. There are three groupings apparent from the diagram. The 1995 endemic and release assemblages are grouped together, the three 1994 assemblages are grouped together and although not as closely associated as the other two groups, the two 1995 epidemic assemblages are grouped together. These groupings are represented along both the first and second axes for all groups except the 1995 epidemic assemblages which are

separated along axis two. The parasitoid species in the diagram are mostly clustered around the centre of the diagram, closest to the epidemic assemblages from both 1994 and 1995. The parasitoid species *E. montanus* and *M. trachynotus* are exceptions to this as they are further removed from the centre of the diagram than any of the other parasitoid species, and are closer to the release and 1995 endemic sites than are any other species. *Mesopolobus tortricis* and *A. morrisi* are responsible for pulling the 1994 epidemic sites together and away from other sites. This occurs because *M. tortricis* was collected only in the two epidemic sites and only in 1994 and *A. morrisi* was collected only in 1994 and only in the epidemic 1 site (Table 7).

A second correspondence analysis was performed on the data found in Tables 7 and 8. The parasitoid species *A. morrisi*, *A. fumiferanae* and *G. fumiferanae* all attack overwintering budworm larvae. When the release site was set up, larvae were released in the spring of 1995 and therefore it would have been impossible to collect these species from this site. Therefore, to allow effective comparisons with the release site, *A. morrisi*, *A. fumiferanae* and *G. fumiferanae* were excluded from this second ordination (Figure 6). The two axes combined have an eigenvalue of 0.301 and represent 71.0% of the variation within the data. The first axis represents 46.3% of the variation within the data and the second axis represents 24.7% of the variation within the data. In this ordination diagram, there are three distinct groups: the 1994 epidemic assemblages, the 1995

epidemic assemblages, and the 1994 endemic, 1995 endemic and release sites which are found together in the third group. The 1994 epidemic sites and the 1995 epidemic sites are both located near the middle of the diagram, separated along both axes due to one or two species. The 1994 epidemic sites are removed from other sites due to their close association with *M. tortricis* (Table 7). *Ephialtes ontario* and *S. aldrichi* are most closely associated with the 1995 epidemic sites (Table 7). The endemic sites from both years and the release site are clearly separated from the epidemic sites near the outer edge of the diagram. *Lypha setifacies*, *M. trachynotus*, and *E. montanus* are positioned closer to the endemic and release sites than the other parasitoid species (Table 7 and Table 8). The remaining parasitoid species are all found clustered between the 1995 and 1994 epidemic sites.

Figure 7 shows the ordination diagram which resulted from the correspondence analysis of the 1994 and 1995 species and site data using count data collected from fir only (Table 10, Table 11, Table 8). The first two axes combined account for 71% of the variation found within the data and have a combined eigenvalue of 0.265. The first axis represents 49.6% of the variation within the data and the second axis represents 21.4% of the variation found within the data. The diagram is very similar to what was seen in Figure 5. The release and 1995 fir endemic assemblages are grouped together along the first axis and are separated from all the other sites. *Enytus montanus* and *M. trachynotus* are

most closely associated with these two sites (Table 11). The fir assemblages from both the 1994 epidemic and 1994 endemic sites are also grouped together. Again, as in Figure 5, the 1994 sites are clustered close to *A. morrisi* and *M. tortricis* (Table 10). The two epidemic sites from 1995 are separated along the second axis although they are grouped together along axis one. *Phaeogenes maculicornis hariolis, E. ontario, S. aldrichi,* and *M. verditer* were all associated with the 1995 epidemic assemblages as in Figure 5 (Table 11).

A fourth correspondence analysis was done using the 1994 and 1995 site and species count data, including the release site in 1995, and excluding the species *A. morrisi, A. fumiferanae* and *G. fumiferanae* (Table 8, Table 10, Table 11). These three species were again excluded for better comparisons of the release site to the other sites. This analysis included only data collected from fir host trees (Figure 8). In this ordination diagram, the first two axes combined have an eigenvalue of 0.298 and represent 70.1 % of the variation within the data. The first axis represents 46.1 % of the variation within the data and axis two represents 24.0 % of the variation within the data. The site groupings and the parasitoid species associated with each group are the same as in Figure 6, indicating that the groupings are not an artifact of different host tree sources in different sites. The 1994 endemic site is in a different position from what was seen in Figure 7 due to the removal of *A. fumiferanae*. Without *A. fumiferanae* in the ordination, the only species influencing the 1994 endemic site is *L. setifacies*.

Figure 9 shows the ordination diagram resulting from the 1994 and 1995 site and parasitoid count data, but only uses parasitoid assemblages collected from white spruce (Table 10, Table 11). In this diagram, the first two axes combined have an eigenvalue of 0.623 and represent 83.3 % of the variation within the data. The first axis represents 58.0% of the variation within the data and the second axis represents 25.3% of the variation within the data. This diagram does not differ much from the preceding diagrams. The 1995 epidemic 1 site, 1994 endemic site, 1994 epidemic 2 site and the 1995 epidemic 2 site assemblages are all very close to each other along the first axis. This is similar to what was seen in Figures 5 and 7. The 1995 epidemic 2 site assemblage is separated from the rest of the assemblages along axis 2 because it was the only spruce assemblage in either year that was associated with *I. conquisitor* and *E. ontario* (Table 10, Table 11). There were no parasitoids collected from spruce in the 1995 endemic site or from the 1995 release site and therefore these sites do not appear in this diagram. The assemblage for the 1994 epidemic 1 site is pulled away from the others along the first axis as it was the only spruce assemblage in either year to be associated with *A. morrisi* (Table 10). The 58% variation accounted for by axis one seems to be related solely to the two individuals of *A. morrisi* collected from spruce in the epidemic 1 site. Therefore, the information provided by this diagram regarding the other sites and species is limited.

Figure 10 illustrates the ordination diagram produced from a correspondence

analysis performed on the count data for both the 1994 and 1995 species and site data, including the release site, separated into tree species (Table 8, Table 10, Table 11). The combined axes account for 64.7% of the variation in the data and have a combined eigenvalue of 0.471. The first axis represents 37.4% of the variation within the data and the second axis represents 27.3% of the variation within the data. All sites, with the exception of the 1994 epidemic 1 site spruce assemblage, are closely aligned along axis one. The 1994 spruce assemblage from the epidemic 1 site is removed from all other assemblages along axis one due to the close association of *A. morrisi* with this assemblage (Table 10). Therefore, the variation in the data explained by axis one is largely accounted for by the two *A. morrisi* individuals that were collected in 1994.

Due to the heavy influence of *A. morrisi* in Figure 10, a second correspondence analysis was performed on the same data excluding *A. morrisi* (Figure 11). The first two axes have a combined eigenvalue of 0.302 and together account for 65.1% of the variation within the data. The first axis represents 43.5% of the variation within the data and the second axis represents 21.6% of the variation within the data. There are no spruce assemblages associated with the 1995 release site or with the 1995 endemic site as there were no parasitoids collected from spruce in either of these sites in 1995. The patterns seen in Figure 11 are very similar to those seen in Figure 5. The fir assemblage from the 1995 endemic site and the fir assemblage from the 1995 release site are at the

positive end of axis one and separated from all other assemblages. *Enytus montanus* and *M. trachynotus* are most closely associated with these two assemblages (Table 11). The 1994 endemic spruce and fir assemblages are located together (Table 10). They are separated from the 1995 endemic assemblages along the first axis but are close to them along the second axis. Although the epidemic assemblages from both years are all grouped closely to each other along the first axis, the group is separated into spruce assemblages fir assemblages along axis two (Table 10, Table 11).

Mortality on spruce

Linear regression

The percentage of budworm collected from spruce on each sampling occasion tended to decline over the season in both 1994 (Figure 12) and 1995 (Figure 13). There was a significant linear regression between the percentage of budworm collected from spruce and sampling date in both the 1994 ($F = 14.28$, $df = 1$, $p < 0.001$) and 1995 ($F = 15.71$, $df = 1$, $p < 0.001$) regressions.

In contrast, there was evidence that the percentage of spruce branches sampled on each sampling occasion exhibited a seasonal trend in 1995 (Figure 14); and a linear regression between percentage of spruce branches collected and sampling date ($F = 0.01$, $df = 1$, $p = 0.92$) was not significant. Data for percent of spruce branches sampled were not recorded in 1994. The trends depicted in the

graphs produced using the LOWESS technique (Figure 12, Figure 13, Figure 14) support the linear regression results.

Comparison of fir and budworm development with temperature and parasitoid occurrence.

For the two epidemic sites in 1995, graphical comparisons were made of the day degree accumulation (DDC) with the bud development of fir, development of budworm instars and the occurrence of parasitoids (Figure 15, Figure 16). The thickness of the individual parasitoid species lines (vertical scale) represents the percentage of the total number of parasitoids collected on each sampling date. The budclass and instar portions of the graph indicate the average budclass or instar stage present on each collection date. Figure 15 shows the results from the epidemic 1 site and Figure 16 show the results from the epidemic 2 site. The DDC accumulation was faster in the epidemic 1 site. The difference was smaller earlier in the summer and increased as the summer progressed. The accumulation of 250 DDC occurred between May 31 and June 5 in the epidemic 1 site and by June 5 in the epidemic 2 site. It took the epidemic 2 site until June 22 to accumulate 500 DDC whereas the epidemic 1 site reached 500 DDC just prior to June 19. The epidemic 1 site reached 750 DDC in the first week of July. The epidemic 2 site did not reach 750 DDC until the second week of July. The fifth and final budclass was recorded in both sites on June 5. The sixth instar budworm were first recorded in both sites on June 8, although pupae were first

recorded June 14 in the epidemic 1 site and June 19 in the epidemic 2 site. Only three parasitoid species occurred in the early stages of fir and budworm development: *A. fumiferanae*, *G. fumiferanae* and *E. montanus* (Figure 15, Figure 16) The majority of the parasitoids occurred in the later instars and pupal stage of the spruce budworm. Although DDC accumulated at a faster rate in the epidemic 1 site, budworm instars, budclass, and parasitoid species all occurred on, or very close to, the same dates in both sites.

Table 3. **The mean density (±SEM) and average age (±SEM) of each tree species in each site**

	Epidemic 1		Epidemic 2		Endemic	
Tree Species	**Number / ha**	**Years**	**Number / ha**	**Years**	**Number / ha**	**Years**
Abies balsamea (L.) Mill. Balsam fir	940 ± 2.60	56 ± 3.13	860 ± 4.37	48 ± 1.97	2800 ± 7.48	55 ± 6.49
Picea glauca (Moench) Voss White spruce	20 ± 0.20	80[1]	100 ± 0.55	91 ± 1.42	260 ± 0.68	94 ± 2.01
Populus tremuloides Michx. Trembling aspen	300 ± 0.89	64 ± 10.22	100 ± 0.55	57 ± 5.50	120 ± 0.80	55 ± 29.50
Betula papyrifera Marsh. White birch	80 ± 0.80	51[1]	40 ± 0.40	44[1]	40 ± 0.24	49 ± 3.00
Pinus banksiana Lamb. Jack pine	20 ± 0.20	53[1]	60 ± 0.60	99[1]	20 ± 0.20	26[1]

[1] Tree species was only found in one sample and therefore SEM is not included.

Table 4. **Estimated percent cover of bare ground and vegetation (herbaceous and shrub) found in the three sampled sites.**

Bare Ground/Vegetation Species	Percent Cover		
	Epidemic 1	Epidemic 2	Endemic
Bare Ground	78.7	16.5	41.8
[1]Common Herbaceous Species:			
Cornus canadensis L. (bunchberry)	3.7	23.0	9.1
Vaccinium angustifolium Ait. (blueberry)	5.5	7.0	0.0
Ledum groenlandicum Oeder (labrador Tea)	0.0	5.0	0.0
Fragaria virginiana Dcne. (smooth wild strawberry)	0.3	0.0	6.9
[2]Other Herbaceous Species:			
Smilacina stellata (L.) Desf. (star flowered-solomon's-seal)	0.3	0.5	0.9
Galium boreale L. (northern bedstraw)	0.1	0.3	0.1
Arctostaphylos uva-ursi (L.) Spreng. (bearberry)	0.0	0.3	0.0
Rosa arkansana Porter (low prairie rose)	1.0	0.0	1.0
Aralia nudicaulis L. (wild sarsaparilla)	0.4	0.0	0.3
Mitella nuda L. (bishop's-cap)	0.0	0.0	1.8
Trientalis borealis Raf. (northern starflower)	0.0	0.0	0.5
Clintonia borealis (Ait.) Raf. (bluebead-lily)	0.2	0.5	0.5
Maianthemum canadense Desf. var. *interius* Fern. (lily of the valley)	0.2	2.0	0.1
Linnaea borealis L. var. *americana* (Forbes) Rehder (twinflower)	0.0	0.0	0.5
[1]Common Shrubs:			
Alnus crispa (Ait.) Pursh (alder)	39.0	4.5	3.4
[2]Other Shrubs:			
Rubus idaeus L. var. *aculeatissimus* Regel & Tiling (raspberry)	0.0	2.0	0.3
Cornus alba L. (red osier dogwood)	0.0	0.0	4.0
Juniperus communis L. (juniper)	0.0	0.0	1.0
Amelanchier alnifolia Nutt. (saskatoon)	3.0	0.0	0.0

[1]. "Common" species are those which were 5% or greater cover in at least one site. Herbaceous and shrub vegetation were sampled separately using different sized quadrats. For this reason, shrub vegetation was not measured in the herbaceous quadrats and vice versa. Therefore, neither the percent covers for herbaceous vegetation, nor the percent covers for the shrub vegetation, add up to 100.

[2]. "Other" species are those which did not have 5% or greater cover in at least one site.

Table 5. Standardized mean light intensity in each site in 1994 and 1995

Sites	Light Intensity			
	1994		1995	
	Mean Light Intensity (Microeinsteins $m^{-2}sec^{-1}$)	$CV_{(x)}$ Light Intensity[1]	Mean Light Intensity (Microeinsteins $m^{-2}sec^{-1}$)	$CV_{(x)}$ Light Intensity
Epidemic 1	2536	0.955	5553	1.067
Epidemic 2	2382	1.039	4089	1.027
Endemic	1052	1.073	1526	1.249

[1] $CV_{(x)}$ = SD/Mean

Table 6. The numbers of spruce budworm collected each year on each tree species in each site.

Site	Epidemic 1				Epidemic 2				Endemic				Release	
Year	1994		1995		1994		1995		1994		1995		1995	
Tree Species	BF[1]	WS[2]	BF	WS	BF	WS	BF	WS	BF	WS	BF	WS	BF	WS
Larvae and pupae[3]	1210	49	1291	52	834	369	1046	272	41	14	67	1	135	0
Egg masses collected	64	8	12	1	77	46	8	4	0	0	0	0	0	0

[1] BF = Balsam fir
[2] WS = White spruce
[3] Includes larvae and pupae

Table 7. Parasitoid species and numbers collected in each site in each year.

	1994			1995		
Parasitoid Species	**Epidemic 1**	**Epidemic 2**	**Endemic**	**Epidemic 1**	**Epidemic 2**	**Endemic**
Hymenoptera: Braconidae						
Apanteles fumiferanae Vier.	86	82	4	48	51	2
Apanteles morrisi Mason	3	0	0	0	0	0
Meteorus trachynotus Vier.	4	1	0	14	4	2
Ichneumonidae						
Glypta fumiferanae (Vier.)	29	21	0	31	13	0
Phaeogenes maculicornis hariolus (Cress.)	27	21	0	33	13	0
Itoplectis conquisitor (Cush.)	11	14	0	13	2	0
Ephialtes ontario (Cress.)	4	9	0	34	18	1
Enytus montanus (Ashmead)	0	0	0	0	3	1
Pteromalidae						
Mesopolobus verditer (Norton)	5	4	0	16	1	0
Mesopolobus tortricis (Brues)	1	6	0	0	0	0
Trichogrammatidae						
Trichogramma minutum Riley	5	21	0	1	8	0
Diptera: Tachinidae						
Phryxe pecosensis (Tns.)	29	29	0	19	26	0
Lypha setifacies (West)	9	12	1	11	5	1
Eumea caesar (Aldr.)	7	11	0	16	4	0
Winthemia fumiferanae Toth.	6	9	0	3	3	0
Sarcophagidae						
Sarcophaga aldrichi Park.	0	0	0	7	6	0

Table 8. **The number of each parasitiod species collected from the release site in 1995.**

Parasitoid Species	Number collected
Meteorus trachynotus	9
Lypha setifacies	4
Phaeogenes maculicornis hariolus	4
Ephialtes ontario	1
Winthemia fumiferanae	1
Enytus montanus	1

Table 9. **The stages of spruce budworm attacked by the parasitoids collected in 1994 and 1995.**

Spruce budworm stage attacked	Insect Order of Parasitoids	
	Hymenoptera	**Diptera**
Early Larval	*Apanteles fumiferanae* *Apanteles morrisi* *Glypta fumiferanae*	
Late Larval	*Enytus montanus* *Meteorus trachynotus*	*Lypha setifacies* *Winthemia fumiferanae*[1] *Eumea caesar*[2] *Phryxe pecosensis*[2]
Pupal	*Ephialtes ontario* *Itoplectis conquisitor* *Phaeogenes maculicornis* *hariolus* *Mesopolobus tortricis* *Mesopolobus verditer*	*Sarcophaga aldrichi*[3]
Egg	*Trichogramma minutum*	

[1] *W. fumiferanae* attacks late larvae, but emerges from pupae.
[2] These species emerged from both late instar larvae and from pupae.
[3] *Sarcophaga aldrichi* may attack late instar and pupae.

Table 10. **The apparent rate of parasitism and numbers of spruce budworm at risk for the parasitoid species collected in all three sites in 1994.**

Parasitoid Species	Percentage parasitism					
	Epidemic 1		Epidemic 2		Endemic	
	BF[1]	WS[2]	BF	WS	BF	WS
Apanteles fumiferanae	8.7 (971)[3]	4.2 (48)	6.4 (676)	11.9 (328)	8.3 (36)	7.1 (14)
Apanteles morrisi	0.1 (971)	4.2 (48)	0.0 (676)	0.0 (328)	0.0 (36)	0.0 (14)
Glypta fumiferanae	3.0 (971)	0.0 (48)	2.1 (676)	2.1 (328)	0.0 (36)	0.0 (14)
Phryxe pecosensis	4.2 (684)	0.0 (7)	5.1 (528)	1.7 (117)	0.0 (19)	0.0 (13)
Phaeogenes maculicornis hariolus	5.7 (456)	50.0 (2)	6.1 (314)	5.9 (34)	0.0 (5)	–[4]
Itoplectis conquisitor	2.4 (456)	0.0 (2)	4.5 (314)	0.0 (34)	0.0 (5)	–
Lypha setifacies	2.1 (437)	0.0 (5)	2.6 (388)	1.8 (111)	7.1 (14)	0.0 (13)
Eumea caesar	1.2 (684)	0.0 (7)	1.7 (528)	1.7 (117)	0.0 (19)	0.0 (13)
Mesopolobus verditer	1.1 (456)	0.0 (2)	0.7 (456)	2.9 (34)	0.0 (5)	–
Mesopolobus tortricis	0.2 (456)	0.0 (2)	1.1 (456)	2.9 (34)	0.0 (5)	–
Winthemia fumiferanae	0.9 (684)	0.0 (7)	1.1 (528)	2.6 (117)	0.0 (19)	0.0 (13)
Ephialtes ontario	0.9 (456)	0.0 (2)	2.9 (314)	0.0 (34)	0.0 (5)	–
Meteorus trachynotus	1.0 (437)	0.0 (5)	0.3 (388)	0.0 (111)	0.0 (14)	0.0 (13)
Sarcophaga aldrichi	0.0 (684)	0.0 (7)	0.0 (528)	0.0 (117)	0.0 (19)	0.0 (13)
Enytus montanus	0.0 (729)	0.0 (5)	0.0 (563)	0.0 (179)	0.0 (29)	0.0 (13)

[1] BF = balsam fir
[2] WS = white spruce
[3] Number of spruce budworm at risk
[4] No spruce budworm at risk collected in this category.

Table 11. **The apparent rate of parasitism and numbers of spruce budworm at risk for the parasitoid species collected in 1995, excluding the release site.**

Parasitoid Species	Percentage parasitism					
	Epidemic 1		Epidemic 2		Endemic	
	BF[1]	WS[2]	BF	WS	BF	WS
Apanteles fumiferanae	5.8 (717)[3]	12.0 (50)	6.9 (554)	6.1 (246)	4.7 (43)	0.0 (2)
Glypta fumiferanae	2.4 (1291)	0.0 (51)	1.0 (1045)	1.1 (270)	0. (15)	0.0 (2)
Phryxe pecosensis	2.7 (731)	0.0 (7)	4.3 (608)	0.0 (70)	0.0 (37)	–[4]
Phaeogenes maculicornis hariolus	10.3 (320)	0.0 (2)	3.5 (340)	5.6 (18)	0.0 (8)	–
Itoplectis conquisitor	4.0 (322)	0.0 (2)	0.4 (241)	7.1 (14)	0.0 (8)	–
Lypha setifacies	2.7 (407)	0.0 (7)	1.4 (356)	0.0 (68)	3.2 (31)	–
Eumea caesar	2.2 (731)	0.0 (9)	0.5 (608)	1.4 (70)	0.0 (37)	–
Mesopolobus verditer	4.4 (322)	100.0 (2)	0.4 (240)	0.0 (14)	0.0 (8)	–
Winthemia fumiferanae	0.4 (741)	0.0 (10)	0.2 (604)	2.3 (86)	0.0 (37)	–
Ephialtes ontario	10.6 (320)	0.0 (2)	6.3 (240)	21.4 (14)	100.0 (1)	0.0 (7)
Meteorus trachynotus	3.4 (407)	0.0 (7)	1.1 (356)	0.0 (68)	6.5 (31)	–
Sarcophaga aldrichi	0.9 (741)	0.0 (10)	1.0 (604)	0.0 (86)	0.0 (37)	–
Enytus montanus	0.0 (435)	0.0 (7)	0.8 (383)	0.0 (70)	3.0 (33)	–

[1] BF = balsam fir
[2] WS = white spruce
[3] Number of spruce budworm at risk
[4] No spruce budworm at risk collected in this category.

Table 12. **The relative abundance of each parasitoid species in the parasitoid guilds collected on each host in each site in 1994. Each species is expressed as a percentage of the total number of parasitoids collected on the host in that site.**

Parasitoid Species	Percent of guild					
	Epidemic 1		Epidemic 2		Endemic	
	BF[1]	WS[2]	BF	WS	BF	WS
Apanteles fumiferanae	38.7	40.0	26.9	66.1	75.0	100
Apanteles morrisi	0.5	40.0	0.0	0.0	0.0	0.0
Glypta fumiferanae	13.4	0.0	8.8	11.9	0.0	0.0
Phryxe pecosensis	13.4	0.0	16.9	3.4	0.0	0.0
Phaeogenes maculicornis hariolus	12.0	20.0	11.9	3.4	0.0	0.0
Itoplectis conquisitor	5.1	0.0	8.8	0.0	0.0	0.0
Lypha setifacies	4.1	0.0	6.3	3.4	25.0	0.0
Eumea caesar	3.2	0.0	5.6	3.4	0.0	0.0
Mesopolobus tortricis	0.5	0.0	3.1	1.7	0.0	0.0
Mesopolobus verditer	2.3	0.0	1.9	1.7	0.0	0.0
Winthemia fumiferanae	2.8	0.0	3.8	5.1	0.0	0.0
Ephialtes ontario	1.8	0.0	5.6	0.0	0.0	0.0
Meteorus trachynotus	1.8	0.0	0.6	0.0	0.0	0.0
Sarcophaga aldrichi	0.0	0.0	0.0	0.0	0.0	0.0
Enytus montanus	0.0	0.0	0.0	0.0	0.0	0.0
Total parasitoids collected	217	5	160	59	4	1

[1] BF = balsam fir
[2] WS = white spruce

Table 13. **The relative abundance of each parasitoid species in the parasitoid guilds collected on each host in each site in 1995. Each species is expressed as a percentage of the total number of parasitoids collected on the host in that site.**

Parasitoid Species	Percent of guild					
	Epidemic 1		Epidemic 2		Endemic	
	BF[1]	WS[2]	BF	WS	BF	WS
Apanteles fumiferanae	17.6	75.0	30.4	53.6	28.6	0.0
Glypta fumiferanae	13.0	0.0	8.0	10.7	0.0	0.0
Phryxe pecosensis	8.4	0.0	20.8	0.0	0.0	0.0
Phaeogenes maculicornis hariolus	13.9	0.0	9.6	3.6	0.0	0.0
Itoplectis conquisitor	5.5	0.0	0.8	3.6	0.0	0.0
Lypha setifacies	4.6	0.0	4.0	0.0	14.3	0.0
Eumea caesar	6.7	0.0	2.4	3.6	0.0	0.0
Mesopolobus verditer	5.9	25.0	0.8	7.1	0.0	0.0
Winthemia fumiferanae	1.3	0.0	0.8	7.1	0.0	0.0
Ephialtes ontario	14.3	0.0	12.0	10.7	14.3	0.0
Meteorus trachynotus	5.9	0.0	3.2	0.0	28.6	0.0
Sarcophaga aldrichi	2.9	0.0	4.8	0.0	0.0	0.0
Enytus montanus	0.0	0.0	2.4	0.0	14.3	0.0
Total parasitods collected	238	8	125	28	7	0

[1] BF = balsam fir
[2] WS = white spruce

Table 14. **Parasitoid species in which the apparent rate of parasitism was significantly affected by site in 1995**

Site Interaction				% Parasitism in 1995					
Species	df	G value	p	Epidemic 1		Epidemic 2		Endemic	
				BF[1]	WS[2]	BF	WS	BF	WS
G. fumiferanae	2	7.89	p < 0.025	2.4[3] (1291)[4]	0.0 (51)	1.0 (1045)	1.1 (270)	0.0 (15)	0.0 (2)
P. maculicornus hariolus	2	11.75	p < 0.01	10.3 (320)	0.0 (2)	3.5 (340)	5.6 (18)	0.0 (8)	-[5]
I. conquisitor	2	6.56	p < 0.025	4.0 (322)	0.0 (2)	0.4 (241)	7.1 (14)	0.0 (8)	-
M. verditer	2	11.41	p < 0.01	4.4 (322)	100.0 (2)	0.4 (240)	0.0 (14)	0.0 (8)	-
M. trachynotus	2	9.14	p < 0.025	3.4 (407)	0.0 (7)	1.1 (356)	0.0 (68)	6.5 (31)	-
E. montanus	2	7.1	p < 0.025	0.0 (435)	0.0 (7)	0.8 (383)	0.0 (70)	3.0 (33)	-

[1] BF = balsam fir
[2] WS = white spruce
[3] Percent of at risk hosts collected that were parasitized
[4] # of spruce budworm collected that were at risk of being parasitized
[5] No spruce budworm at risk were collected in this category.

Table 15. **Parasitoid species in which the apparent rate of parasitism was significantly affected by tree species in 1995.**

Tree Species Interaction				% Parasitism in 1995					
Species	**df**	**G value**	**p**	**Epidemic 1**		**Epidemic 2**		**Endemic**	
				BF[1]	**WS[2]**	**BF**	**WS**	**BF**	**WS**
I. conquisitor	1	6.04	$p < 0.025$	4.0[3] (322)[4]	0.0 (2)	0.4 (241)	7.1 (14)	0.0 (8)	-[5]
M. verditer	1	12.4	$p < 0.001$	4.4 (322)	100.0 (2)	0.4 (240)	0.0 (14)	0.0 (8)	-
W. fumiferanae	1	8.91	$p < 0.01$	0.4 (741)	0.0 (10)	0.2 (604)	2.3 (86)	0.0 (37)	-

[1] BF = balsam fir
[2] WS = white spruce
[3] Percent of at risk hosts collected that were parasitized
[4] # of spruce budworm collected that were at risk of being parasitized
[5] No spruce budworm at risk were collected in this category.

Table 16. **Parasitoid species with significantly different apparent rates of parasitism between 1994 and 1995.**

	Year Interactions			% Parasitism					
Species	**df**	**G value**	**p**	**Epidemic 1**		**Epidemic 2**		**Endemic**	
				1994	**1995**	**1994**	**1995**	**1994**	**1995**
M. trachynotus	1	8.93	$p < 0.01$	0.9[1] (442)[2]	3.4 (414)	0.2 (499)	0.9 (424)	0.0 (27)	6.5 (31)
E. ontario	1	40.01	$p < 0.001$	0.9 (458)	10.6 (322)	2.6 (348)	7.1 (254)	0.0 (5)	12.5 (8)
E. montanus	1	4.31	$p < 0.025$	0.0 (734)	0.0 (442)	0.0 (742)	0.7 (453)	0.0 (42)	3.0 (33)
M. verditer	1	6.61	$p < 0.025$	1.1 (458)	4.9 (324)	0.8 (490)	0.4 (254)	0.0 (5)	0.0 (8)
S. aldrichi	1	9.64	$p < 0.01$	0.0 (691)	0.9 (751)	0.0 (645)	0.9 (632)	0.0 (32)	0.0 (37)

[1] Percent of at risk hosts that were parasitized.
[2] # of spruce budworm that were at risk of being parasitized.

Table 17. Parasitoid species with significant interactions of apparent parasitism rates between sites, tree species and year.

Site x Tree x Year Interaction				% Parasitism											
Species	df	G value	p	Epidemic 1				Epidemic 2				Endemic			
				1994		1995		1994		1995		1994		1995	
				BF[1]	WS[2]	BF	WS	BF	WS	BF	WS	BF	WS	BF	WS
A. fumiferanae	2	12.94	p < 0.01	8.7 (971)	4.2 (48)	5.8 (717)	12.0 (50)	6.4 (676)	11.9 (328)	6.9 (554)	6.1 (246)	8.3 (36)	7.1 (14)	4.7 (43)	0.0 (2)
A. morrisi	2	9.56	p < 0.01	0.1 (971)	4.2 (48)	0.0 (717)	0.0 (50)	0.0 (676)	0.0 (328)	0.0 (554)	0.0 (246)	0.0 (36)	0.0 (14)	0.0 (43)	0.0 (2)
M. trachynotus	2	16.21	p < 0.001	1.0 (437)	0.0 (5)	3.4 (407)	0.0 (7)	0.3 (388)	0.0 (111)	1.1 (356)	0.0 (68)	0.0 (14)	0.0 (13)	6.5 (31)	-
E. ontario	2	12.90	p < 0.01	0.9 (456)	0.0 (2)	10.6 (320)	0.0 (2)	2.9 (314)	0.0 (34)	6.3 (240)	21.4 (14)	0.0 (5)	-	100.0 (1)	0.0 (7)
E. montanus	2	13.41	p < 0.01	0.0 (729)	0.0 (5)	0.0 (435)	0.0 (7)	0.0 (563)	0.0 (179)	0.8 (383)	0.0 (70)	0.0 (29)	0.0 (13)	3.0 (33)	-
L. setifacies	2	16.09	p < 0.001	2.1 (437)	0.0 (5)	2.7 (407)	0.0 (7)	2.6 (388)	1.8 (111)	1.4 (356)	0.0 (68)	7.1 (14)	0.0 (13)	3.2 (31)	-
E. caesar	2	13.74	p < 0.01	1.2 (684)	0.0 (7)	2.2 (731)	0.0 (9)	1.7 (528)	1.7 (117)	0.5 (608)	1.4 (70)	0.0 (19)	0.0 (13)	0.0 (37)	-
W. fumiferanae	2	15.18	p < 0.01	0.9[3] (684)	0.0 (7)[4]	0.4 (741)	0.0 (10)	1.1 (528)	2.6 (117)	0.2 (604)	2.3 (86)	0.0 (19)	0.0 (13)	0.0 (8)	-
S. aldrichi	2	16.87	p < 0.001	0.0 (684)	0.0 (7)	0.9 (741)	0.0 (10)	0.0 (528)	0.0 (117)	1.1 (546)	0.0 (86)	0.0 (19)	0.0 (13)	0.0 (37)	-

[1] BF = balsam fir
[2] WS = white spruce
[3] Percent of at risk hosts that were parasitized.
[4] # of spruce budworm collected that were at risk of being parasitized.
[5] No spruce budworm at risk were collected in this category.

Table 18. **Parasitoid species with significantly different apparent rates of parasitism between sites and year.**

Species	Site and Year Interactions			% Parasitism					
	df	G value	p	Epidemic 1		Epidemic 2		Endemic	
				1994	1995	1994	1995	1994	1995
I. conquisitor	2	8.47	$p < 0.025$	2.4[1] (458)[2]	4.0 (324)	4.0 (348)	0.8 (255)	0.0 (5)	0.0 (8)
E. caesar	2	6.06	$p < 0.05$	1.0 (691)	2.2 (740)	1.7 (645)	0.6 (678)	0.0 (32)	0.0 (37)

[1] Percent of at risk hosts that were parasitized.
[2] # of spruce budworm that were at risk of being parasitized.

Figure 4. The 1994 site and vegetation species data, including herbaceous plants, shrubs, trees, and bare ground, Correspondence analysis ordination diagram with site scores (o) and vegetation species scores (•); first axis (horizontal) has an eigenvalue of 0.207 = 65.7% and the second axis (vertical), has an eigenvalue of 0.108 = 34.3%. The vegetation species are: Cc = *Cornus canadensis*, Lg = *Ledum groenlandicum*, Fv = *Fragaria virginiana*, Va = *Vaccinium angustifolium*, Ra = *Rosa arkansana*, Mc = *Maianthemum canadense*, Ac = *Alnus crispa*, Ri = *Rubus idaeus* var. *aculeatissimus*, Ca = *Cornus alba*, Jc = *Juniperus communis*, Aa = *Amelanchier alnifolia*, Bg = bare ground, Ab = *Abies balsamea*, Pg = *Picea glauca*, Pt = *Populus tremuloides*, Bp = *Betula papyrifera*, Pb = *Pinus banksiana*. The sites are 94Ep 1 = 1994 epidemic 1 site, 94Ep 2 = 1994 epidemic 2 site, 94End = 1994 endemic site.

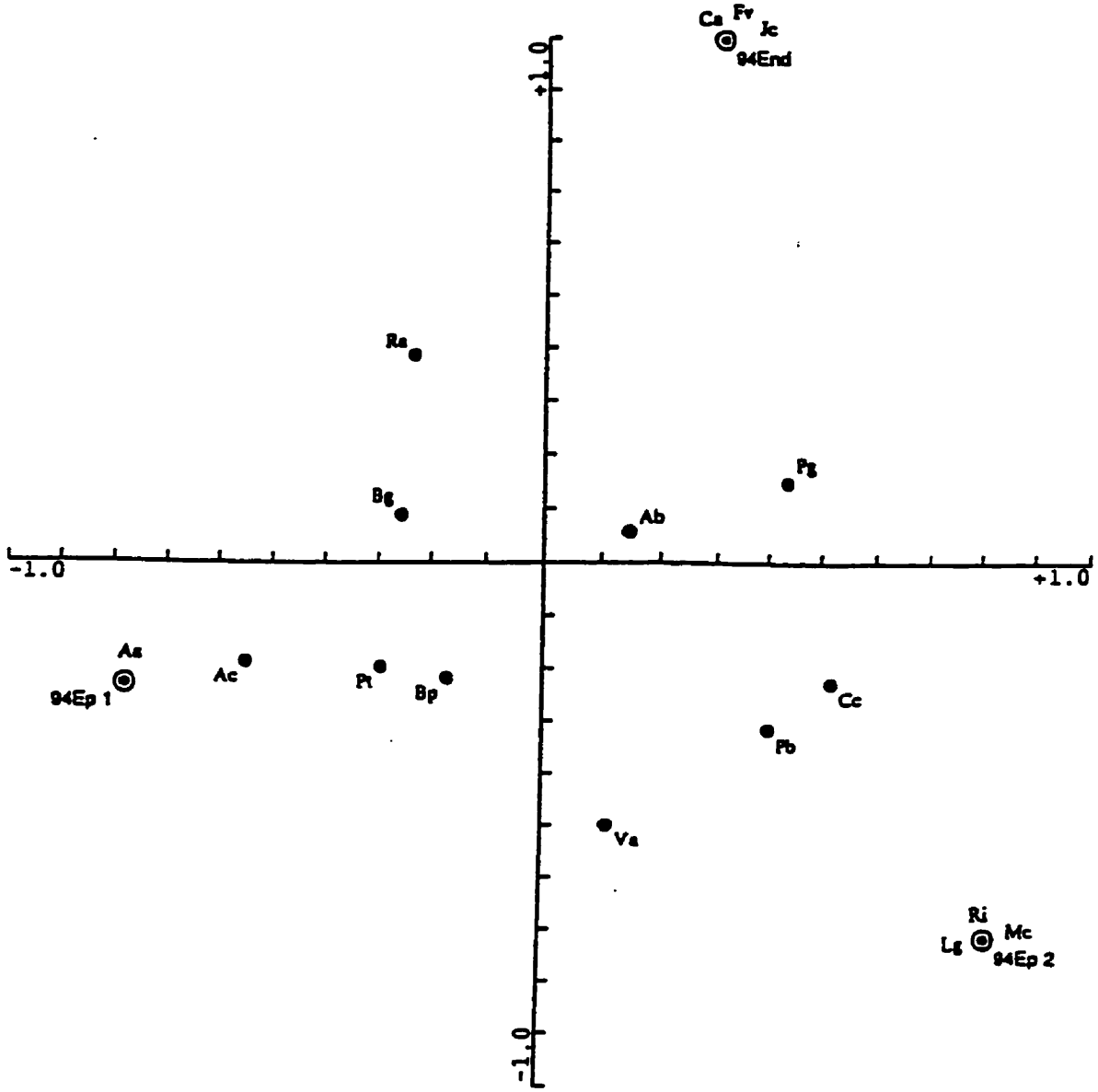

Ca Fv Jc
94End
+1.0
Ra
Pg
Bg
Ab
-1.0
+1.0
As
94Ep 1
Ac
Pt
Bp
Cc
Pb
Va
Ri
Lg Mc
94Ep 2
-1.0

Figure 5. The 1994 and 1995 site and parasitoid species data, including the release site. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.190 = 52.3% and the second axis (vertical), has an eigenvalue of 0.083 = 22.9%. The parasitoid species are: A.f. = *Apanteles fumiferanae*, A.m. = *Apanteles morrisi*, G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*. The sites are: 94Ep 1 = 1994 Epidemic site 1, 94Ep 2 = 1994 Epidemic site 2, 94End = 1994 Endemic site, 95Ep 1 = 1995 Epidemic site 1, 95Ep 2 = 1995 Epidemic site 2, 95End = 1995 Endemic site, Rel = Release site.

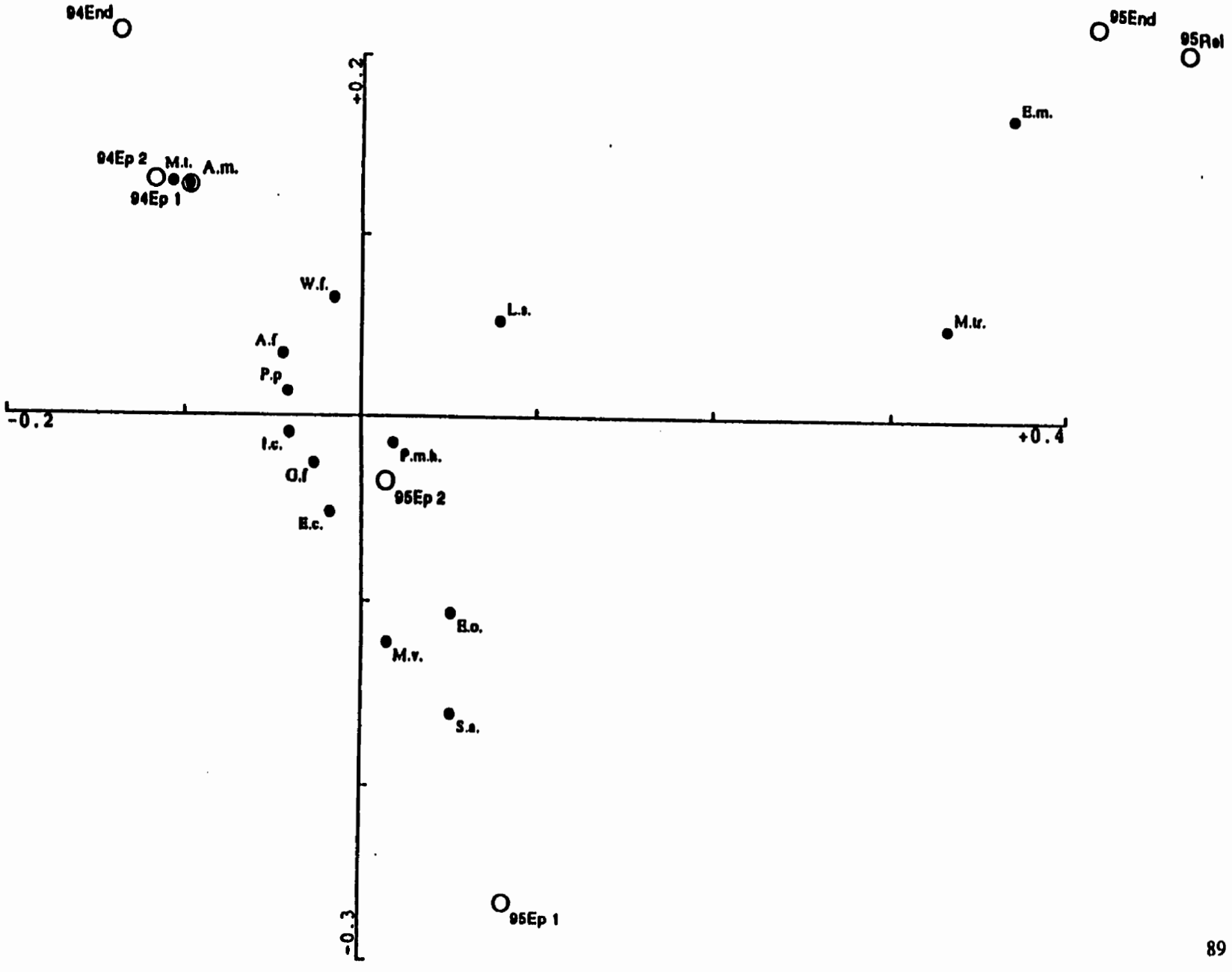

94End
95End
95Rel
+0.2
E.m.
94Ep 2
M.t.
A.m.
94Ep 1
W.f.
L.s.
M.tr.
A.f
P.p
-0.2
+0.4
I.c.
P.m.h.
O.f
95Ep 2
E.c.
E.o.
M.v.
S.s.
-0.3
95Ep 1

Figure 6. The 1994 and 1995 site and parasitoid species data, including release site, excluding the parasitoid species *Apanteles fumiferanae, Apanteles morrisi* and *Glypta fumiferanae*. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.196 = 46.3% and the second axis (vertical), has an eigenvalue of 0.105 = 24.7%. The parasitoid species are: P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*. The sites are: The sites are: 94Ep 1 = 1994 Epidemic site 1, 94Ep 2 = 1994 Epidemic site 2, 94End = 1994 Endemic site, 95Ep 1 = 1995 Epidemic site 1, 95Ep 2 = 1995 Epidemic site 2, 95End = 1995 Endemic site, Rel = Release site.

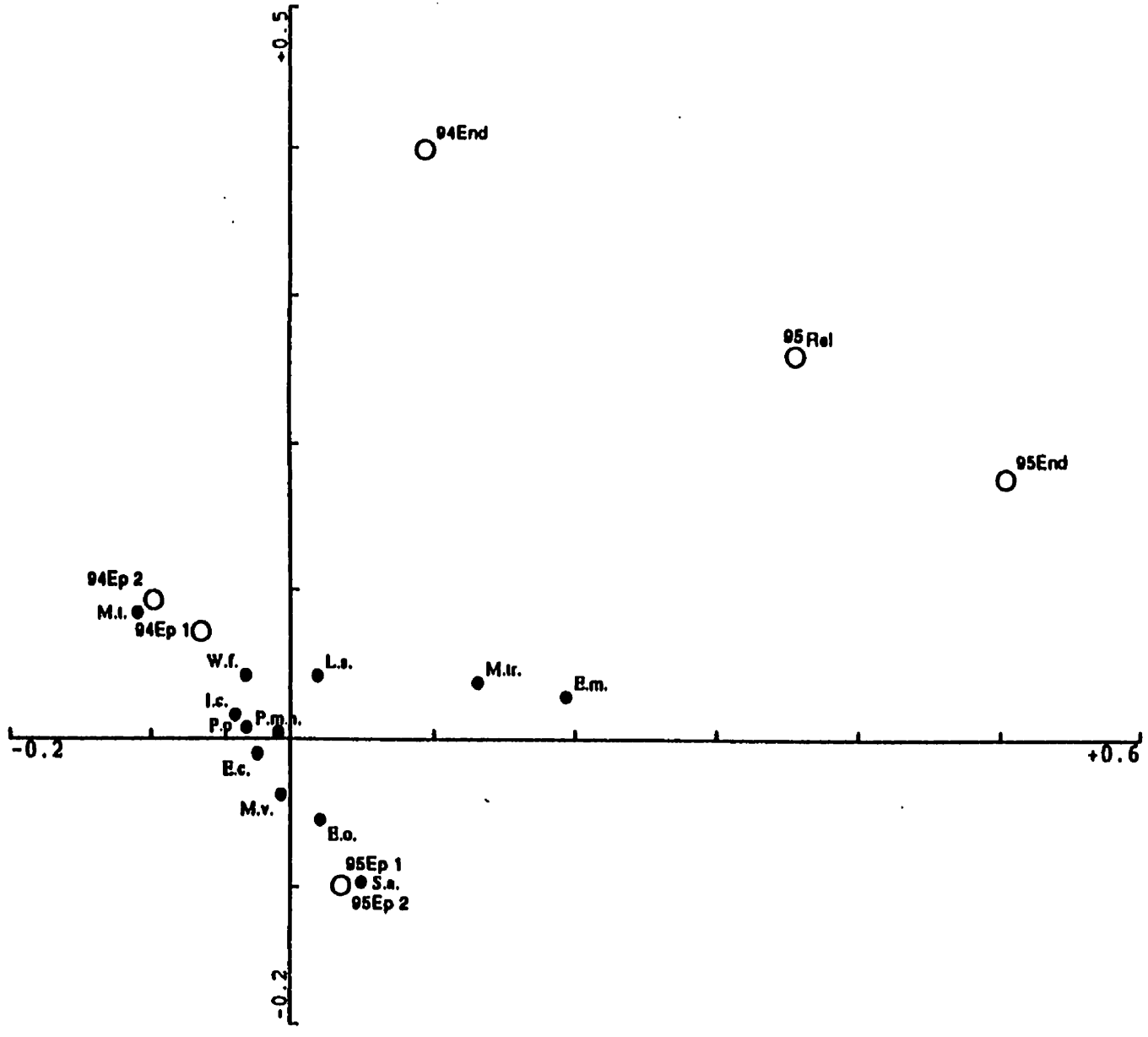

+0.5
-0.2
-0.2
+0.6
94End
95Rel
95End
94Ep 2
M.l.
94Ep 1
W.f.
L.s.
M.tr.
B.m.
I.c.
P.p
P.m.n.
E.c.
M.v.
B.o.
95Ep 1
S.a.
95Ep 2

Figure 7. The 1994 and 1995 site and parasitoid species data, including the release site, but only including parasitoid assemblages collected from fir. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.185 = 49.6% and the second axis (vertical), has an eigenvalue of 0.080 = 21.4%. The parasitoid species are: A.f. = *Apanteles fumiferanae*, A.m. = *Apanteles morrisi*, G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*. The sites are: 94FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 94FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 94FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 95FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 95FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FRel = Parasitoid species that emerged from spruce budworm collected from fir trees in the Release site.

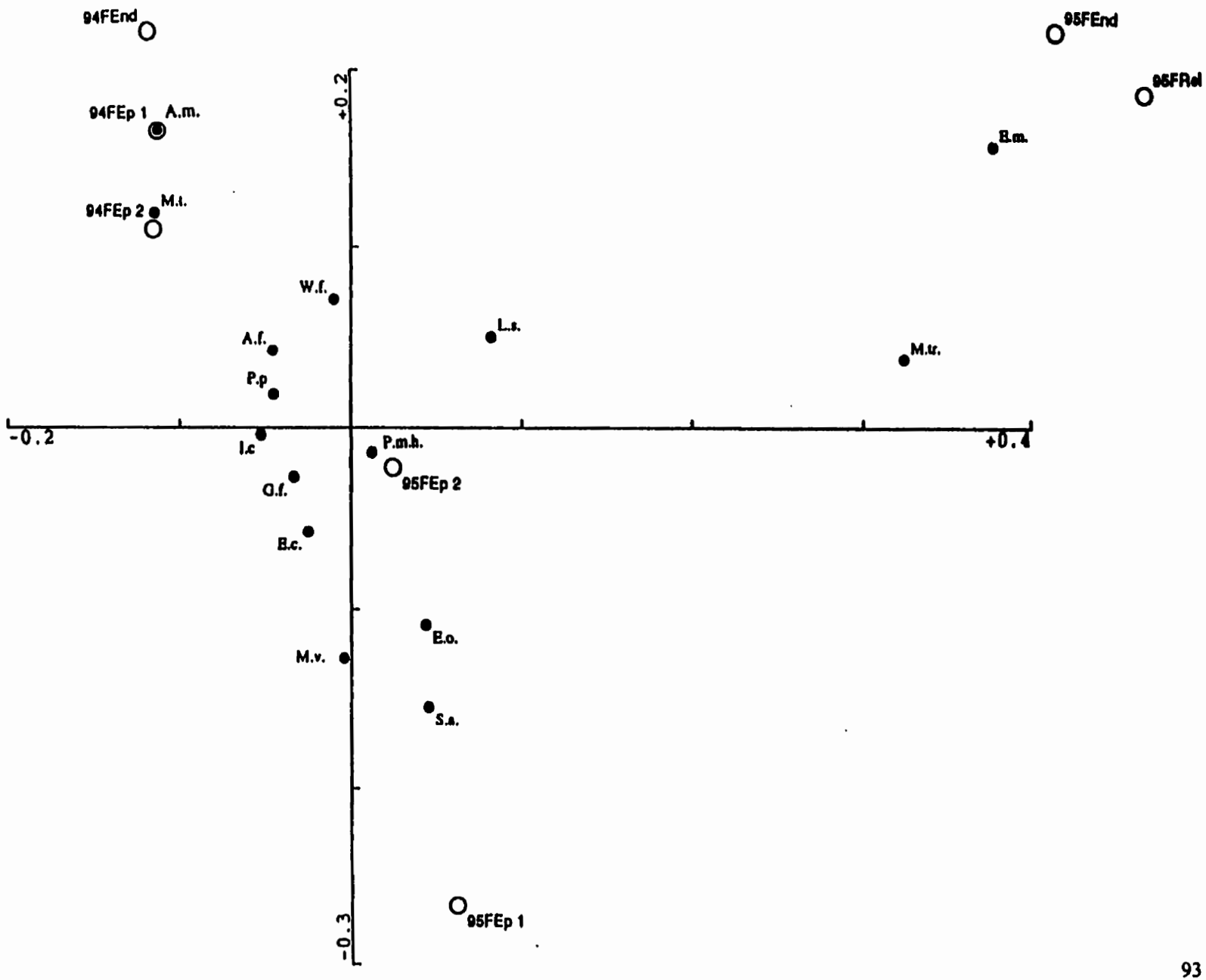

94FEnd
95FEnd
95FRel
94FEp 1
A.m.
B.m.
94FEp 2
M.t.
W.f.
L.s.
A.f.
M.tr.
P.p
+0.2
-0.2
+0.4
I.c
P.m.h.
95FEp 2
O.f.
E.c.
E.o.
M.v.
S.s.
95FEp 1
-0.3

Figure 8. The 1994 and 1995 site and parasitoid species data, including release site, but only including assemblages collected from fir trees and excluding the parasitoid species *Apanteles fumiferanae, Apanteles morrisi* and *Glypta fumiferanae*. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.196 = 46.1% and the second axis (vertical), has an eigenvalue of 0.102 = 24.0%. The parasitoid species are: P.p. = *Phyrxe pecosensis*, P.m.h. = Phaeogenes maculicornis hariolus, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*. The sites are: The sites are: 94FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 94FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 94FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 95FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 95FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FRel = Parasitoid species that emerged from spruce budworm collected from fir trees in the Release site.

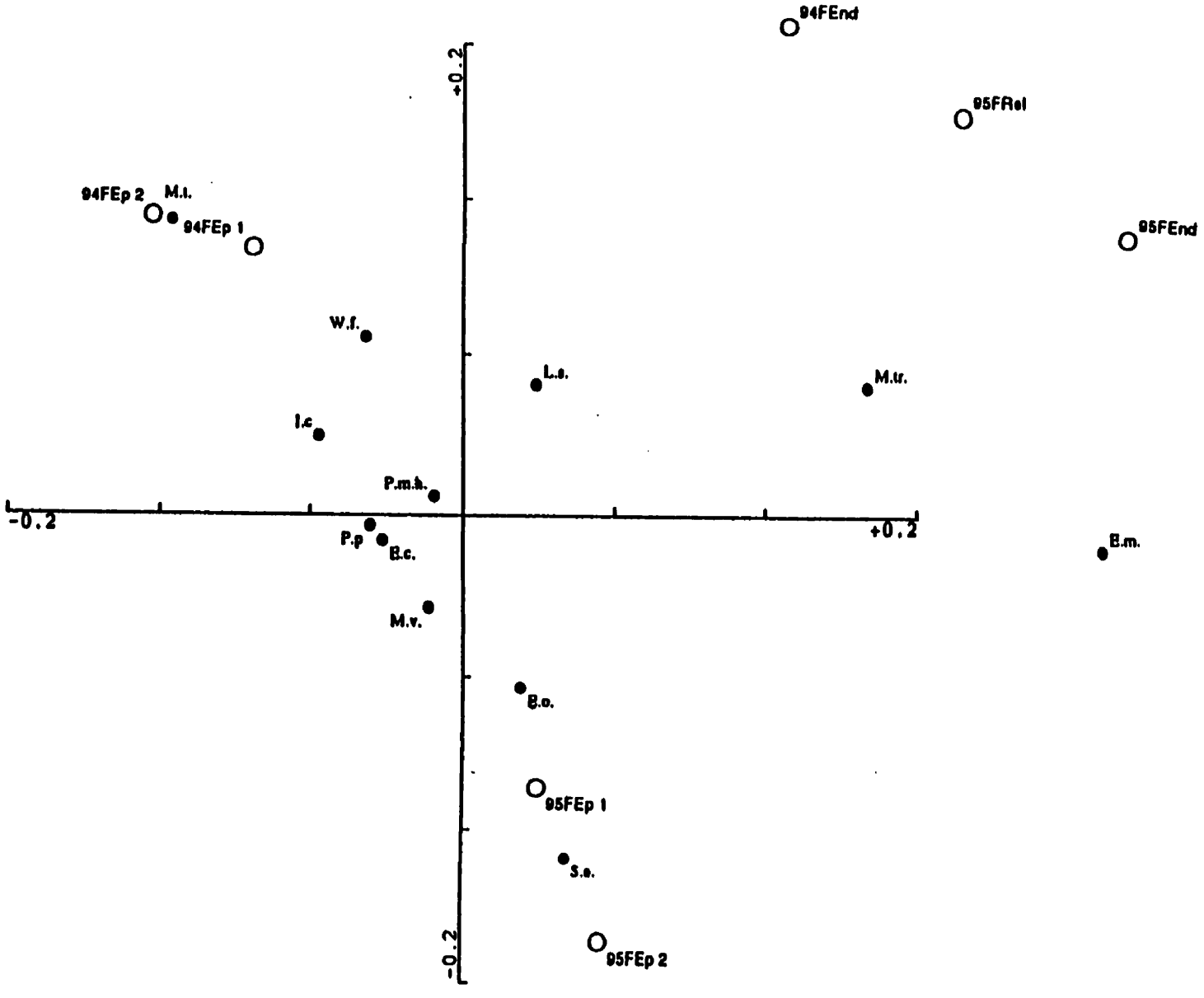

94FEnd
95FRel
95FEnd
94FEp 2
M.t.
94FEp 1
W.f.
L.s.
M.tr.
I.c.
P.m.h.
P.p
B.c.
M.v.
B.m.
B.o.
95FEp 1
S.s.
95FEp 2
+0.2
-0.2
-0.2
+0.2

Figure 9. The 1994 and 1995 site and parasitoid species data, but only including parasitoid assemblages collected from white spruce. Correspondence analysis ordination diagram with site scores (o) and parasitoid species scores (•); first axis (horizontal) has an eigenvalue of 0.434 = 58.0% and the second axis (vertical), has an eigenvalue of 0.189 = 25.3%. The parasitoid species are: A.f. = *Apanteles fumiferanae*, A.m. = *Apanteles morrisi*, G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*. The sites are: 94SEp 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in epidemic site 1 in 1994, 94SEp 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in epidemic site 2 in 1994, 94SEnd = Parasitoid species that emerged from spruce budworm collected from spruce trees in the endemic site in 1994, 95SEp 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in epidemic site 1 in 1995, 95SEp 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in epidemic site 2 in 1995. There were no parasitoid species collected from spruce trees in 1995 in the endemic site, nor from the release site.

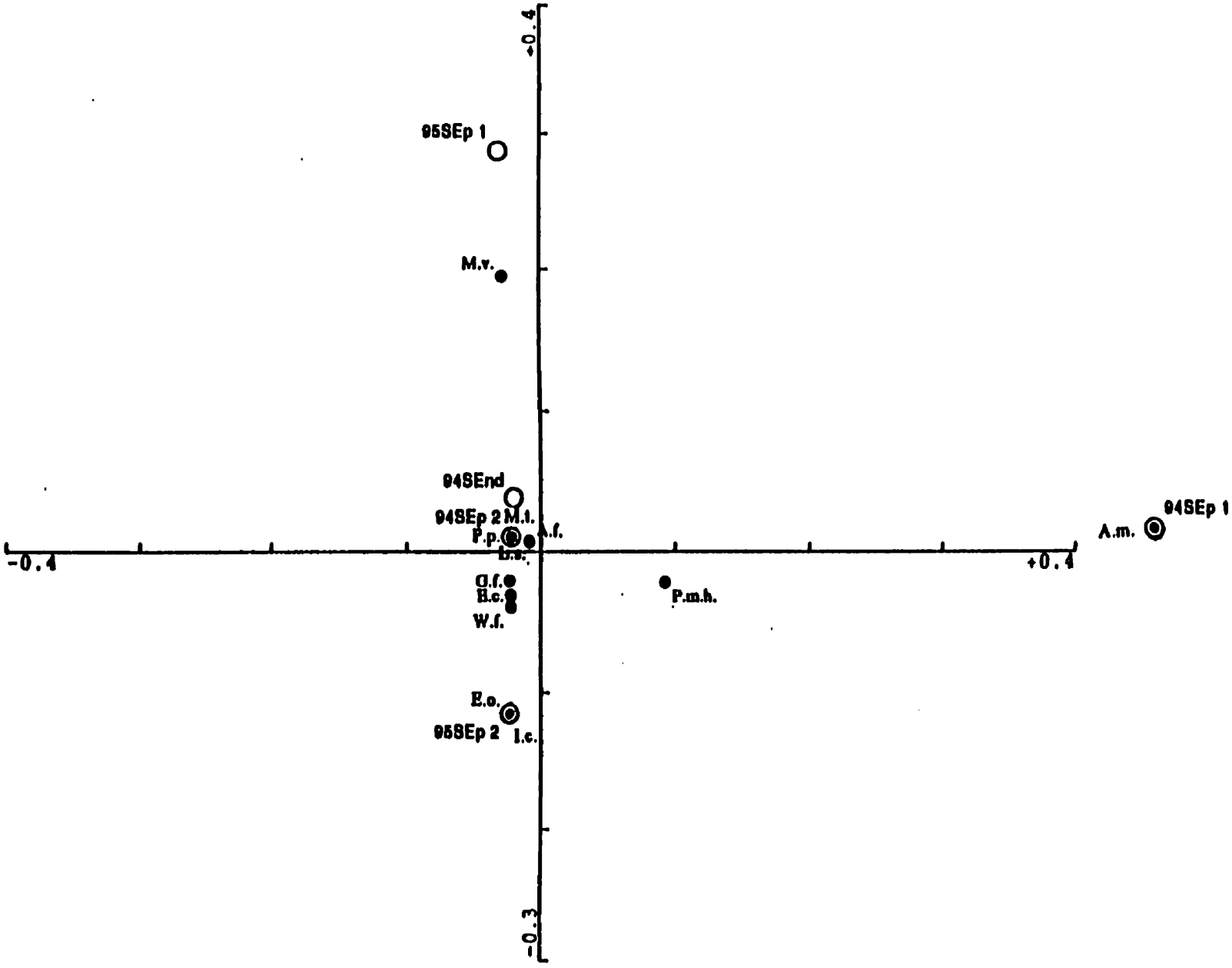

+0.4
95SEp 1
M.v.
94SEnd
94SEp 2
M.l.
P.p.
A.f.
L.o.
-0.4
+0.4
94SEp 1
A.m.
G.f.
H.c.
W.f.
P.m.h.
E.o.
95SEp 2
I.c.
-0.3

Figure 10. The 1994 and 1995 site and parasitoid species data, with the sites divided into assemblages based on tree species. This includes the release site. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.272 = 37.4% and the second axis (vertical), has an eigenvalue of 0.199 = 27.3%. The parasitoid species are: A.f. = *Apanteles fumiferanae*, A.m. = *Apanteles morrisi,* G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus,* E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi.* The sites are: 94FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 94Sep 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 1, 94Sep 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 2, 94FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 94FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 94SEnd = Parasitoid species that emerged from spruce budworm collected from spruce trees in the Endemic site, 95FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 95Sep 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 1, 95Sep 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 2, 95FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 95FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FRel = Parasitoid species that emerged from spruce budworm collected from fir trees in the Release site.

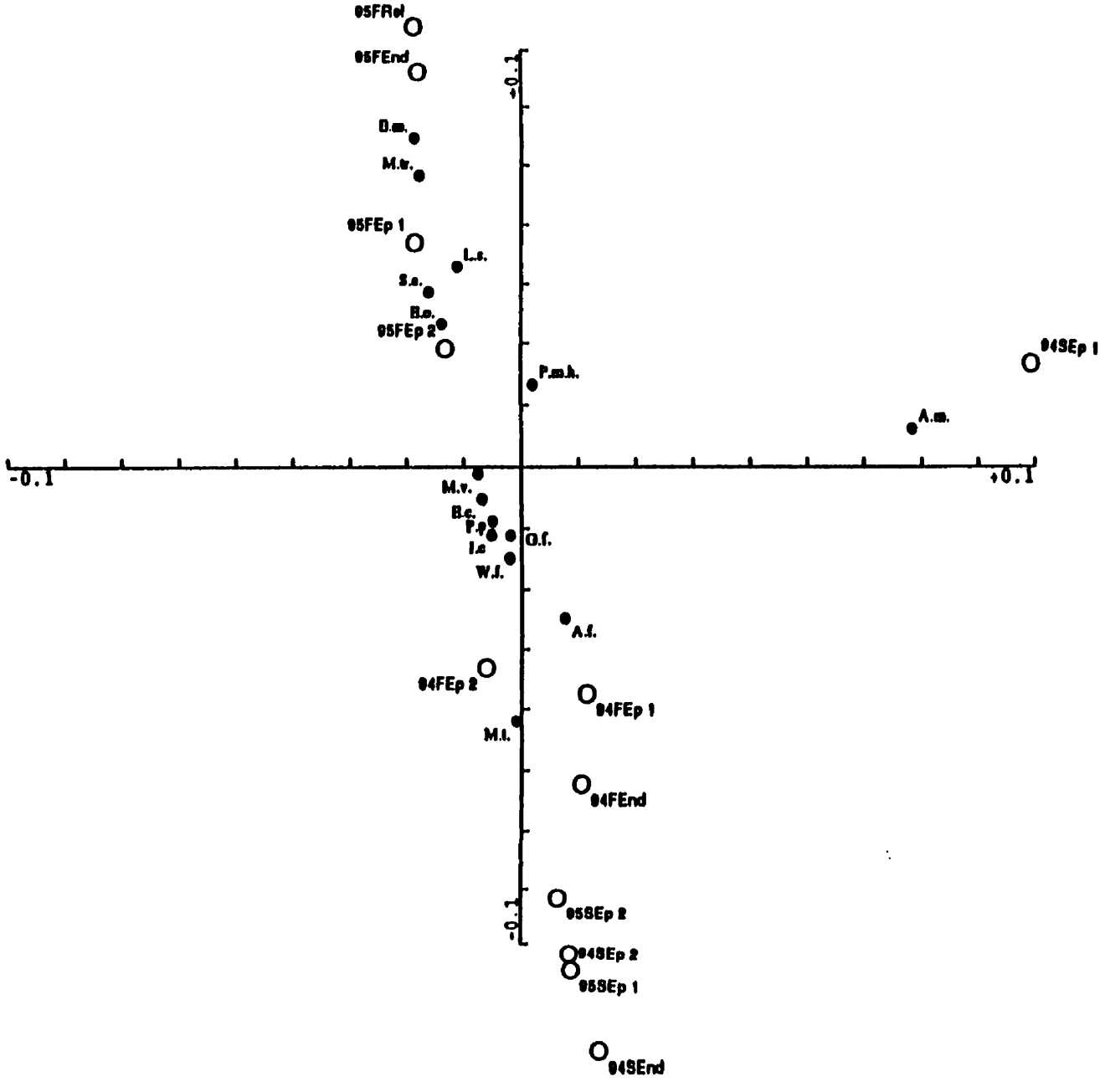

95FRel
95FEnd
D.m.
M.v.
95FEp 1
L.s.
S.s.
B.s.
95FEp 2
94SEp 1
P.m.h.
A.m.
-0.1
+0.1
M.v.
B.c.
P.p.
I.s
W.f.
O.f.
A.f.
94FEp 2
94FEp 1
M.f.
94FEnd
95SEp 2
94SEp 2
95SEp 1
94SEnd
+0.1
-0.1

Figure 11. The 1994 and 1995 site and parasitoid species data, with the sites divided into assemblages based on tree species. This includes the release site and excludes *Apanteles morrisi*. Correspondence Analysis ordination diagram with site scores (○) and parasitoid species scores (●); first axis (horizontal) has an eigenvalue of 0.272 = 37.4% and the second axis (vertical), has an eigenvalue of 0.199 = 27.3%. The parasitoid species are: A.f. = *Apanteles fumiferanae*, G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.tr. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*. The sites are: 94FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 94Sep 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 1, 94Sep 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 2, 94FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 94FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 94SEnd = Parasitoid species that emerged from spruce budworm collected from spruce trees in the Endemic site, 95FEp 1 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 1, 95Sep 1 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 1, 95Sep 2 = Parasitoid species that emerged from spruce budworm collected from spruce trees in Epidemic site 2, 95FEp 2 = Parasitoid species that emerged from spruce budworm collected from fir trees in Epidemic site 2, 95FEnd = Parasitoid species that emerged from spruce budworm collected from fir trees in the Endemic site, 95FRel = Parasitoid species that emerged from spruce budworm collected from fir trees in the Release site.

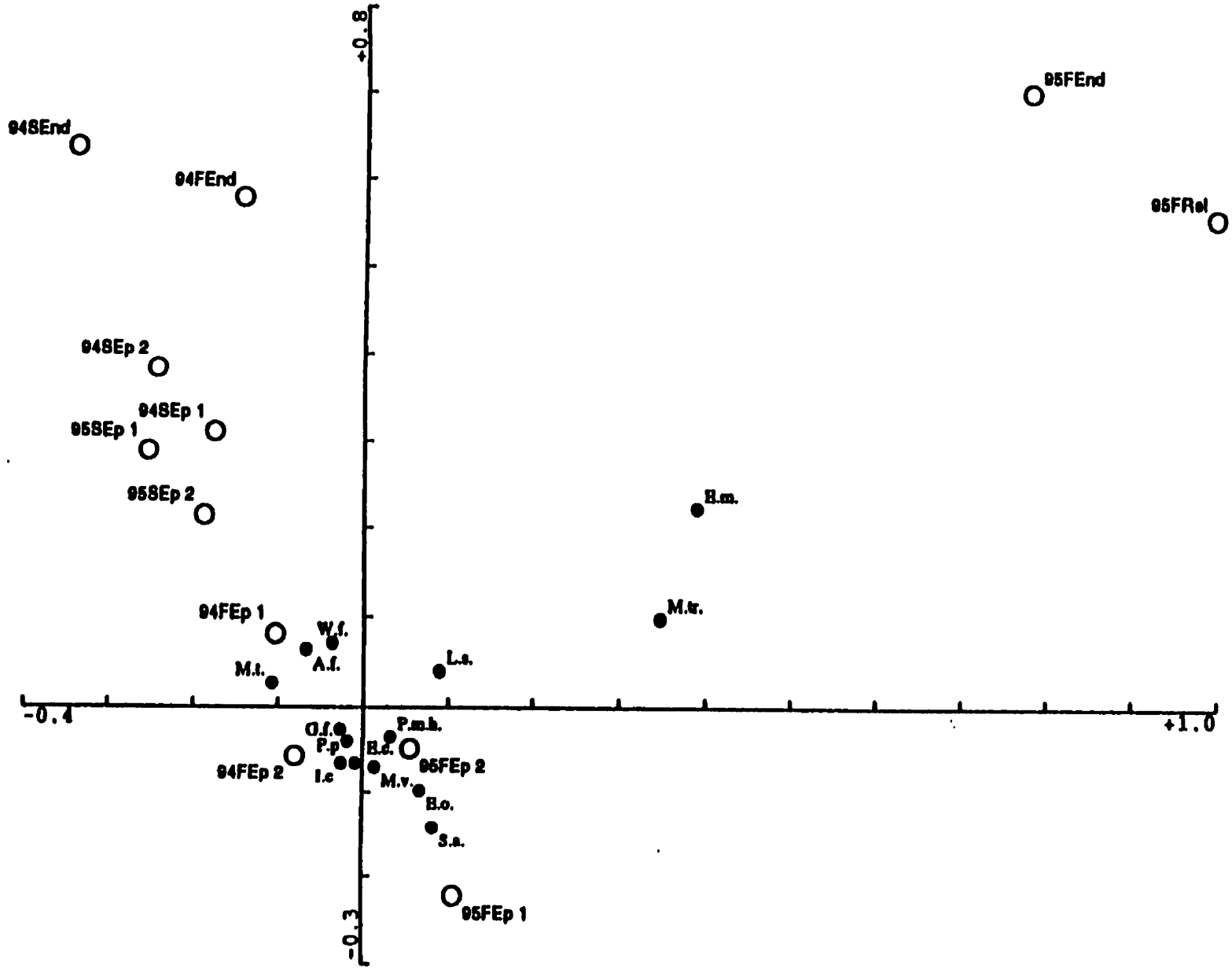

+0.8
-0.3
-0.4
+1.0
94SEnd
94FEnd
95FEnd
95FRel
94SEp 2
94SEp 1
95SEp 1
95SEp 2
94FEp 1
94FEp 2
95FEp 2
95FEp 1
H.m.
M.tr.
L.s.
W.f.
A.f.
M.t.
O.f.
P.p
I.c
P.m.h.
H.c.
M.v.
B.o.
S.a.

Figure 12. Percentage of budworm collected from spruce on each sampling occasion in the pooled epidemic sites in 1994. Data weighted based on the total number of budworm collected on each sampling date: ◯ = > 250 budworm collected; ○ = 200 - 250 budworm collected; o = 150 - 200 budworm collected; ∘ = 100 - 150 budworm collected; • = 50 - 100 budworm collected. Trend line was fitted by LOWESS procedure (Wilkinson, 1992).

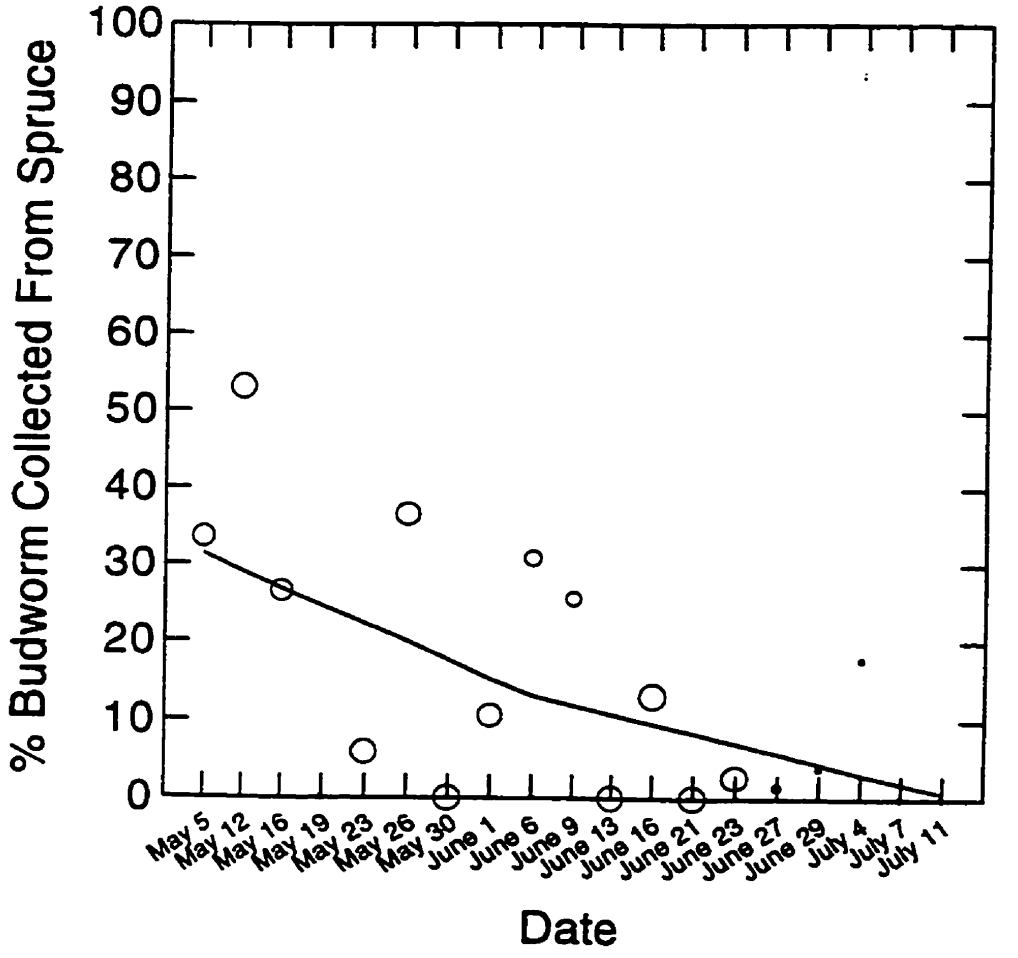

% Budworm Collected From Spruce
100
90
80
70
60
50
40
30
20
10
0
May 5
May 12
May 16
May 19
May 23
May 26
May 30
June 1
June 6
June 9
June 13
June 16
June 21
June 23
June 27
June 29
July 4
July 7
July 11
Date

Figure 13. Percentage of budworm collected from spruce on each sampling occasion in the pooled epidemic sites in 1995. Data weighted based on the total number of budworm collected on each sampling date: ◯ = > 250 budworm collected; ○ = 200 - 250 budworm collected; o = 150 - 200 budworm collected; ∘ = 100 - 150 budworm collected; • = 50 - 100 budworm collected. Trend line was fitted by LOWESS procedure (Wilkinson, 1992).

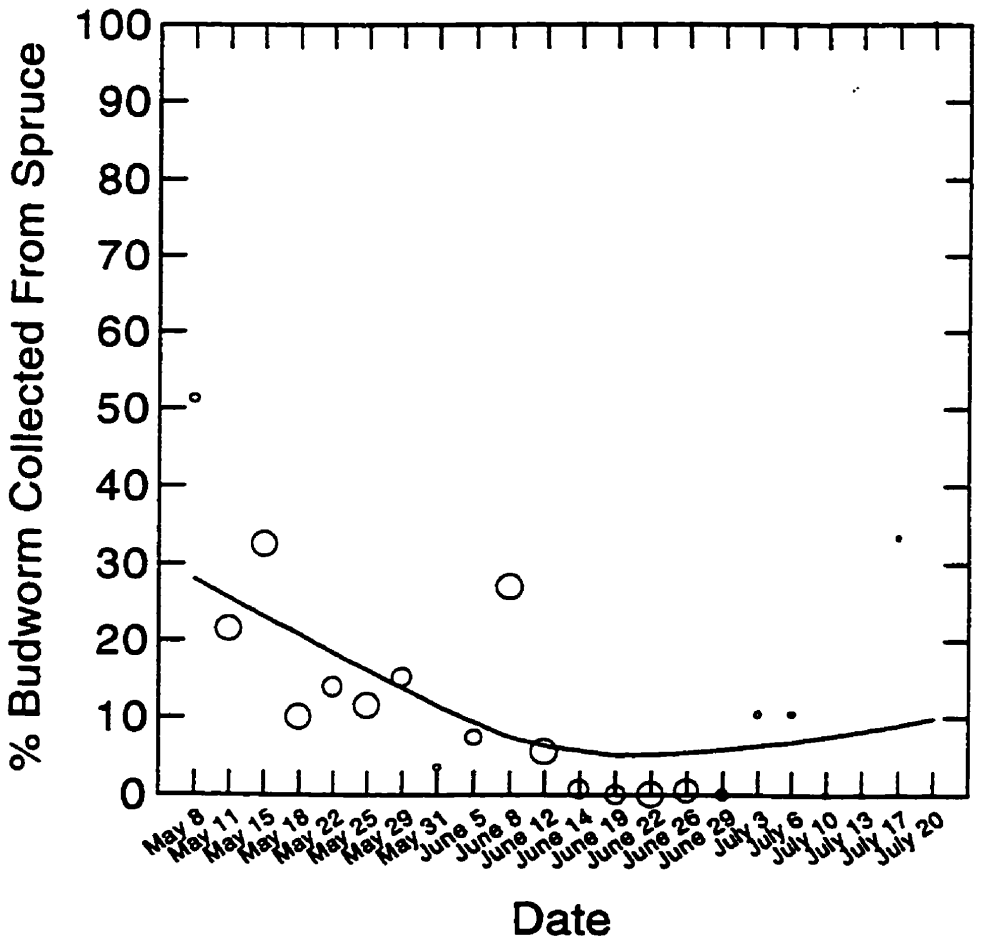

% Budworm Collected From Spruce
100
90
80
70
60
50
40
30
20
10
0
May 8
May 11
May 15
May 18
May 22
May 25
May 29
May 31
June 5
June 8
June 12
June 14
June 19
June 22
June 26
June 29
July 3
July 6
July 10
July 13
July 17
July 20
Date

Figure 14. Percentage of spruce branches collected on each sampling occasion in the pooled epidemic sites in 1995. Trend line was fitted by LOWESS procedure (Wilkinson, 1992).

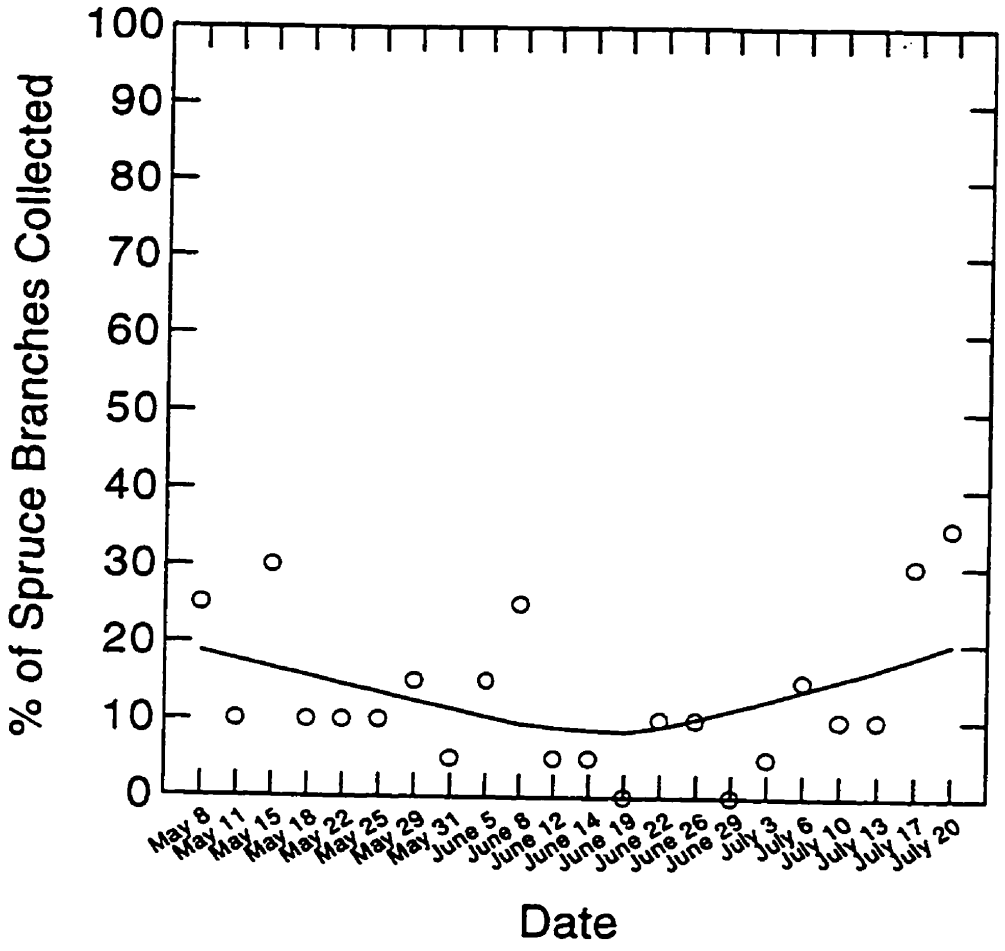

% of Spruce Branches Collected
100
90
80
70
60
50
40
30
20
10
0
May 8
May 11
May 15
May 18
May 22
May 25
May 29
May 31
June 5
June 8
June 12
June 14
June 19
June 22
June 26
June 29
July 3
July 6
July 10
July 13
July 17
July 20
Date

Figure 15. A comparison of day degree accumulation with balsam fir bud phenology, spruce budworm larval development and the occurrence of parasitoid species in the epidemic 1 site in 1995. A.f. = *Apanteles fumiferanae*, G.f. = *Glypta fumiferanae*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.t. = *Mesopolobus tortricis*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.t.r. = *Meteorus trachynotus*, S.a. = *Sarcophagus aldrichi*, M.v. = *Mesopolobus verditer*.

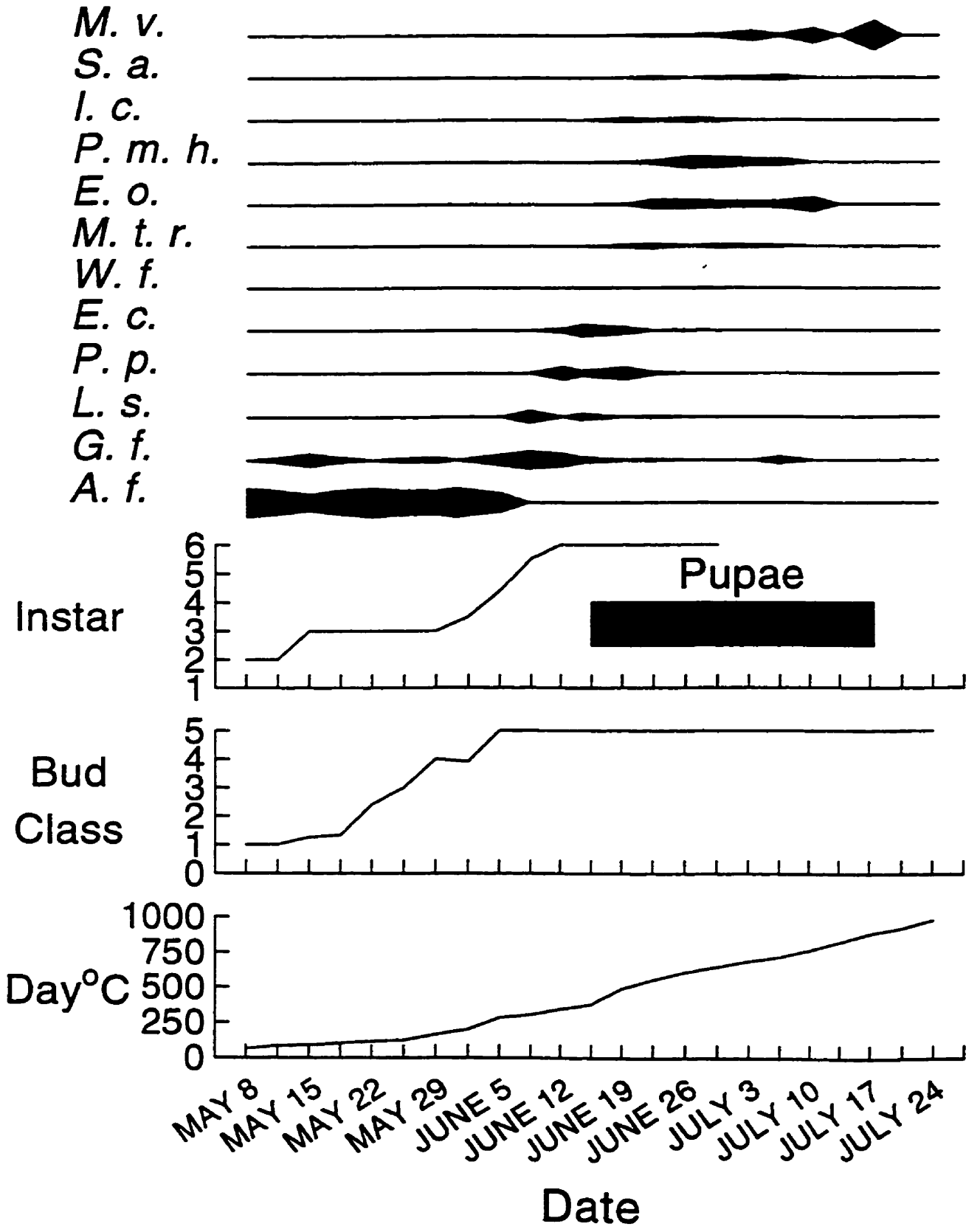
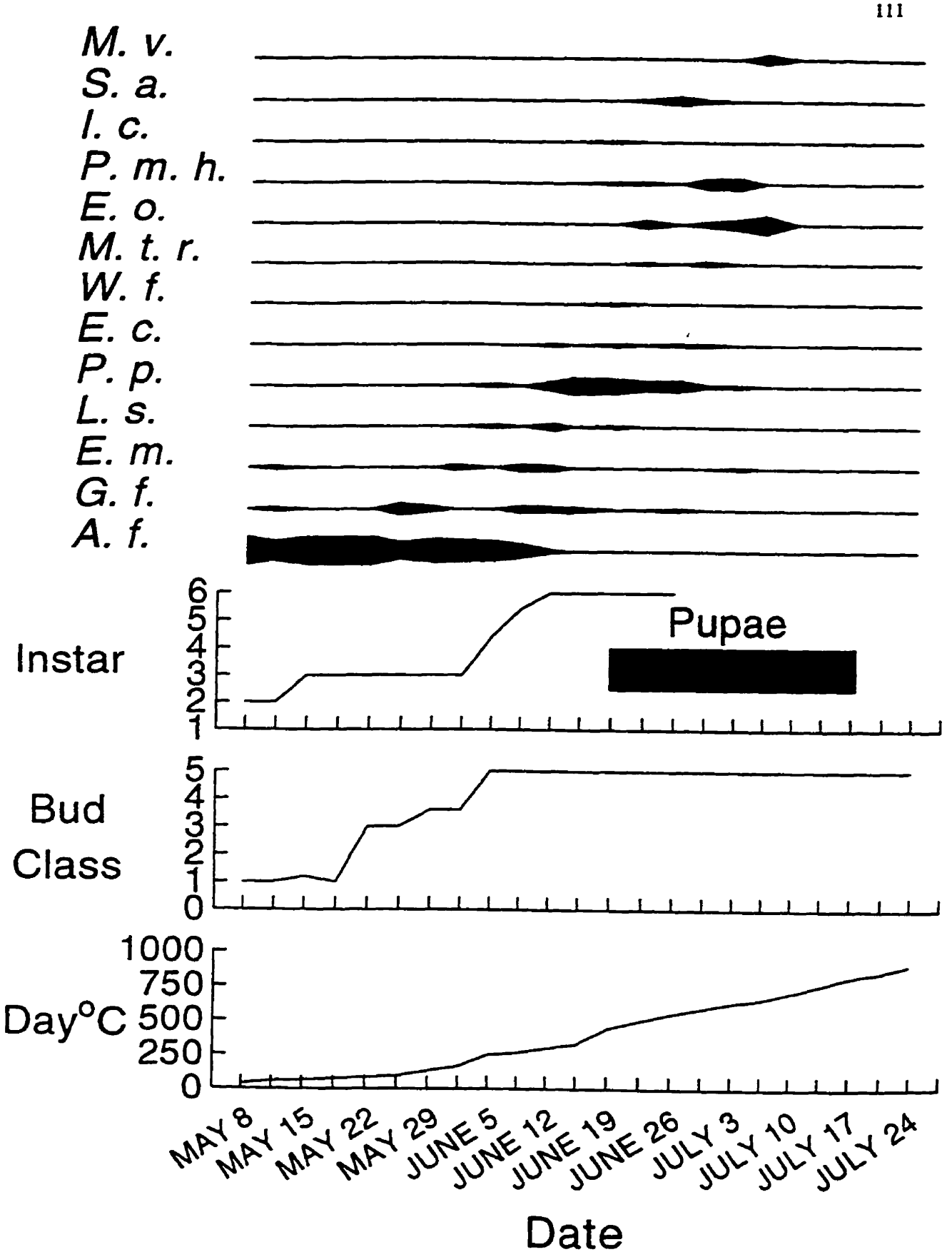

M. v.
S. a.
I. c.
P. m. h.
E. o.
M. t. r.
W. f.
E. c.
P. p.
L. s.
G. f.
A. f.
Instar
6
5
4
3
2
1
Pupae
Bud
Class
5
4
3
2
1
0
Day°C
1000
750
500
250
0
MAY 8
MAY 15
MAY 22
MAY 29
JUNE 5
JUNE 12
JUNE 19
JUNE 26
JULY 3
JULY 10
JULY 17
JULY 24
Date

Figure 16. A comparison of day degree accumulation with balsam fir bud phenology, spruce budworm larval development and the occurrence of parasitoid species in epidemic 2 site in 1995. A.f. = *Apanteles fumiferanae*, G.f. = *Glypta fumiferanae*, E.m. = *Enytus montanus*, P.p. = *Phyrxe pecosensis*, P.m.h. = *Phaeogenes maculicornis hariolus*, I.c. = *Itoplectis conquisitor*, L.s. = *Lypha setifacies*, E.c. = *Eumea caesar*, M.v. = *Mesopolobus verditer*, W.f. = *Winthemia fumiferanae*, E.o. = *Ephialtes ontario*, M.t.r. = *Meteorus trachynotus*, E.m. = *Enytus montanus*, S.a. = *Sarcophagus aldrichi*.


M. v.
S. a.
I. c.
P. m. h.
E. o.
M. t. r.
W. f.
E. c.
P. p.
L. s.
E. m.
G. f.
A. f.
Instar
6
5
4
3
2
1
Pupae
Bud
Class
5
4
3
2
1
0
Day°C
1000
750
500
250
0
MAY 8
MAY 15
MAY 22
MAY 29
JUNE 5
JUNE 12
JUNE 19
JUNE 26
JULY 3
JULY 10
JULY 17
JULY 24
Date

Discussion

Parasitoid species found in Manitoba

Epidemic populations

There have been many parasitoid species observed to attack outbreak populations of the spruce budworm. Wilkes et al. (1948) determined that of the 45 species collected in their study, only 15 species could be considered important elements of the British Columbia parasitoid complex (Table 1). Several other studies in different regions of Canada and the United States have found these same species (Dowden et al., 1948; McGugan and Blais, 1959; Blais, 1960; Miller, 1963b). McGugan and Blais (1959) hypothesize that the parasitoid species considered important elements in any spruce budworm outbreak will generally be found among the 15 species noted in Table 1, regardless of the location in North America. There are often differences found between the parasitoids that occasionally attack the spruce budworm, however, when intensive studies are done in different localities (McGugan and Blais, 1959; Miller and Renault, 1976). All of the parasitoids found in this study have previously been found attacking spruce budworm in other studies. Eight of the 15 species listed in Table 1 were collected in this study. The seven species which I did not collect were: *Phytodietus fumiferanae* Rohw., *Itoplectis quadricingulata* (Provancher), *Ceromasia auricaudata* Tns., *Agria affinis* (Fall.), *Cyzenis incrassata* (Smith), *Madremyia saundersii* (Will.), and *Nilea erecta* (Coquillet).

Although *A. affinis* was not collected in this study, there is evidence that it is present in Manitoba or was at one time. It was released into Manitoba as part of an experiment to establish high profile parasitoids from western Canada (i.e. B.C.) into eastern Canada. This species was also released into Ontario, Quebec, New Brunswick and Newfoundland at the same time (Coppel et al., 1959). Lejeune (1939) collected parasitoids, apparently from jack pine budworm, during the summer of 1938 in the Sandilands Forest Preserve in southeastern Manitoba. During this study, *A. affinis* was collected. This collection of *A. affinis* took place before the release which occurred in 1946 (Coppel et al., 1959), and therefore it would appear that *A. affinis* was naturally present in Manitoba. *Agria affinis* attacks a large number of insect families (Thompson, 1951). There is no evidence however that it requires an alternate host to complete its development and it is suspected that it overwinters on the ground as a puparium (Coppel et al., 1959). Therefore its absence from this study is not likely due to a lack of alternate hosts. Lejuene's study took place in a jack pine forest as opposed to the balsam fir/white spruce mix used in this study. Different forest types could affect *A. affinis* abundance. It may also be that *A. affinis* is simply rare in Manitoba. Unfortunately, Lejuene does not give the abundance of *A. affinis* in his study and therefore it is unknown how abundant *A. affinis* was at the time of his research. Although not abundant, *A. affinis* was found in New Brunswick (Miller, 1963b), Quebec and Ontario (Coppel et al., 1959) and therefore Miller (1963b) suspects that *A. affinis* may be native to

eastern North America.

Table 19 compares the parasitoid species collected from spruce budworm outbreak populations in different localities outside Manitoba to those collected from outbreak populations in Manitoba in 1994 and 1995. Although parasitoids of spruce budworm have been collected from Minnesota, the publication which lists these parasitoid species (Wilson and Bean, 1964) includes only hymenopterous parasitoids and does not indicate abundance. Therefore, in Table 19, the hymenopterous parasitoids under Minnesota are only listed as being present or absent, not as abundant, common or rare as was done for the other localities. Lejeune's study (1939) on parasitoids of budworm in Manitoba was not included in Table 19 as the host insect examined in this study was most likely jack pine budworm and not spruce budworm. In addition, the relative abundance for some of the species was not given (Lejeune, 1939). Of the 28 parasitoid species collected by Lejeune (1939), only six parasitoid species were also collected in the current study. These six species include: *T. minutum, M. trachynotus, P. maculicornis hariolus, I. conquisitor, M. tortricis and S. aldrichi.* These six species, and *A. affinis*, were the only species Lejeune's 1939 study had in common with the studies listed in Table 19. Table 19 shows that the Manitoba collections in the current study were very similar to those from other localities, both in terms of species and abundance. The locality most similar to Manitoba was Maine.

Apanteles morrisi was only collected in three locations, and was rare in all three places. *Apanteles fumiferanae* was abundant in all locations except for British Columbia where it was common (Table 19). There is a possibility that, because several new species of *Apanteles* were identified by Mason (1974), many of the specimens classified as *A. fumiferanae* in the studies included in Table 19 may have actually been other *Apanteles* species that were misidentified. This is likely, as with the exception of the present study and one other, all the studies on parasitoid abundance used in Table 19 took place before 1974.

Table 19. The abundance of different parasitoid species found in epidemic spruce budworm populations in Manitoba in the present study compared to the abundance of parasitoid species found in epidemic spruce budworm populations in different localities.

Parasitoid Species	Manitoba	[1]British Columbia	[2]Ontario	[3]Quebec	[4]New Brunswick	[5]Colorado	[6]New York	[7]Maine	[8]Oregon	[9]Minnesota
Hymenoptera: Braconidae										
Apanteles fumiferanae Vier.	[a]A	[b]C	A	A	A	A	A	A	A	X
Apanteles morrisi Mason	[c]R	[d]-	R	-	-	-	-	R	-	-
Meteorus trachynotus Vier.	C	R	A	A	A	-	A	C	R	X
Ichneumonidae										
Glypta fumiferanae (Vier.)	C	A	A	A	A	A	A	C	A	X
Phaeogenes maculicornis hariolus (Cress.)	A	C	A	C	C	A	C	C	A	X
Phytodietus fumiferanae Rohw.	-	A	-	-	-	-	-	-	C	-
Itoplectis conquisitor (Say)	C	R	A	C	C	C	A	R	-	X
Itoplectis quadricingulata (Provancher)	-	C	-	-	-	A	-	-	-	-
Ephialtes ontario (Cress.)	A	C	A	A	C	C	A	C	C	X
Enytus montanus (Ashmead)	R	-	R	-	C	-	-	R	-	-
Synetarius sp.	-	-	R	-	C	-	-	R	-	-
Exochus sp.	-	-	R	-	A	-	-	-	R	X
Pteromalidae										
Mesopolobus verditer (Norton)	C	R	C	R	C	-	C	-	A	X
Mesopolobus tortricis (Brues)	R	-	C	-	C	-	-	-	-	X
Trichogrammatidae										
Trichogramma fumiferanae Riley	A	C	R	C	C	[e]-	A	A	C	X
Diptera: Tachinidae										
Phryxe pecosensis (Tns.)	C	C	C	A	C	-	A	C	R	NA
Lyphe setifacies (West)	C	C	A	A	C	-	R	C	C	NA
Eumea caesar (Aldr.)	C	R	C	A	C	-	A	C	R	NA
Winthemia fumiferanae Tothill	R	C	A	C	-	C	R	C	A	NA
Winthemia amoena (Mg.)	-	-	-	R	A	-	-	-	-	NA
Cyzenis incrassata (Smith)	-	C	-	-	-	-	-	-	C	NA
Nilea erecta (Coquillet)	-	C	R	R	-	-	-	-	R	NA
Madremyia saundersii (Will.)	-	C	-	-	C	A	R	-	A	NA
Ceromasia auricaudata Tns.	-	C	-	-	-	C	-	-	A	NA
Actia interrupta Curran	-	-	R	A	C	-	R	R	R	NA
Sarcophagidae										
Sarcophaga aldrichi Park.	R	-	R	A	-	-	-	-	-	NA
Agria affinis (Fall.)	-	A	C	R	R	-	R	-	C	NA

a A = abundant; at least 5% of budworms were parasitized at one collection point.
b C = common; were collected in small numbers.
c R = rare; were collected only occasionally.
d - = was not collected
e No eggmass sampling was done in this study.
1 Coppel, 1946; Wilkes et al., 1948.
2 McGugan and Blais, 1959.
3 Blais, 1960; Blais, 1965.
4 Macdonald, 1959; Miller, 1963b.
5 Dowden et al., 1948.
6 Dowden et al., 1948; Dowden and Carolin, 1950.
7 Jaynes and Drooz, 1962; Tilles and Woodley, 1984.
8 Carolin and Coulter, 1959.
9 Wilson and Bean, 1964. Wilson and Bean (1964) only include Hymenoptera species and do not give relative abundance. Therefore, for the Minnesota column, X = present, - = absent and NA = presence absence not available. In addition to the species indicated on the table, the following species were found only in Minnesota: *Braconidae: Apanteles petrovae* Walley, *A. polychrosidis* Vier., *Eubadizon gracile* Prov., *Mecrocentrus iridescens* French, *M. paronese* Mues.; Encyrtidae: *Copidosoma deceptor* Miller; Eulophidae: *Euplectrus frontalis* Howard, *Hyssopus johannseni* (Cwfd.), *Pediobius tarsalis* (Ashm.), *Tetrastichus caerulescens* Ashm., T. *silvaticus* Gah.; Ichneumonidae: *Coccygomimus pedalis* (Cress.), *Scambus alboricta* (Cress.); Pteromalidae: *Habrocytus phycidis* Ashm

Endemic populations

A comparison between the parasitoid species found in the Manitoba endemic population and what was found in the other endemic studies in the literature (Fye, 1963, 1965; Miller and Renault, 1976; Hanson, 1982) is shown in Table 20. The data from the Ontario study is only listed as presence/absence and therefore Table 20 was prepared in a presence/absence format for comparison purposes. When comparing these studies, it should be noted that both the Ontario and New Brunswick studies looked at endemic populations following budworm population collapses. Only the current study and the Vermont study focused on endemic budworm populations unassociated with recent outbreaks. The study from New Brunswick differed from the other studies in that it focused mainly on overwintering and small larvae. Parasitoids that attack later stages were only examined in a cursory manner (Miller and Renault, 1976).

The endemic population parasitoid lists from Vermont and New Brunswick are larger than the lists from Manitoba and Ontario. This is likely due to the sampling effort used in the Vermont study and the length of the New Brunswick study. The study in Vermont took place over two years and 10-12 people were employed on each sampling occasion (Hanson, 1982). The study in New Brunswick took place from 1960 to 1971 and therefore consists of data compiled over many years. Several species thought to be of minor importance in outbreak spruce budworm populations have been reared from endemic populations.

Table 20. The presence of different parasitoid species found in endemic spruce budworm populations in Manitoba in the present study compared to the presence of parasitoid species found in endemic spruce budworm populations in other localities.

Parasitoid Species	Parasitoid Abundance			
	Manitoba	[1]Ontario	[2]New Brunswick	[3]Vermont
Hymenoptera: Braconidae				
Apanteles fumiferanae Vier.	x		x	x
Apanteles absonus Mues.			x	x
Apanteles petrovae Wall.			x	
Apanteles morrisi Mason			x	
Apanteles milleri Mason			x	
Apanteles renaulti Mason			x	
Meteorus trachynotus Vier.	x		x	x
Agathis binominata Mues.				x
Charmon gracilis (Prov.)				x
Clinocentrus fumiferanae Mues.				x
Ichneumonidae				
Glypta fumiferanae (Vier.)			x	x
Phaeogenes maculicornis hariolus (Cress.)				x
Ephialtes ontario (Cress.)	x			x
Enytus montanus (Ashmead)	x	x	x	
Synetaeris tenuifemur (Wfy.)		x	x	
Exochus nigripalpis tectulum Tow. & Tow.		x	x	x
Elachertus cacoeciae How.		x	x	
Horogenes cacoeciae (Vier.)		x		
Tranosema rostrale rostrale Brischke			x	x
Mesochorus sylvarum Curtis				x
Chorinaeus excessorius Davis				x
Coccygomimus (=Pimpla) tanuicornis (Cress.)				x
Stictopisthus flaviceps (Prov.)				x
Ptaromalidae				
Mesopolobus vendilar (Norton)			x	
Diptera: Tachinidae				
Phryxe pecosensis Tns.				x
Schizactia vitemarvis (Thompson)				x
Actia interrupta Curran			x	x
Lypha setifacies (West)	x			

1 - Fye, 1963; Fye, 1965.
2 - Miller and Renault, 1976; This study only looked at parasitoids attacking overwintering larvae and young larvae - parasitoids attacking later stages were not studied.
3 - Hanson, 1962.

These include *Apanteles absonus* Mues., *Tranosema rostrale rostrale* Brischke, *Enytus montanus* (Ashmead), *Exochus nigripalpis tectulum* Tow. & Tow., *Synetaeris tenuifemur* Wly., and *Actia interrupta* Curran (Fye, 1963; Miller and Renault, 1976). Of these species, only *E. montanus* was found in Manitoba.

Synetaeris tenuifemur is a univoltine species which overwinters as a cocoon. It attacks small spruce budworm larvae and is not recorded as having any alternative hosts (Krombein et al., 1979). The distribution for this species is listed as being New Brunswick, Ontario and eastern British Columbia (Krombein et al., 1979). This suggests a cross canada distribution. It is unknown why it was not collected from Manitoba. Even with the extensive sampling effort in Vermont this species was not recorded there either (Hanson, 1982).

Apanteles absonus, *T. rostrale rostrale*, and *E. nigripalpis tectulum* all have distribution records that include Manitoba and all three are recorded as having several alternative hosts to the spruce budworm (Krombein et al., 1979). However, none of these species were collected in this study. *Exochus nigripalpis tectulum* attacks late instar larvae and emerges from pupae. The small number of individuals collected from the endemic site in these stages may be one reason why *E. nigripalpis tectulum* was not collected in this study.

Although there are no definitive studies on the budworm stages attacked by *A.*

absonus, it was hypothesized by Miller and Renault (1976) that it attacks the budworm during the same time period as *A. fumiferanae*. *Apanteles absonus* has been recorded from the spruce budworm with much less frequency than *A. fumiferanae* (Mason, 1974). *Apanteles fumiferanae* is found in almost every study of spruce budworm parasitoids in both epidemic and endemic populations. One factor that could influence presence of *A. absonus* is that it does have alternate hosts and its presence or abundance could be regulated by the density of alternate hosts (Mason, 1974; Miller and Renault, 1976). In describing the distribution of *A. absonus*, a number of locations, including Hawk Lake, Manitoba have been included by Mason (1974) as known northern limits for the species. Mason (1974) does not indicate which host species *A. absonus* was collected from at each of these northern limits. Therefore, while this implies that *A. absonus* has been collected from Manitoba, it does not clarify whether it was collected from spruce budworm or from one of its alternate hosts. Therefore, assuming *A. absonus* is present in Manitoba, its absence from this study is unknown. It may simply be that *A. absonus* was too uncommon to be detected given the intensity of the sampling effort in this study.

Lypha setifacies was collected from the endemic population in Manitoba, but not from any of the other three endemic studies reported on in the literature. Therefore, this study is the first to record *L. setifacies* from an endemic population of spruce budworm (Fye, 1963; Fye, 1965; Miller and Renault, 1976;

Hanson, 1982). This species is common or abundant in most epidemic budworm populations where it has been collected, including Ontario and New Brunswick (Table 19). No record was found of this species being collected from Vermont. *Lypha setifacies* is not noted in the literature as being associated with endemic or light spruce budworm populations. It has, however, been recorded as showing an increase in parasitism as budworm density decreases (Miller, 1963b). It has also been associated with collapsing populations of jack pine budworm, *Choristoneura pinus pinus* Free. (Nealis, 1991). *Lypha setifacies*, which overwinters in the pupal stage (Coppel, 1946), was collected in both years from the Manitoba endemic site and was one of only two species collected from the endemic population in the first year of sampling. Due to the small number of spruce budworm collected in the endemic site in the first sampling year, and in particular the small number of late instar larvae and pupae collected, it seems logical to assume that only the more abundant species in the population would be found in the samples collected. The fact that *L. setifacies* was also collected in the second year of sampling reinforces the fact that this species was a feature of this population. The Manitoba endemic site was located within a few kilometres of epidemic budworm populations and therefore it is possible that the *L. setifacies* individuals found in the endemic site had immigrated from nearby epidemic populations. However, if this was the case, it would be expected that *L. setifacies* would have also been collected from the endemic sites in Ontario and New Brunswick. *Lypha setifacies* has been recorded from epidemic

populations in both Ontario and New Brunswick, and the endemic studies in both of these regions were in relatively close proximity to epidemic populations (Fye, 1963; Fye, 1965; Miller and Renault, 1976). Additional research is needed understand more clearly the role of *L. setifacies* in endemic parasitoid guilds.

The endemic study in New Brunswick took place in an endemic population created following the collapse of a spruce budworm outbreak. Miller and Renault (1976) speculate that studying an endemic population created by a collapse, as opposed to studying a stable endemic population, may influence the parasitoids that are found and their abundance. The study from Ontario also took place after a population collapse (Fye, 1963; Fye, 1965). If the comparison is only done between the two studies which looked at stable endemic populations, this study and the Vermont study, there are still many differences between the species that were found. Therefore, although the parasitoid species commonly associated with epidemic spruce budworm populations are quite uniform regardless of location (McGugan and Blais, 1959), based on the data presented from the four studies on endemic populations I would agree with Hanson (1982): the parasitoids associated with endemic populations are much less predictable.

Hyperparasitoids

There are three species of *Baryscapus* recorded as parasitizing the genus *Choristoneura* or its parasitoids. Two of the species are undescribed and cannot

be named until the genus in North America is revised (Huber et al., 1996). *Baryscapus coerulescens* (Ashmead) has been recorded as a secondary and tertiary parasitoid of Lepidoptera and other insect orders through Ichneumonoidea or Chalcidoidea (Huber et al., 1996). *Baryscapus* sp. 2. (Huber et al., 1996) was reared from *C. fumiferana* via *M. tortricis* whereas *Baryscapus* sp.1. was reared from *C. fumiferana* via *A. fumiferanae* and *M. trachynotus*. The *Baryscapus* individual in this study was reared from a pupa also containing *M. verditer*. Therefore, it most likely parasitized *M. verditer* or *M. tortricis* (as both *M. verditer* and *M. tortricis* have been reared from the same pupa) and is most likely *B. coerulescens*, or *Baryscapus* sp. 2.

Parasitoid guilds in epidemic versus endemic budworm populations

There is a difference between the parasitoid guilds found in the epidemic populations and the endemic population sampled in this study. Even when higher numbers of spruce budworm were released (release site), the parasitoid guild collected showed differences from the epidemic site. The release site and the endemic sites are clearly aligned together in both Figures 5 and 6. The separation is clearer in Figure 6 in which *A. morrisi*, *A. fumiferanae* and *G. fumiferanae* were removed from the ordination. The removal of *A. fumiferanae* brought the 1994 endemic site closer to the release and 1995 endemic sites. This occurred because *A. fumiferanae* constituted a higher proportion of the endemic collection in 1994 than in 1995 (Table 7). *Enytus montanus* and *M.*

trachynotus were not collected from the endemic site in 1994 (Table 7). Therefore, in Figure 5, the 1994 endemic site is pulled closer to *A. fumiferanae* than the 1995 endemic and release sites, and is pushed away from *E. montanus* and *M. trachynotus*. When *A. fumiferanae*, *G. fumiferanae* and *A. morrisi* are removed in Figure 6, the 1994 endemic site moves closer to the 1995 endemic and release site due to their shared association with *L. setifacies*. Therefore, the difference between the parasitoid guilds found in the epidemic and endemic populations appears to centre around three species: *L. setifacies*, *M. trachynotus* and *E. montanus*. Although all three of these species were collected in both epidemic and endemic populations, they comprised a much higher proportion of the endemic parasitoid guild than they did of the epidemic parasitoid guild in the years that they were collected (Table 12, Table 13). *Enytus montanus*, which was only collected in 1995, showed significant interaction between parasitism and year (Table 16). Its apparent rate of parasitism showed significant interaction with site in 1995 (Table 14) as well. When this significant interaction was examined further, the apparent rate of parasitism in the pooled 1995 epidemic sites was significantly different than the apparent rate of parasitism in the 1995 endemic site ($G = 5.89$, $df = 1$, $p < 0.025$). *Meteorus trachynotus* also showed a significantly higher apparent rate of parasitism in 1995 (Table 16). The apparent rate of parasitism of *M. trachynotus* showed significant interaction with site in 1995 (Table 14). Upon further examination however, the significant interaction was found to be between the two epidemic sites and not the pooled

epidemic sites and the endemic site ($G = 5.60$, $df = 1$, $p < 0.025$). *Lypha setifacies*, while comprising a higher proportion of the endemic parasitoid guild, than of epidemic parasitoid guilds in both 1994 and 1995 (Table 12, Table 13), did not show any significant interaction between site and apparent rate of parasitism. There was significant interaction between apparent rate of *L. setifacies* parasitism, site, tree species and year, but this significant interaction was more likely influenced by differences between collection from spruce in 1994 than by differences in apparent rates of parasitism between sites (Table 17). Therefore, the differences between the epidemic and endemic parasitoid guilds appear to be due to the relative importance of these three species within the endemic guild (Table 12, Table 13), rather than on the apparent rate of parasitism of these species within epidemic and endemic budworm populations.

Although Miller and Renault (1976) found differences between the epidemic and endemic parasitoid guilds in New Brunswick, they were not the same as were found in Manitoba. Miller and Renault (1976) traced the differences to three species: *A. fumiferanae*, *M. trachynotus*, and *S. tenuifemur*. They concluded that *A. fumiferanae* and *M. trachynotus* are common during the collapse of an outbreak. Populations then decline as the endemic phase is reached. *Synetaeris tenuifemur* was common during the endemic phase, but did not respond to increases in the budworm population. Overall, *S. tenuifemur* was the most abundant species in the endemic population in New Brunswick.

There was a large difference between the numbers of budworm collected from spruce versus the number of budworm collected from fir in this study. Figures 7, 8 and 9 were used to confirm that the separations between epidemic and endemic/release sites in Figures 5 and 6 were not an artifact of different host tree sources in different samples. Figures 7 and 8, using only samples collected from fir, are very similar to Figures 5 and 6. Figure 9, using only samples collected from spruce, differed from the separations shown in Figures 7 and 6 but numbers of budworm collected from spruce were small and therefore this ordination has diminished discriminatory power. The 1995 endemic and release sites are missing from Figure 9 as there were no parasitoids collected from spruce in these sites in 1995. As the release site was excluded from the spruce ordination analysis, it was not necessary to do a separate ordination excluding *A. fumiferanae*, *A. morrisi* and *G. fumiferanae*.

Some differences in site separation in Figure 9 were observed, but it does not appear that the separation between epidemic and endemic guilds is an artifact of different host tree sources in different samples. The separations are consistent when spruce assemblages are removed from the ordination analyses. There were only five species which showed significant interactions between rates of parasitism and tree species; only one of these, *A. fumiferanae*, was collected in the endemic site. Thus, I conclude that assemblage differences between epidemic and endemic sites were not the result of different host tree sources in

different samples.

Parasitoid guilds attacking budworm on spruce and fir

Figure 10 examines differences in the parasitoid guilds attacking budworm feeding on spruce versus budworm feeding on fir. Although Figure 10 appears to show some separation of tree species assemblages along axis 2, most of the assemblages are quite closely associated along axis 1. This configuration is due to the heavy influence of *A. morrisi* on the spruce assemblage from the 1994 epidemic 1 site. In order to see the relationships between the spruce and fir parasitoid guilds more clearly, *A. morrisi* was removed from the ordination (Figure 11). In Figure 11, there is a clear separation between the fir and spruce assemblages. There is also a clear separation between the 1995 endemic and release sites and the epidemic sites from both years. The 1994 fir and spruce endemic assemblages are both closely associated with the epidemic spruce assemblages from both years. There were only two parasitoid species collected from the endemic site in 1994: *A. fumiferanae* and *L. setifacies*. *Lypha setifacies* was only collected from fir in the 1994 endemic site; *A. fumiferanae* was collected from both spruce and fir (Table 10). In the epidemic sites, *L. setifacies* was only collected from spruce in 1994 and only from the epidemic 2 site (Table 10). *Apanteles fumiferanae* however, was collected from spruce in every site in both years (Table 10, Table 11) with the exception of the 1995 endemic (Table 11) and release sites (Table 8). Therefore, it would appear that the 1994

endemic assemblages are closely associated with the epidemic spruce assemblages from both years due to the shared association with *A. fumiferanae*. *Apanteles fumiferanae* was also collected from fir in every site in both years with the exception of the 1995 release site. When the data from 1994 and 1995 are pooled for the epidemic sites, the relative abundance of each parasitoid species within spruce and fir guilds can be compared (Table 21). *Apanteles fumiferanae* has the greatest abundance in each guild, however, its relative abundance is higher in the spruce than in the fir guild (Table 21). In addition, many of the late larval and pupal parasitoids have lower relative abundances in the spruce guild than in the fir guild. This would point to the conclusion that the separation of spruce and fir guilds in Figure 11 is due to both the stronger influence of *A. fumiferanae* and the weaker influence of many of the late larval and pupal parasitoids in the spruce assemblages compared to the fir assemblages. Therefore, although there does not seem to be a clear influence of host tree species on the parasitoid species attacking budworm, there do seem to be some differences in the relative abundance of species.

Table 21: **Relative abundance of parasitoids of different species in fir and spruce parasitoid guilds from the pooled data of the epidemic 1 and epidemic 2 sites.**

Parasitoid Species	Percentage parasitism	
	Percent of Guild	
	Fir	Spruce
Apanteles fumiferanae	27.9	62.0
Apanteles morrisi	0.1	2.0
Glypta fumiferanae	11.0	10.0
Phryxe pecosensis	13.8	2.0
Phaeogenes maculicornis hariolus	12.0	4.0
Itoplectis conquisitor	5.0	1.0
Lypha setifacies	4.7	2.0
Eumea ceasar	4.9	3.0
Mesopolobus tortricis	0.8	1.0
Mesopolobus verditer	3.1	3.0
Winthemia fumiferanae	2.0	5.0
Ephialtes ontario	8.0	3.0
Meteorus trachynotus	3.0	0.0
Sarcophaga aldrichi	1.7	0.0
Enytus montanus	0.4	0.0

The differences in relative abundance seen between the parasitoid species attacking budworm on spruce versus fir does not appear to be due to the parasitoid species having a preference for one tree species over another. There is only one reference in the literature where preference for one host tree over another by budworm parasitoids has been examined. Miller (1959) found that *A. fumiferanae* shows a preference for white spruce foliage over severely defoliated balsam fir in olfactometer experiments. The preference for white spruce in that experiment however, may have really been an attraction to defoliated versus undamaged foliage, and not really an attraction to spruce over fir. In the current study, only five parasitoid species showed significant interactions with tree species. In 1994, both *A. morrisi* ($G = 8.16$, $df = 1$, $p < 0.01$) and *A. fumiferanae* ($G = 5.31$, $df = 1$, $p < 0.025$) showed significant interaction between apparent rate of parasitism and tree species. In 1995, *M. verditer*, *I. conquisitor* and *W. fumiferanae* showed significant interaction between tree species and apparent rate of parasitism (Table 15). However, this interaction was not significant for any of these species in both years, and only *W. fumiferanae* showed the same trend in both years (Table 10, Table 11). Therefore, it is likely that these significant interactions may be due to the small numbers at risk collected from spruce versus fir rather than a consistent preference for one host tree species over another.

Examination of Table 22 offers an alternative explanation to host tree preference for the heavy influence of *A. fumiferanae* in the spruce guild. Table 22 shows that there are lower numbers of spruce budworm at risk for parasitoids attacking later stages of the budworm. If the numbers at risk for late attacking parasitoids are compared to the numbers at risk for early attacking parasitoids, the numbers at risk on spruce appear to be decreasing at a faster rate than on fir. In other words, the budworm population appears to be declining on spruce at a much faster rate than on fir. Graphical examination (Figures 12 and 13) and regression analysis of this decrease confirms that there was a decline in the percentage of budworm collected from spruce and sample date in both 1994 and 1995. It could be argued that this decline might be the result of less spruce samples collected at the end of the field season. This seems unlikely however as the sampled trees were all selected randomly and therefore the number of spruce trees sampled at the beginning of the season should not differ overly from the number of spruce trees sampled at the end of the season. Figure 14 and the associated linear regression confirm that the number of spruce trees sampled in 1995 did not differ significantly between the beginning and end of the field season.

Table 22: **Relative abundance of parasitoids of different species in fir and spruce guilds and percentage parasitism within hosts at risk from pooled data of the epidemic 1 and epidemic 2 sites.**

Parasitoid Species	Percentage parasitism			
	Percent of Guild		Percent of At Risk Hosts	
	Fir	Spruce	Fir	Spruce
Early larval parasitoids				
Apanteles fumiferanae	27.9	62.0	7.1 (2918)[1]	9.5 (672)
Apanteles morrisi	0.1	2.0	<0.1 (2918)	0.3 (672)
Glypta fumiferanae	11.0	10.0	2.1 (3983)	1.4 (697)
Late larval parasitoids				
Enytus montanus	0.4	0.0	0.1 (2110)	0.0 (261)
Meteorus trachynotus	3.0	0.0	1.4 (1588)	0.0 (191)
Lypha setifacies	4.7	2.0	2.2 (1588)	1.0 (191)
Phryxe pecosensis	13.8	2.0	4.0 (2551)	1.0 (201)
Eumea ceasar	4.9	3.0	1.4 (2551)	1.5 (203)
Winthemia fumiferanae	2.0	5.0	0.6 (2557)	2.3 (220)
Pupal parasitoids				
Phaeogenes maculicornis hariolus	12.0	4.0	6.3 (1430)	7.1 (56)
Itoplectis conquisitor	5.0	1.0	3.0 (1333)	2.0 (52)
Mesopolobus tortricis	3.9	4.0	2.0 (1474)	7.7 (52)
Mesopolobus verditer	3.1	3.0	1.6 (1474)	5.8 (52)
Ephialtes ontario	8.0	3.0	5.7 (1330)	5.7 (52)
Sarcophaga aldrichi	1.7	0.0	0.5 (2499)	0.0 (220)

[1]The number of budworm at risk for each parasitoid species

Although the reasons for the observed increased mortality on spruce are unknown, there are a number of applicable hypotheses in the literature. In an experiment where egg masses were introduced to fir and spruce trees, a higher survival rate was found in larvae on the fir trees than those on white spruce (Fye, 1965). Fye (1965) indicates that unpublished data suggests that larger populations of predators inhabit white spruce than balsam fir. During Fye's (1965) study, he observed that of 128 eggs known to have been lost to predators, 95 were from white spruce whereas only 33 were from balsam fir. This tends to corroborate the suggestion that there are larger predator populations on white spruce than on fir (Fye, 1965).

Thomas (1987) showed under laboratory conditions that as foliage age increased in white spruce, mortality of budworm increased and then decreased. The white spruce shoots changed from a suitable to an unsuitable food source during the period when 6th-instar larvae were feeding. The change in food quality was associated with a rapid decrease in total nitrogen content of the foliage (Thomas, 1987). This could also explain the increased budworm mortality seen in late budworm stages in the current study. It is the opinion of other authors that the effects of hosts can be significant and that the current knowledge regarding the role of host in the development and survival of budworm populations is lacking (Volney and Cerezke, 1992). More work is needed to further our understanding in this area.

Watt (1963) found that budworm mortality is proportionately more severe at low than high budworm densities. Watt (1963) suggests that there are some factors present which kill a relatively constant number of budworm at all densities, and therefore kill a greater proportion at low densities. Specifically, Watt (1963) proposes that this may be caused by low-numerical response predators. The current study did not record the density of budworm larvae per unit sampled on fir and spruce. Therefore, it is possible that the number of budworm on spruce in this study may have been smaller to begin with. In the current study, low numbers were seen in endemic budworm populations versus epidemic populations. Therefore, the question of proportionately higher mortality at low densities could be examined using the results for the endemic population. Watt's explanation could account for the difficulty in obtaining good data for parasitoids of late larvae and pupae in the endemic population in 1994 as the numbers at risk for the early larval parasitoids is much higher than for the late larval and pupal parasitoids (Table 7, Table 10). However, the same does not seem to be true for 1995 (Table 7, Table11). In 1995, in the endemic site, the number of budworm at risk for the early larval parasitoids was not appreciably higher than the numbers at risk for the late larval or pupal parasitoids. Therefore it is reasonable to conclude that Watt's explanation may not be the correct explanation for the decreased budworm at risk for late larval and pupal parasitoids on spruce versus fir, even if there were lower numbers on spruce to begin with.

The current study was not designed to examine predation or population dynamics of the spruce budworm and therefore the above hypotheses regarding mortality on spruce could not be tested. Although the reasons for this higher mortality of late season larvae on spruce in this study is not known, its effects on parasitism can be seen. The increased mortality on spruce reduced the late season host availability for late larval and pupal parasitoids. This caused the relative abundance of early season parasitoids to be much higher in the spruce parasitoid guild versus the fir parasitoid guild.

Day degree accumulation

The rate of day degree accumulation was slightly faster in the epidemic 1 site. The fir in this site achieved bud class four ahead of the epidemic 2 site, although both sites reached bud class five by June 5th. Although the epidemic 2 site had a slower accumulation of DDC, the budworm in this site achieved each of the instars from second instar through to sixth instar on the same dates as in the epidemic 1 site. This result may be due to the methodology used in sampling temperature. The temperature measurements were taken at a height of 2 m. The budworm however, would have been located much higher in the canopy and therefore, the DDC accumulation recorded at 2 m may not accurately reflect the actual DDC experienced by the budworm in the epidemic sites. This may account for the budworm instar being present on the same dates in both sites, but having different levels of DDC accumulation on those dates.

Integrated management

In the past, spruce budworm outbreaks have been treated with chemicals such as DDT (Macdonald, 1959; Blais and Martineau, 1960; Blais, 1963; Blais and Parks, 1964), phosphamidon, dimethoate, menazon (Randall, 1962), and mexacarbate (Leonard and Simmons, 1974) among others. These insecticides often reduced any budworm parasitoids and predators present at the time of spraying (Webb, 1959; Leonard and Simmons, 1974). A newer control agent, *Bacillus thuringiensis* (*B.t.*), has been shown to be effective against lepidopterous larvae, including the spruce budworm (Klein and Lewis, 1966; Smirnoff, 1963; and Smirnoff, 1973). *Bacillus thuringiensis* has a high degree of host selectivity as only certain Lepidoptera provide the enzymes and pH conditions in the gut that are required for *B. thuringiensis* to initiate infection (Niwa et al., 1987). Nealis and van Frankenhuyzen (1990) demonstrated that parasitized larvae are more likely to survive exposure to *B. thuringiensis* as they feed less than non-parasitized budworm and are therefore less likely to ingest a lethal dose of the bacterium. Delaying the timing of spraying until the fourth to sixth instars increases the rate of parasitism of *A. fumiferanae* while still providing adequate protection of the current year's foliage (Nealis et al., 1992). Based on this information and the results of the current study, conservation of *A. fumiferanae* in Manitoba, could be achieved if spraying were delayed until approximately June 12. This date may vary depending on DDC accumulation in any particular year. In recent years, the actual spray dates in the Whiteshell

area of Manitoba have been within the first two weeks of June (Knowles and Matwee, 1995; 1996; 1997). Therefore the current spray practices in Manitoba may already be achieving conservation of *A. fumiferanae*. Future studies examining parasitoids within spray blocks could confirm how successful current spray dates are at conserving budworm parasitoids.

The previously mentioned studies which examine conservation of *A. fumiferanae* all looked at spray operations utilizing *B. thuringiensis.* The current budworm control program in Manitoba is moving towards increased use of Mimic® (K. Knowles, Manitoba natural Resources - Forestry Branch, Pers. comm.). Mimic® has shown a residual effect in some spray areas (K. Knowles, Manitoba natural Resources - Forestry Branch, Pers. comm.). Future studies looking at integrated budworm control in Manitoba should focus on areas sprayed with Mimic®. In particular, how the residual effects of Mimic® may influence parasitoid populations should be investigated.

Conclusions

The parasitoid species collected from epidemic budworm populations in Manitoba were similar to the parasitoid species collected from epidemic populations in other localities. The relative abundances of these species in Manitoba was also similar to what was found in other studies.

The parasitoid guild collected from the endemic population in this study differed from what has been found in other studies. Several species found to be of importance in endemic budworm populations in localities other than Manitoba were not collected in this study. *Lypha setifacies,* which was collected in the endemic site in Manitoba, has not been previously recorded from an endemic budworm population. The results from this study, regarding parasitoid species associated with endemic populations, agree with that of previous studies: the parasitoid species associated with endemic populations are much less predictable than those associated with epidemic populations. Future investigations into parasitoids of endemic budworm populations are needed to understand this unpredictability. In addition, more knowledge is needed about the biology of many of the parasitoid species attacking budworm. This information is needed to predict and understand when and where different parasitoid species will be present.

There was a difference between parasitoid guilds in epidemic populations and

endemic populations in Manitoba. The difference in the two guilds centres around three species: *L. setifacies*, *M. trachynotus*, and *E. montanus*. All three of these species were collected in both epidemic and endemic populations, but all three comprised a much higher proportion of the endemic parasitoid guild than of the epidemic guild. The difference between these two guilds is the importance of these species within each guild rather than in the apparent rates of parasitism.

The parasitoid guilds attacking budworm feeding on spruce differed from that attacking budworm feeding on fir. The difference resulted from decreased late season host availability on spruce for late larval and pupal parasitoids. This was caused by a higher rate of mortality on spruce than on fir. This resulted in early larval parasitoids comprising a much higher proportion of the parasitoid guild attacking spruce than in the guild attacking fir.

The DDC accumulation in the current study suggests that delaying spraying for spruce budworm until early June would help conserve the parasitoid *A. fumiferanae* in Manitoba. Current spray practices in Manitoba may already be achieving this. Future studies examining parasitoid species present in recently sprayed areas would help to confirm the level of parasitoid conservation currently acheived.

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IMAGE EVALUATION
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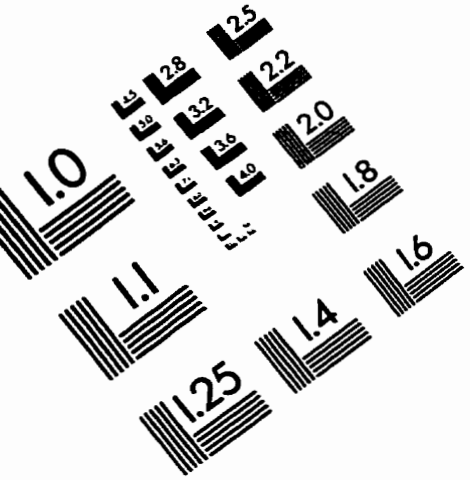

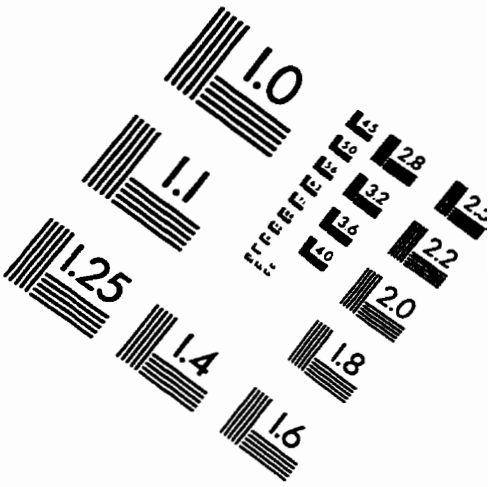

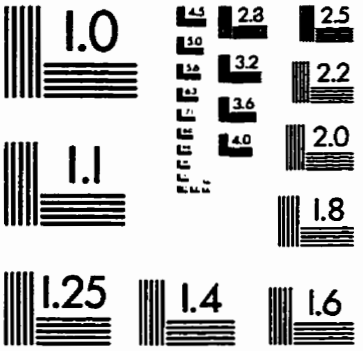

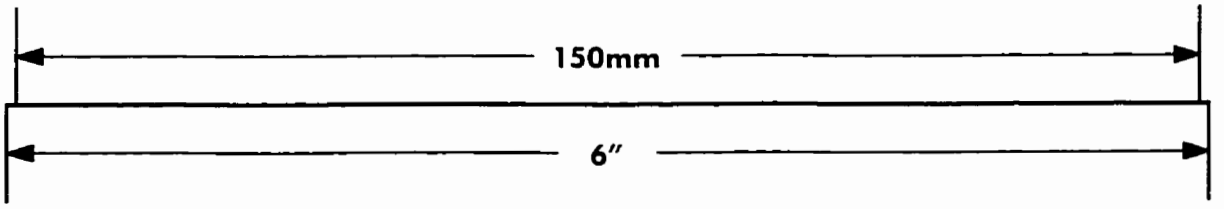

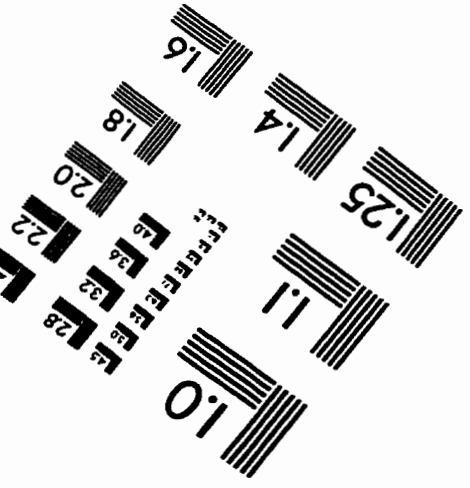

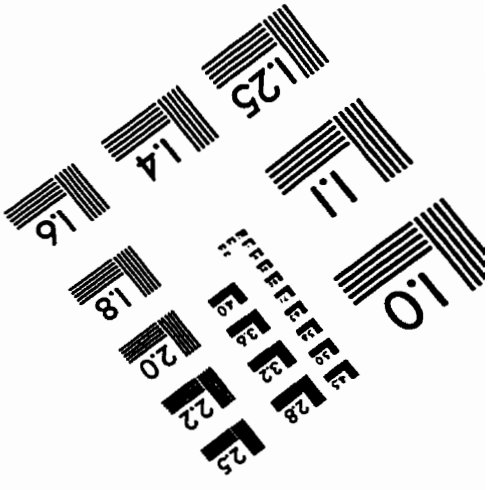

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