STUDIES ON THE FALL CANKERWORM,

ALSOPHILA POMETARIA (HARRIS)

(LEPIDOPTERA: GEOMETRIDAE) IN MANITOBA,

WITH REFERENCE TO PERFORMANCE ON DIFFERENT

HOST TREES, DEFOLIATION INTENSITY

AND HOST PLANT SELECTION

A Thesis

Submitted to the Faculty

of

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by

Blaine Herbert Leslie Timlick

In Partial Fulfillment of the

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of

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BLAINE HERBERT LESLIE TIMLICK

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

MASTER OF SCIENCE

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To my friends, who make life so interesting.

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Abstract

Studies were conducted to examine the performance of the fall cankerworm, <u>Alsophila</u> <u>pometaria</u> (Harris), when reared under various conditions, and also to examine adult host selection cues upon eclosion. Fall cankerworm larvae were reared on two age classes of foliage from four species of trees. Cankerworm larvae were also reared on foliage from trees of one species that were under three different degrees of defoliation. Indices of performance were survival, duration of the larval feeding life, prepupal weight, pupal duration, and fecundity of the females. Studies were conducted in both laboratory and field settings.

Results indicate that fall cankerworm larvae reared on young foliage have greater performance than do larvae reared on more mature foliage; in general the disadvantage of feeding on mature foliage was less on birch (Betula x sargentii Dugle) and willow (Salix lutea [Nutt.]) than on oak (Quercus macrocarpa Michx.) and elm (Ulmus americana L.). Results suggest that fall cankerworm responds to the changes in foliar quality of <u>Betula x sargentii</u> (Dugle), but it is not clear whether all of these changes are induced by the level of defoliation intensity, or whether other stresses, such as drought, are involved. Results also indicate that both male and female fall cankerworm adults are attracted to vertical silhouettes. The factors influencing the differences and their evolutionary implications are discussed.

CHAPTER I

INTRODUCTION

The fall cankerworm, *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae), is a defoliator of hardwoods in the forests of eastern North America (Fedde 1977), but in Canada outbreaks have been most prevalent in the prairie provinces (Palaniswamy et al. 1986). It is a polyphagous insect that feeds on many deciduous trees including species of *Quercus*, *Ulmus*, *Malus*, *Acer*, and *Tilia* (Palaniswamy et al. 1986). In Manitoba, recent outbreaks have caused severe defoliation to elms (*Ulmus*) along river banks and boulevards.

The larvae hatch early in the spring and feed on young foliage (Lawson et al. 1984). There are four larval instars, with the fourth instar consuming the greatest amounts of foliage (Hinds 1901). Feeding on young foliage is characteristic of a number of insects related to the fall cankerworm, such as autumnal moth, *Epirrita autumnata* (Bk.) (Haukioja et al. 1988) and winter moth, *Operophtera brumata* (L.) (Feeny 1970; Holliday 1977). Feeding on young foliage is thought to be an advantage for these insects because young leaves are more succulent and nutritious than mature foliage (Lawson et al. 1984; Scriber and Slansky 1981), and may contain lower amounts of defensive compounds (Feeny 1970). It has also been suggested that defensive compounds are induced by herbivore feeding (Haukioja 1982), and may last several years (Tuomi et al. 1984). How effective

these defensive compounds are, may dictate how well the lepidopterous larvae perform.

In A. pometaria a primary determinant of the feeding site is the site of oviposition. The resulting newly hatched larvae must either feed on the host or spin silk and disperse on the wind to find alternative resources. Therefore, the mechanisms by which the female chooses the oviposition site are important for the success of her offspring. Palaniswamy et al. (1986) suggest that fall cankerworm orients to vertical silhouettes. This has has been proven for winter moth , Operophtera brumata (Grison and de Sacy 1954) and for gypsy moth, Lymantria dispar (Richerson et al. 1976).

It has been suggested that insects like the fall cankerworm evolved in a cold climate because of aptery, and that wing reduction is a mechanism which the insects adapted to avoid heat loss (Dierl and Reichholf 1977). In cold environments such as those present at the recession of the last glaciers, or in treed tundra today, the most dominant woody vegetation are dwarf willow and birch trees (Pennington 1969; Ritchie 1984). It has been suggested that the evolution of these geometrids with flightless females took place in treed tundra; the current distribution in the deciduous woodland biome is a recent occurrence. In this study, Quercus macrocarpa (Michx.) and Ulmus americana (L.) are chosen as current hosts, and Salix lutea (Nutt.) and Betula x sargentii (Dugle) were chosen as possible prefered hosts in recent evolution.

Objectives

The studies were approached with the following objectives:

    i.   To investigate whether foliage of different tree species affects survival, development and subsequent egg production of <u>Alsophila pometaria</u>.

    ii.   To determine if survival, development and egg production of fall cankerworm are affected by the age of the foliage in the larval diet.

    iii.   To test whether inducible defence against herbivores occurs in hybrid bog birch, <u>Betula x sargentii</u>.

    iv.   To determine if vertical silhouettes are attractive to adult fall cankerworm

Thesis Organization

This thesis is a report of research work carried out in controlled laboratory environments and in the field in Manitoba in 1986 and 1987. Chapter II is a review of literature pertinent to the research. Chapter III presents detailed reports of the research in three parts, each written in scientific paper style suitable for publication. It is anticipated that papers from this chapter will be submitted to The Canadian Entomologist. Chapter IV contains a general discussion.

CHAPTER II

LITERATURE REVIEW

Distribution and Description

The fall cankerworm, <u>Alsophila pometaria</u> (Harris), is a geometrid moth of the subfamily Oenochrominae, and is indigenous to North America (Johnson and Lyon 1976). It is found as far south as North Carolina and north to central Saskatchewan (McGuffin 1988). In the United States, fall cankerworm is found along the east coast south to North Carolina and is also found in Kansas, Colorado and California (Forbes 1948). In Canada, fall cankerworm is found from Nova Scotia in the east to the east side of the Rocky Mountains in Alberta (McGuffin 1988); in the Canadian prairies, the distribution of fall cankerworm closely follows that of Manitoba Maple, <u>Acer negundo</u> (L.) (Prentice 1963).

Egg masses contain an average of about 200 eggs, but numbers range from several to several hundred. Eggs are laid together in rows, usually in one layer to form the mass. Individual eggs are approximately 0.6 mm long and 0.45 mm in diameter at the top (Hinds 1901). The base of each egg is somewhat narrower than the top, so that eggs resemble inverted cones with rounded basal edges. Eggs are grey with a darker depression in the centre of the top.

There are four larval instars, all of which feed. The larvae have 10 abdominal segments with prolegs on abdominal segments 7 and 10, and with a pair of vestigial prolegs on the sixth abdominal

segment (Hinds 1901). The first instar larva is approximately 1.8 - 4.5 mm long and is light green with a faint light-colored lateral stripe (McGuffin 1988). The second instar larva is approximately 8 mm long when fully fed, is slightly darker than the previous instar and has a dorsal stripe of dark green (McGuffin 1988). The third instar is about 12 mm long, and this and the fourth instar exhibit color polymorphism. Schneider (1979) recognized six color morphs ranging from light green through various striped patterns to black. Schneider considered increased pigmentation to be correlated with population density; however, in Manitoba, darkly pigmented individuals sometimes occured when larvae were reared singly (Timlick, unpublished data). The fourth larval instar grows to about 18 - 20 mm in length; in this instar, larvae feed almost constantly. Larvae then enter a prepupal stage, in which they are lethargic and become shorter in length and wider in diameter. Prepupae burrow into the soil or surface litter to pupate. Pupation occurs within a hardened cocoon; inside the cocoon the pupa is dark brown and is about 10 - 12 mm long (Hinds 1901).

Upon eclosion, adults emerge as winged males and wingless females. The head and body of males are light grey to light brown; females are grey. Wings of the males are grey to light brown with an expanse of 24 - 35 mm (McGuffin 1988). Adults eclose with non-functional mouthparts and therefore, do not feed.

Phenology

Eggs are laid in the autumn and are the overwintering stage. Fall cankerworm eggs are laid on many surfaces, including potential

host trees and the sides of buildings. On host trees eggs are usually laid on branch terminals, with a mean twig diameter of 6.2 mm (Talerico 1971).

Larvae emerge in the early spring at about the same time as the bud burst of many of the deciduous trees (Hildahl and Peterson 1974). This occurs on various calendar dates depending on the geographic location and on climatic factors. The larval stage lasts about one month; the first instar lasts 4-5 days, the second 5-7 days, the third 6-8 days, and the fourth instar, including the non-feeding prepupal stage, lasts 9-12 days (Hinds 1901) .

In Manitoba, moths of the fall cankerworm emerge from their cocoons during late September to early October, usually after the first severe autumn frost (Hildahl and Peterson 1974). The wingless females walk to vertical surfaces, mate and then crawl up the selected vertical object to deposit their eggs. Winged males fly to vertical objects and are aided in finding mates by the release by females of sex-attractant pheromones (Palaniswamy et al. 1986).

Synchronization of Hatch to Host Bud Burst

Spring feeding caterpillars, in which hatch is synchronized with bud burst may have evolved this pattern of phenology for a number of reasons. The most studied insect with this type of life style is another geometrid, the winter moth. Winter moths suffer considerable mortality if they hatch only a few days before the bud burst of their hosts (Embree 1965, Varley and Gradwell 1958). When fall cankerworm hatch long before the host bud burst there is

dispersal and mortality (Schneider 1979). In forests in Nova Scotia, there is a correlation between synchronization with host bud burst and larval population densities of winter moth (Embree 1965). The density of winter moth larvae in apple trees is related to the degree of development of the buds, this is the result of larvae leaving trees with closed buds, and colonizing trees with open buds (Holliday 1977).

Delay of hatch exposes larvae to a diet of more mature leaves, and this is detrimental. Indirect evidence from Schneider's (1979) research suggests that a delay of hatch by only a few days significantly reduces fecundity of fall cankerworm feeding on red maple. Reduced fecundity has been attributed to the reduced nutritional quality of the mature foliage (Schneider 1979; Feeny 1970; Drooz 1970), and constitutes a selection pressure favoring earlier hatch. There is evidence that the fall cankerworm requires large amounts of foliage because of low digestive efficiency. This strategy has been termed "consumption over efficiency" (Lawson et al. 1984). As a result, the earlier the cankerworm can hatch in relation to the host, the more time it has to feed before the quality of the foliage becomes reduced.

Host Plant

Different host plant species have different defence mechanisms which affect the insects ability to consume or digest the foliage. For example, _Rheumaptera hastata_ (L.), performs best on birch, _Betula papyrifera_ (Marsh.) although it will also survive and reproduce on _Alnus_ spp., _Salix_ spp., and _Rosa_ spp. (Werner 1979). Gypsy moth ,

Lymantria dispar (L.) performs better on Quercus spp. than on Alnus spp. (Hough and Pimental 1978); this was attributed to differences in water and nitrogen content and in leaf toughness. Winter moth performs better on Quercus spp. (Wint 1983) and Malus (Holliday 1975) than on other species. Dispersal of winter moth larvae from unacceptable hosts results in aggregations on more acceptable hosts, however, some larvae remain on less acceptable hosts. This spread of larvae across hosts with different phenologies, or varying in other attributes affecting host acceptability, results in a hatch time which is related to the average time of bud burst of the hosts in an area, rather than to the bud burst of individual trees (Wint 1983).

Host Plant Defence

The performance of tree-feeding insects can be affected by the condition of the host plant and the intensity of defoliation which has taken place before or during the insect's feeding life. Reduction in water content and available nitrogen, and accumulation of various chemical compounds in maturing foliage are thought to be deleterious to many herbivorous insects. Nitrogen and water content generally exhibit decreases as leaves age, and simultaneously the toughness of the foliage increases (Feeny 1970, Scriber and Slansky 1981; Schultz et al. 1982). Phenolic substances such as tannins are toxic to some insects and are present in higher amounts in the mature foliage of many temperate region tree species such as Quercus (Feeny 1970) and Betula (Haukioja et al. 1985); in contrast phenolic compounds can be high in the young foliage of many

tropical tree species (Coley 1983; Macauley and Fox 1980; Oates et al. 1980). However, while they bind with various gut proteins, tannins do not inhibit digestion in all insects (Bernays 1978). Lawson et al. (1984) suggest that tannins and other phenols do not influence the nutritional indices of the fall cankerworm.

The chemical factors responsible for resistance to insect herbivores in plants are thought to be either continuously occurring or inducible. Haukioja (1982) identified two types of inducible defences in birch foliage. One type occurs in foliage that has suffered chewing or mechanical damage; this defence is induced within hours or days of injury, and relaxes approximately two weeks after its cessation. The other type occurs in the leaf generations following defoliation and may take a number of years to relax. Haukioja (1982) suggested that the two types of defence have opposite effects on the stability of a herbivore population using these trees as a preferred food source. The rapidly inducible defences have a stabilizing effect and are strongest when pest densities are high. Resistance in further years is a potential destabilizing agent which is thought to drive the periodicity of outbreaks of the autumnal moth, <u>Epirrita autumnata</u> on birch in northern Europe. Tuomi et al. (1984) predicted that the long relaxation time of resistance would be nutrient dependent, given adequate water, and demonstrated that fertilization in connection with defoliation of birches shortened the relaxation time of resistance to the autumnal moth.

In some trees, defences are thought to be induced when defences of neighboring trees of the same species are induced by herbivore attack (Rhoades 1983; Baldwin and Schultz 1983, Haukioja

et al. 1985). This communication is proposed to happen via aerial transmission. Volatile compounds such as ethylene exude from wounded tissue (Yang and Pratt 1978), and are reported to affect the synthesis of alleochemicals in receptor trees (Boller 1982). Fowler and Lawton (1985) criticized the "talking tree" explanation and proposed that the insects on uninjured trees in Rhoades (1983) experiments were diseased and Baldwin and Schultz's (1983) experiment was incorrectly analysed. Haukioja et al. (1985) prevented insect -spread diseases and felt that the transfer of triggering cues via roots or through the soil could also not be excluded as a means of communication.

Constraints imposed by leaf development and damage are thought to have influenced the life histories of many herbivorous insects feeding on trees (Feeny 1970; Niemela and Haukioja 1982; Mattson 1980). In addition to the advantages of early feeding on juvenile leaves which have increasing but non-induced defences, early hatch could be advantageous when there are inducible defences. By feeding on young leaves, the insects might avoid the induced defences that would be encountered by later infesting herbivores; such a trait would also minimize the time that the feeding larvae are exposed to predators and parasites (Price et al. 1980).

Host Selection by Females

Like fall cankerworm, female winter moths are flightless and unable to feed. Winter moth females seek mating and oviposition sites by orienting themselves visually to vertical silhouettes (Grison

and de Sacy 1954). If hatching winter moth larvae find the host plants foliage unapparent or unacceptable, then they disperse by ballooning in the wind on spun silk (Holliday 1977). Such dispersal would be facilitated if oviposition on terminal twigs is high in the canopy. While insects like the winter moth have a preferred host, they are also polyphagous and this increases the probability that wind-borne larvae will encounter a suitable host (Wint 1983). The fall cankerworm has similar characteristics to the winter moth and also produces silk which may function in dispersal. It seems likely that the adult fall cankerworm females, like winter moth females can maximize their fitness by laying the largest number of eggs compatible with placing them high in the trees. Because of the similar constraints of the two species, it seems reasonable to conjecture that fall cankerworm females orient to oviposition sites using similar visual responses to those seen in winter moth by Grison and de Sacy (1954).

CHAPTER III

Part i

The Effect of Leaf Maturity and Host Plant Species on the Performance of *Alsophila pometaria*

(Lepidoptera: Geometridae)

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The Effect of Leaf Maturity and Host plant Species on the Performance of *Alsophila pometaria* (LEPIDOPTERA: GEOMETRIDAE)

Abstract

Performance of the fall cankerworm, Alsophila pometaria was measured when larvae were reared on two ages of foliage of four species of tree. Indices of performance were survival, duration of feeding, prepupal weight, pupal duration and fecundity of females. On all tree species, performance was better on newly emerged foliage than on more mature foliage. Larvae reared on young foliage had greater survival, shorter feeding duration, and greater prepupal weights than did those which were reared on more mature foliage. Fecundity strongly correlated with prepupal weight. Differences in the performance indices also occured between the tree species. Factors influencing these differences, and their evolutionarily implications are discussed.

Introduction

The physical and chemical changes that take place in maturing tree foliage change the nutritional value for many species of herbivorous insects. (Feeny 1970, Schultz et al. 1982, Coley 1983). These changes in food are postulated to have influenced the evolution and development of many species of insects (Feeny 1970; Haukioja and Niemela 1977; Niemela and Haukioja 1982; Hough and Pimental 1978; Mattson 1980). Generally, young foliage is nutritionally superior to more mature foliage, as the water content (Scriber 1977), and the nitrogen content (Feeny 1970) are often higher in young foliage than in more mature leaves. Larvae feeding on young foliage may also develop into larger pupae, and more fecund females (Haukioja and Neuvonen 1985). Feeding on younger leaves may also allow immature insects to grow rapidly and so reach pupation more rapidly (Ayres and McClean 1987). This would minimize the exposure time of the feeding insects to predators and parasitoids (Price et al. 1980).

Polyphagous herbivorous insects such as the fall cankerworm, Alsophila pometaria (Harris), feed on a wide range of hosts, however, many polyphagous insects perform differently when fed foliage from different hosts (Beck and Reese 1976). Individual plants of the same species may vary in nutritional quality and quantity of secondary metabolites from site to site, year to year, individual to individual or even part to part. These secondary metabolites affect the growth and survival of insects which ingest them while feeding (Rice 1974; Coley

1983; Haukioja 1982; Feeny 1976). Polyphagous lepidopterous larvae reared on leaves of various tree species differ in survival and developmental rates (Werner 1979; Hough and Pimental 1978; Futuyma and Saks 1981).

This paper deals with the performance on four species of deciduous trees of fall cankerworm which hatch at bud burst or later than bud burst. The objective was to determine if, on any of the tree species there is an advantage to the fall cankerworm of hatching at bud burst. The length of the larval feeding life, weight at prepupation and the fecundity of the females were used as indices of performance. Performance is a component of fitness, and so differences in performance may be evidence for selection pressure on the fall cankerworm.

Methods and Materials

Two trees of each species were used in the experiment. The species are American elm, Ulmus americana L., scrub oak, Quercus macrocarpa Michx., a hybrid bog birch, Betula x sargentii Dugle and yellow willow, Salix lutea (Nutt.). The elm, oak and birch trees were located on the Fort Garry campus of the University of Manitoba in Winnipeg, and the willow trees were on the edge of a water dugout on the Glenlea Research Farm approximately 16 km south of the campus. Preliminary sampling of these trees indicated that they were all under a very low level of herbivore pressure. The hybrid bog birch trees were caged because they were involved in a defoliation intensity study (Chapter III, part ii of this thesis).

However, it was determined that the difference in defoliation intensity between the caged and uncaged trees was negligible.

Fall cankerworm eggs for this study were collected from Acer and Ulmus spp. in Winnipeg during the winter of 1985 - 1986 and 1986 - 1987. Eggs were kept outdoors until April 22 in 1986, and April 23 in 1987, which was approximately 21 days before the anticipated date of bud burst of the host plants; after which they were stored in the dark at 5 ° C. During storage, egg masses were kept in polyethylene bags and were misted with water every 2 days.

Egg masses were allocated randomly to one of four groups before they were removed from 5 ° C storage. Two groups were to hatch shortly after the bud burst of the host; one of these was to be fed excised leaves in the laboratory, while the other group was to be placed in cages on trees in the field. The trees used in the field were those from which the excised leaves came. The second two groups of egg masses were treated as above, but were to hatch 14 days after bud burst.

Laboratory study

Newly-hatched larvae were placed in groups of five in 2.5 x 8 cm clear plastic vials, and assigned a diet of foliage from one of the four tree species. Each day, larvae were monitored for survival and fresh excised leaves were provided. After 5 to 7 days, survivors from each tube were placed individually into 10 cm petri dishes with moistened filter paper and fresh foliage; monitoring and feeding took place daily as before (Fig. 1). Larvae in vials and dishes were kept at 17.5° C and 16:8 h L:D photoperiod (Fig. 2).

Before pupation, larvae enter a non-feeding prepupal stage; prepupae are shorter and fatter than feeding larvae. Prepupae were weighed to the nearest 0.1 mg and placed individually into petri dishes with moistened vermiculite. The petri dishes were placed into a dark container at 20° C. and were monitored weekly until adults began to emerge and then daily until emergence was complete.

To obtain estimates of fecundity, egg laying boxes were set up, each containing one newly emerged male and one newly emerged female. Boxes were of clear plastic, 9 x 9 x 23 cm and contained twigs; they were placed in an incubator at 17.5° C with 16:8 h L:D photoperiod. Egg laying boxes were examined daily until females died, then the eggs were counted and the females were dissected to count any eggs that were not laid.

Field Study

Egg masses in the early and late hatch field treatments were placed in the field at the same time as those in the corresponding laboratory study. Egg masses were initially placed into cloth egg hatch cages (Fig 3), because first instar larvae are small enough to escape through nylon mesh. Egg hatch cages were 30 cm diameter x 60 cm cylindrical sleeve cages of green cotton with a 15 x 30 cm. plastic window and a zipper in the side to allow for monitoring and transfer of larvae. The cages were placed over branches of the trees to be tested and two egg masses were placed in each. Approximately 7 days after hatching, surviving larvae were removed from egg hatch cages and placed into 20 cm diameter x 45 cm larval cages (Fig. 4). Larval cages were also sleeve cages that were mounted over

branches of the test trees, but these cages were of fine nylon mesh with plastic fasteners from Ziplock ™ bags sewn into the sides to allow for access and monitoring. All cages were supported by wire frames to keep them from collapsing.

For each of the four tree species, one egg hatch cage was placed on each of the two test trees. There were five larval cages on oak, elm, and willow test trees, while only one larval cage was used on birch. Five larvae were placed into each cage. Larvae were monitored every 48 hours until they died or reached prepupation. Following prepupation, the insects were removed to the laboratory and weighed; pupal survival and fecundity were estimated as above.

Effects of treatments on larval survival to prepupation were tested using χ^2 contingency tests from the Catmod procedure (SAS Institute 1985). Effects of treatments on prepupal weight, length of feeding life, egg production and the pupal duration were examined using analysis of variance followed where appropriate by contrasts or multiple range tests (REGWQ procedure, SAS Institute 1985). The relationship between the prepupal weights and fecundity of females were examined using regression techniques (SAS Institute 1985;). Except were otherwise indicated, statistical tests were considered significant at $\alpha = 0.05$.

Results

Egg masses were transferred from 5° C to 17.5° C approximately 14 days before the desired hatch dates. Eggs to hatch

at bud burst of the host trees were placed at 17.5 ° C on 6 May in 1986 and on 24 April in 1987. Transfers for the late hatch were made on 22 May in 1986 and on 5 May in 1987. The early treatment eggs began hatching on 15 May in 1986 and on 6 May in 1987. Eggs in the late hatch treatment commenced hatching on 7 June in 1986 and on 13 May in 1987.

With the exception of the birch, all the trees appeared to be in good condition in both years. The birch, which was caged for another experiment (see Chapter III, part ii) was healthy in 1986, but suffered severe drought stress in 1987. In 1987, excised birch leaves were relatively brittle and dry.

Larval Survival

Larval survival was generally lower when egg hatch was delayed, regardless of what type of foliage was consumed (Table 1). In the laboratory, the average survival of cankerworm larvae was 66% for early hatch and 12% for late hatch in 1986 and 61% for early hatch and 10% for late hatch for 1987. In the field experiments, the average survival of the larvae was 59% for the early hatch and 20% for the late hatch in 1986, and 76% for early hatch and 72% for late hatch in 1987. The trend for late hatching larvae to have poorer survival was apparent in all trials except for the 1987 field experiment for willow in which the late hatch group survived better than the early hatch group.

There were differences among the foliage treatments within the laboratory experiments in 1986 and 1987, (Table 1). With the

exception of birch in 1987, late hatching larvae survived better on birch and willow than they did on oak and elm. This is primarily due to the poor survival of the cankerworms reared on late season foliage of oak and elm.

Larvae reared in the field also exhibited differences in survival. In 1986, cankerworm larvae reared on willow survived significantly better than larvae on any other tree (Table 1). Survival in 1987 was significantly greater on birch than for those reared on elm.

Duration of Larval Feeding

In the laboratory in 1986 and in 1987, the duration of feeding was significantly shorter for larvae that hatched early than for those in the late hatch group (Table 2). Results were different for the experiments conducted in the field. In 1986, there was no significant difference, and larval feeding life was significantly longer when hatch was early than when hatch was late, in 1987.

The duration of larval feeding life differed among hatch groups reared on different tree species. In the laboratory in 1986, larvae reared on willow had a shorter feeding life than did those reared on oak or elm. In 1987, larvae reared on elm took longer to complete feeding than did those larvae reared on willow.

Prepupal Weights

In the laboratory in 1986 and 1987, the prepupae in the early hatch group weighed significantly more than those in the late hatch group. Results from the field experiments in 1986 revealed no significant differences. In the field in 1987, the trend was for weights to be significantly higher in the early hatch than the late hatch, however, there was a significant interaction because the mean weight on willow increased from early to late hatch (Table 3).

There were significant differences of mean prepupal weights among the foliar treatments. Fall cankerworms reared on oak have much lower prepupal weights than do those reared on the other foliage treatments, especially when the foliage is more mature. With the exception of birch in 1987, early hatching larvae on birch and willow had higher prepupal weight than did those fed oak and elm. Comparisons in the late hatch treatments are complimented by small numbers, but prepupal weights were always lowest for oak, and were highest for birch in the 1986 laboratory experiment and for willow in the 1987 field experiment.

Pupal Duration

In the laboratory in 1986, there were no significant differences in pupal duration, but treatment effects were significant in 1987. In 1987, pupal duration was significantly longer in pupae from the early hatch group than in the late hatch group (Table 4). In the field experiments in both years, pupal duration was generally longer in the early hatch group than the late hatch group.

In the laboratory in 1987, and in the field in 1986, there were significant differences in pupal duration among tree species. (Table 4). In the early hatch group in the laboratory in 1987, pupal duration for larvae reared on oak and willow was significantly longer than for those reared on birch; there was no significant differences among the treatments in the late hatch group. In the early hatch group from the 1986 field experiment, those fed on oak and willow had a, significantly longer pupal period than did those reared on elm, while in the late hatch group there was no difference in pupal duration among the treatments.

Fecundity

In 1986 in the laboratory and the field, there were no significant differences in the mean fecundity of females between hatch groups (Table 5). However, in the 1987 laboratory experiment on willow, and in the field experiments, there were significantly less eggs produced by adult females in the late hatch group (Table 5).

Results of mean fecundity among females reared on different foliage groups was mixed. Generally, when survival was great enough to produce egg laden females, those reared on more mature oak or elm foliage produced the fewest eggs.

Although the indices of performance of the cankerworm are individually useful, a summary measure of performance is desirable. Such a measure is the estimated number of eggs produced for each original hatched egg. Any number greater than 1 results in an

increasing population and any number less than 1 results in population decline.

The 1986 laboratory experiments exhibit differences in the number of eggs produced for each original hatched egg: from the early hatch group, 26 eggs/egg were produced, but in the late hatch there were only 0.8 eggs/egg produced. The 1987 laboratory experiments showed a similar trend: in the early hatch 37 eggs/egg were produced, while late hatch results produced 6 eggs/egg. All of the eggs produced from the late hatch in 1987 were from larvae reared on willow. Clearly, fall cankerworms will produce more eggs for subsequent generations if they feed on immature rather than mature foliage (Table 6).

Prepupal weight / Fecundity Relationship

The relationship of prepupal weight and fecundity of females from both early and late hatch groups from both laboratory and field experiments were combined for each year. In 1986 (Fig. 5) and in 1987 (Fig. 6), there were significant regressions between prepupal weights and fecundity of fall cankerworm females (1986: $F = 26.6$, d.f. = 1, 79, $P < 0.001$; 1987: $F = 208.5$, d.f. = 1, 247, $P < 0.001$).

Discussion

Although the methods were designed to synchronize egg hatch and bud burst in the early treatment, this synchronization may not have been the same as occurred in nature. Egg hatch was manipulated in the laboratory, based on previous experience of times

of bud burst and of hatching phenology, but, in order to avoid losing a treatment entirely, hatch before bud burst could not be risked. In nature, many early season feeders hatch slightly before the bud burst of the host and starve for a short time, and feed on the new foliage as soon as it is available (Schneider 1979, Wint 1983). In these experiments, larvae were presented leaves from trees which had already come into leaf. This may have affected the results. In 1986, larvae reared on oak in the field had much poorer survival in the early hatch than in 1987; this may indicate that early hatch larvae were better synchronized with oak bud burst in 1987 than they were in 1986. The elm and willow had similar results for both years and this may indicate that, in these species, defenses are less time dependent, or that the synchronization was similar for both years. While the insects reared on the birch had the greatest survival rate in 1986, survival was very low when hatch was early in 1987, and negligible when hatch was late. The severe water stress of the birch trees in 1987 resulted in small leaves which became tough, or dry and brittle, very quickly. These leaves seemed detrimental to A. pometaria larvae, and so the results for the birch in 1987are not considered representative of the normal response of larvae to healthy trees.

The low survival of larvae in some treatments has implications for the analysis and interpretation of other indices of performance. When survival is 0, the other indices cannot be analysed, yet clearly host quality is poorer when there are no survivors than when there are survivors which have low prepupal weight and fecundity.

In the field experiments, the difficulty of manipulating newly hatched larvae forced me to let the larvae remain in the egg hatching cages until they were large enough that they could not escape through the nylon mesh cages. Consequently, survival of larvae in the field was not estimated for the whole larval lifespan but only from second instar to pupation. Both in the laboratory and in the field many larvae died within the first few days after hatching; these larvae died in the egg hatch cages and only survivors of the egg hatch cages were used in the field experiments. The effects of this are especially evident in results from the field in 1987 where survival was larger in the field than in the laboratory in all treatments.

Feeding life, was lengthened when hatch was delayed in the laboratory but was shorter when hatch was delayed in the field experiments. In the field, later hatching larvae were exposed to higher temperatures than were those that hatched early; within the favorable range for the insect, higher temperature would accelerate development. Larvae in the laboratory were all reared at the same constant temperature.

Both in the field and in the laboratory, the performance of fall cankerworm was affected by the synchrony of egg hatch to bud burst. Larvae hatching close to the time of the bud burst of the host had greater survival, had greater prepupal weights and produced more eggs than did those which hatched 10 to 14 days later and fed on more mature foliage. Also, in the absence of temperature effects, more mature foliage extended the duration of the feeding period. In the field, late hatching larvae would probably have even have faster

development times if they did not have to eat a diet that slows their development.

The importance of prepupal weight is that it is directly related to fecundity (Figs. 5 and 6). Larvae hatching early feed for the shortest period and attain the highest weights. Therefore, it may be concluded that the early hatching larvae either can consume more of the resource or are better at converting the resource to produce the greatest number of eggs.

It is evident that the performance of fall cankerworm is impaired when the egg hatch is delayed. There may be a number of reasons for this. Moisture and nitrogen content as well as the build up of defensive chemicals may affect the performance of herbivorous insects. Young foliage is significantly higher in water content and nitrogen than the mature foliage. Moisture content and nitrogen content of tree leaves are positively correlated; decreased leaf moisture results in less available nitrogen for the feeding larvae (Mattson 1980). Low leaf nitrogen is also associated with greater leaf cellulose (Soo Hoo and Fraenkel 1966). Increased leaf cellulose results in tougher leaves causing the larvae to spend more time and energy on consuming the leaf tissue. As leaves mature, concentrations of phenolic compounds such as tannins increase, and these compounds have been associated with diminishing larval performance (Feeny 1970). Tannins are thought to cause a reduction in the digestibility of the available nitrogen that is assimilated by certain insects (Feeny 1976; Rhoades and Cates 1976). Tuomi et al. (1984) show that phenolic content and nitrogen content are inversely related in the mountain birch, Betula pubescens (Ehrh.) and this is

thought to affect the performance of the autumn moth, Epirrita autumnata (Bkh.) adversely. It is also thought that these chemicals are induced when the tree is under defoliation pressure (Haukioja and Hanhimaki 1985).

My studies used a bioassay approach which does not identify biochemical changes, but rather gives a measure of insect performance. Increasing leaf toughness is probably the chief factor preventing fall cankerworm larvae from performing well when they are reared on mature foliage. On oak, the growth rate of fall cankerworm larvae depends on consumption rate rather than the ability to convert biomass efficiently (Lawson et al. 1984). The negative affects of leaf toughness may be exacerbated by the decline in available nitrogen in mature foliage which would result in the larvae not assimilating enough protein. Leaf tannins form complexes with proteins in the gut (Feeny 1970) and this would further reduce nitrogen availability.

Even though the fall cankerworm is a polyphagous insect, results indicate that the foliage of some tree species is more suitable, when larval performance is used as a measure. Differences were observed for all indices tested. Survival was generally the greatest on willow and poorest on oak. Larvae reared on willow had the shortest feeding life and the greatest prepupal weights. Fecundity was found to be poorest on oak, which also had the lower prepupal weights.

Survival of cankerworms reared on oak and elm leaves in the laboratory and the field were similar to that of larvae reared on the other foliage types when hatch was early; when larvae were reared

on late foliage of oak or elm survival declined sharply. Survival of larvae reared on birch and willow did not decline from early to late hatch as much as it did for cankerworm reared on oak and elm. First instar larvae die after four days if deprived of food (Schneider 1979). Since the mean length of life of those that did not survive in these studies was approximately four days it seems likely that larvae were not able to consume the foliage and starved.

The duration of feeding life is generally shorter for cankerworms reared on willow compared to those reared on oak or elm. This is important in species success, especially in spring feeders, in that completion of feeding in the shortest period of time allows for minimal exposure time to predators and parasitoids. A longer feeding time on oak and elm compared to willow suggests that the larvae are being exposed to older tougher tissue that may be higher in chemical compounds that are defensive in nature.

Those fall cankerworm larvae reared on birch and willow generally had greater prepupal weights than those reared on oak and elm (Table 3). There was a relationship between prepupal weights and fecundity (Figs. 5 & 6). Prepupal or pupal weights of females are considered a reliable index of reproductive capacity (Hough and Pimental 1978, Wallner and Walton 1979).

The fall cankerworm is polyphagous and clearly can succeed in producing offspring on any of the tree species tested. But why does fall cankerworm perform better on the willow and birch when it is found primarily on oak and elm trees in southern Manitoba? It may be that over time the fall cankerworm has had to adapt owing to a changing environment.

The aptery of the fall cankerworm suggests that it evolved in a cold environment. Walking allows females to be active at low temperatures. Male flight of the winter moth is inhibited by low temperatures (Alma 1970), however, male behavior enables mating to take place even when temperatures are low (Holliday 1985) and I believe this to be the case for the cankerworm. Thus, I suggest that the fall cankerworm evolved in tundra regions, possibly at times of glaciation.

During times of glaciation the most common woody plants of the tundra were the willows and the scrub birches (Ritchie 1984). Epirrita autumnata is a geometrid similar to the fall cankerworm and is found in the northern and mountainous regions of Norway and Finland, far beyond the Arctic circle (Haukioja et al. 1988) where it eats Betula pubescens Ehrh. which thrives in tundra habitat. Betula nana L. along with some willows and sedges were the most dominant species following the recession of the ice cap in England (Pennington 1969), and dwarf willow and birch trees are the dominant woody vegetation of moderately drained land north of the treeline in the Northwest Territories of Canada (Ritchie 1984). Thus, if fall cankerworm occupied treed tundra during glaciation, it would be likely feeding on birches and willows.

The absence of wings allowed for greater egg production and was an advantage under cold conditions. However, when the glaciers and the tundra environment receded northward, fall cankerworm would be unable to follow because of its limited dispersal ability. With the succession of forests, wingless females would begin ovipositing in large trees, because adult females orientate themselves

to their hosts, at least in part, by visual cues (Chapter III, part iii of this thesis). Fall cankerworm would become trapped into continuing evolution on these larger trees, as its original hosts receded northward.

Table 1. Effect of tree species and date of hatch on survival of
Alsophila pometaria larvae.

EXPERIMENT		DATA				ANALYSIS		
	TREE SPP.	EARLY HATCH		LATE HATCH		SOURCE	d.f.	χ^2
		N	SURVIVAL (%)	N	SURVIVAL (%)			
LABORATORY 1986	BIRCH	152	73	317	28	HATCH	1	422**
	WILLOW	81	69	172	17	TREE	3	41**
	OAK	74	57	216	2	INTER-		
	ELM	123	66	167	2	ACTION	3	10 n.s.
LABORATORY 1987	BIRCH	218	20	153	1	HATCH	1	944***
	WILLOW	326	77	141	28	TREE	3	384***
	OAK	409	75	143	1	INTER-		
	ELM	413	70	117	9	ACTION	3	250***
FIELD 1986	BIRCH	10	55	10	40	HATCH	1	35**
	WILLOW	50	98	50	32	TREE	3	34**
	OAK	50	24	50	4	INTER-		
	ELM	50	60	50	4	ACTION	3	11**
FIELD 1987	BIRCH	10	90	10	80	HATCH	1	36**
	WILLOW	50	52	50	91	TREE	3	10 n.s.
	OAK	50	90	50	54	INTER-		
	ELM	50	72	50	64	ACTION	3	77**

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; n.s = not significant

Table 2. Effect of tree species and hatch date on duration of feeding life (days) of *Alsophila pometaria* larvae.

EXPERIMENT		DATA				ANALYSIS		
	TREE SPP.	EARLY HATCH		LATE HATCH		SOURCE	d.f.	F
		N	MEAN ±SE	N	MEAN ±SE			
LABORATORY								
1986	BIRCH	81	24.4±0.4	89	32.2±0.5	HATCH	1	246***
	WILLOW	55	23.2±0.6	29	29.8±0.2	TREE	3	7 *
	OAK	42	23.8±0.6	3	36.3±0.6	INTER-		
	ELM	81	26.0±0.5	2	31.1±0.1	ACTION	3	2 n.s.
LABORATORY								
1987	BIRCH	43	25.8±0.9			HATCH	1	876***
	WILLOW	251	21.9±0.2	39	32.3±0.9	TREE	3	60**
	OAK	306	20.4±0.1			INTER-		
	ELM	288	20.4±0.1	10	36.1±0.7	ACTION	1	30**
FIELD								
1986	BIRCH	5	28.0±0.5	4	25.8±0.8	HATCH	1	1 n.s.
	WILLOW	24	26.5±0.6	3	26.0±2.0	TREE	3	8 *
	OAK	4	22.5±0.5			INTER-		
	ELM	8	31.4±1.9			ACTION	1	1 n.s.
FIELD								
1987	BIRCH	10	35.8±0.4	9	31.6±2.0	HATCH	1	32**
	WILLOW	26	32.0±0.4	45	29.5±0.5	TREE	3	13**
	OAK	40	34.8±0.3	27	32.7±1.0	INTER-		
	ELM	36	35.3±0.2	32	33.8±1.2	ACTION	3	1 n.s.

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; n.s = not significant

Table 3. Effect of tree species and date of hatch on the mean prepupal weight (±se) (mg) of *Alsophila pometaria*.

EXPERIMENT	TREE SPP.	DATA EARLY HATCH N	MEAN ±SE	LATE HATCH N	MEAN ±SE	ANALYSIS SOURCE	d.f.	F
LABORATORY 1986	BIRCH	81	56.9±1.7	89	39.6±1.1	HATCH	1	58**
	WILLOW	55	50.5±2.2	29	24.8±1.5	TREE	3	31**
	OAK	42	33.4±2.3	3	18.5±3.5	INTER-		
	ELM	81	49.4±2.1	2	31.0±6.0	ACTION	3	1n.s.
LABORATORY 1987	BIRCH	43	36.4±1.7			HATCH	1	66**
	WILLOW	251	63.9±1.1	29	38.9±1.9	TREE	3	59**
	OAK	306	53.0±0.9			INTER-		
	ELM	288	52.2±0.7	4	31.6±2.9	ACTION	1	1 n.s.
FIELD 1986	BIRCH	5	45.6±10.6	4	49.0±6.7	HATCH	1	2 n.s.
	WILLOW	24	36.1±3.3	3	33.5±2.0	TREE	3	1 n.s.
	OAK	4	30.4±4.4			INTER-		
	ELM	8	30.4±3.3			ACTION	1	1 n.s.
FIELD 1987	BIRCH	10	35.9±1.7	9	30.1±1.2	HATCH	1	19**
	WILLOW	26	48.5±2.9	45	50.2±2.2	TREE	3	43**
	OAK	40	40.4±1.5	27	23.6±1.3	INTER-		
	ELM	36	39.4±1.7	32	25.8±1.0	ACTION	3	10**

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; n.s = not significant

Table 4. Effect of tree species and date of hatch on the pupal duration (days) of *Alsophila pometaria.*

EXPERIMENT	TREE SPP.	EARLY HATCH		LATE HATCH		SOURCE	d.f.	F
		N	MEAN ±SE	N	MEAN ±SE			
LABORATORY 1986	BIRCH	81	122±3	89	123±4	HATCH	1	1 n.s.
	WILLOW	55	122±3	29	139±3	TREE	3	2 n.s.
	OAK	42	131±4	3	122±20	INTER-		
	ELM	81	123±3	2	112±0	ACTION	3	0.1 n.s.
LABORATORY 1987	BIRCH	24	125±1			HATCH	1	5 *
	WILLOW	220	132±1	29	126±2	TREE	3	6 *
	OAK	265	134±1			INTER-		
	ELM	215	130±2	4	127±1	ACTION	1	0.1 n.s.
FIELD 1986	BIRCH	5	142±10	4	129±17	HATCH	1	7 *
	WILLOW	24	155±4	3	125±10	TREE	3	4 *
	OAK	4	156±7			INTER-		
	ELM	8	127±8			ACTION	1	1 n.s.
FIELD 1987	BIRCH	10	157±7	9	139±9	HATCH	1	4 n.s.
	WILLOW	26	147±5	45	141±3	TREE	3	2 n.s.
	OAK	40	153±3	27	144±5	INTER-		
	ELM	36	141±4	32	143±4	ACTION	3	1 n.s.

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; n.s = not significant

Table 5. Effect of tree species and date of hatch on the fecundity of *Alsophila pometaria* females (Number of eggs per female).

EXPERIMENT	TREE SPP.	EARLY HATCH N	MEAN ±SE	LATE HATCH N	MEAN ±SE	SOURCE	d.f.	F
			DATA				ANALYSIS	
LABORATORY 1986	BIRCH	35	110±14	7	83±21	HATCH	1	2 n.s.
	WILLOW	20	95±17	1	42	TREE	3	2 n.s.
	OAK	12	76±16			INTER-		
	ELM	29	123±14	1	78	ACTION	2	0.1 n.s.
LABORATORY 1987	BIRCH	10	94±12			HATCH	1	17 **
	WILLOW	64	192±8	29	126±2	TREE	3	21 **
	OAK	82	135±6			INTER-		
	ELM	78	147±5			ACTION	0	
FIELD 1986	BIRCH	1	151	1	141	HATCH	1	2 n.s.
	WILLOW					TREE	1	4 n.s.
	OAK					INTER-		
	ELM	2	112±10			ACTION	0	
FIELD 1987	BIRCH	1	131	4	94±25	HATCH	1	11**
	WILLOW	11	132±12	17	142±8	TREE	3	5 **
	OAK	15	146±9	7	54±5	INTER-		
	ELM	12	122±10	8	87±15	ACTION	3	8 **

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; n.s = not significant

Table 6. Effect of tree species and date of hatch on egg production of *Alsophila pometaria*. Numbers represent the number of eggs per egg that hatched.

EXPERIMENT	TREE SPECIES	N	EARLY HATCH	N	LATE HATCH
LABORATORY 1986	BIRCH	152	34.7	317	1.8
	WILLOW	81	23.5	172	0.2
	OAK	74	12.3	216	0
	ELM	123	29.0	167	0.5
TOTAL EGGS PRODUCED			11655		689
LABORATORY 1987	BIRCH	218	4.3	153	0
	WILLOW	326	37.7	141	25.9
	OAK	409	27.1	143	0
	ELM	413	27.8	117	0
TOTAL EGGS PRODUCED			35792		3652

Fig. 1. *Alsophila pometaria* larva in 10 cm petri dish with fresh
foliage
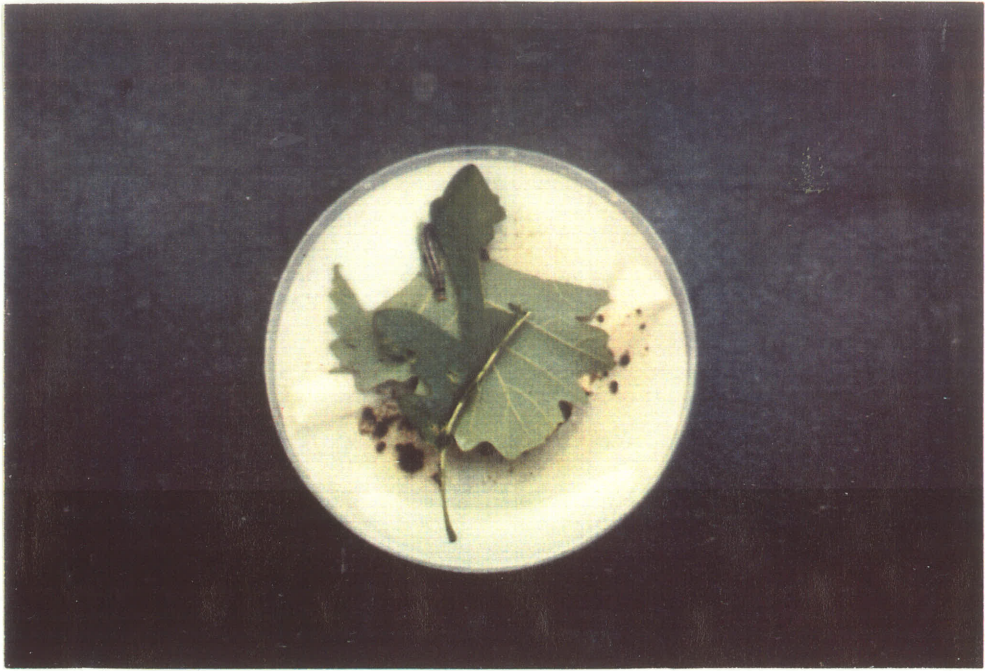
Fig. 2.   Ten cm petri dishes in incubator.

Fig. 3.   Cloth egg hatch cage over branch terminal of test tree.

Fig. 4. Nylon mesh sleeve cage

Fig. 5.   Relationship of prepupal weight and and fecundity of female
Alsophila pometaria . 1986: Fecundity = 2.1 prepupal weight +
8.4.   The dashed lines represent the 95% confidence intervals.

EGGS PRODUCED vs PREPUPAL WEIGHT
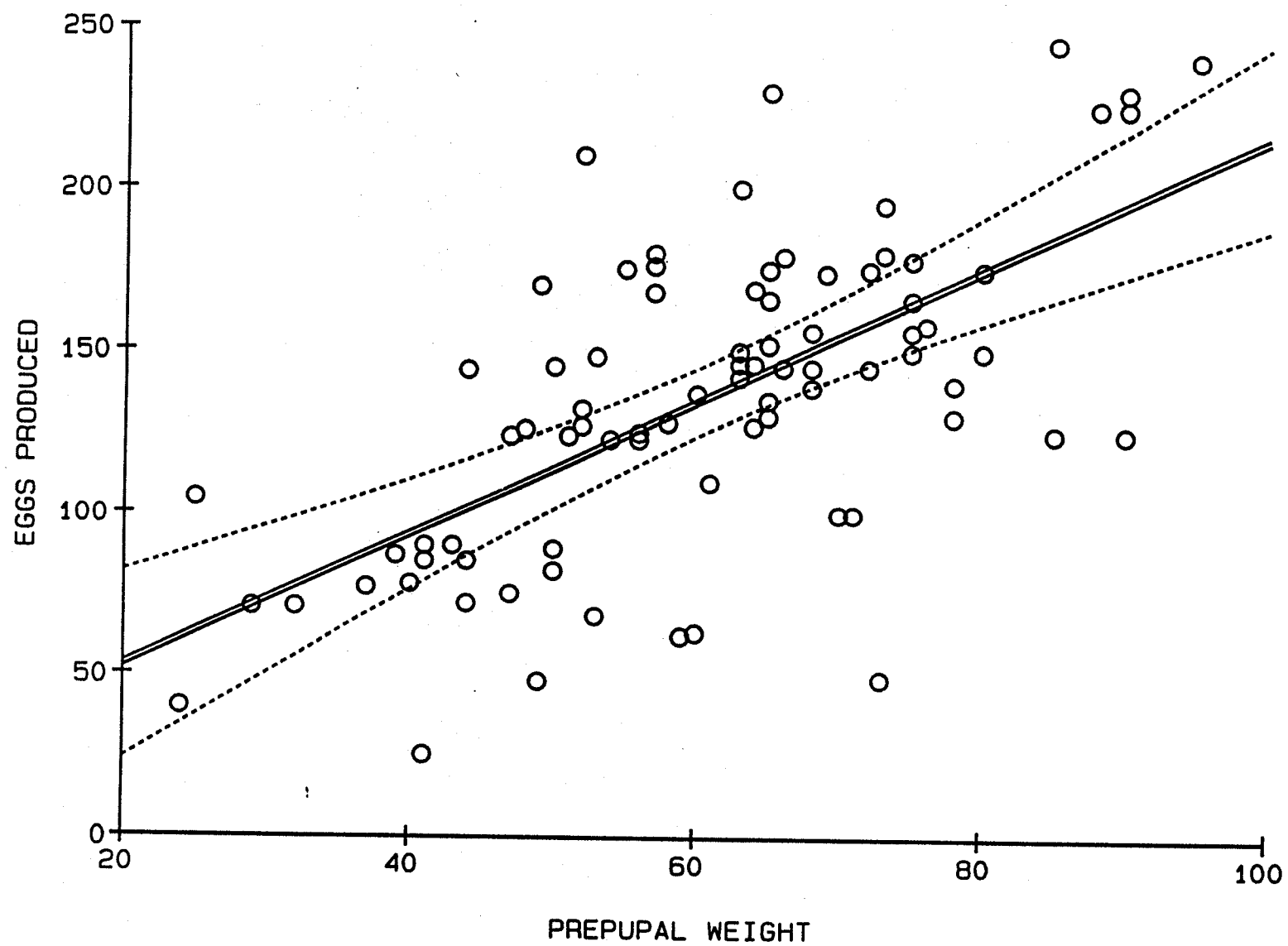
Fig. 6. Relationship of prepupal weight and fecundity of female
Alsophila pometaria. 1987: Fecundity = 2.6 prepupal weight
- 10.5. The dashed lines represent the 95% confidence
intervals.
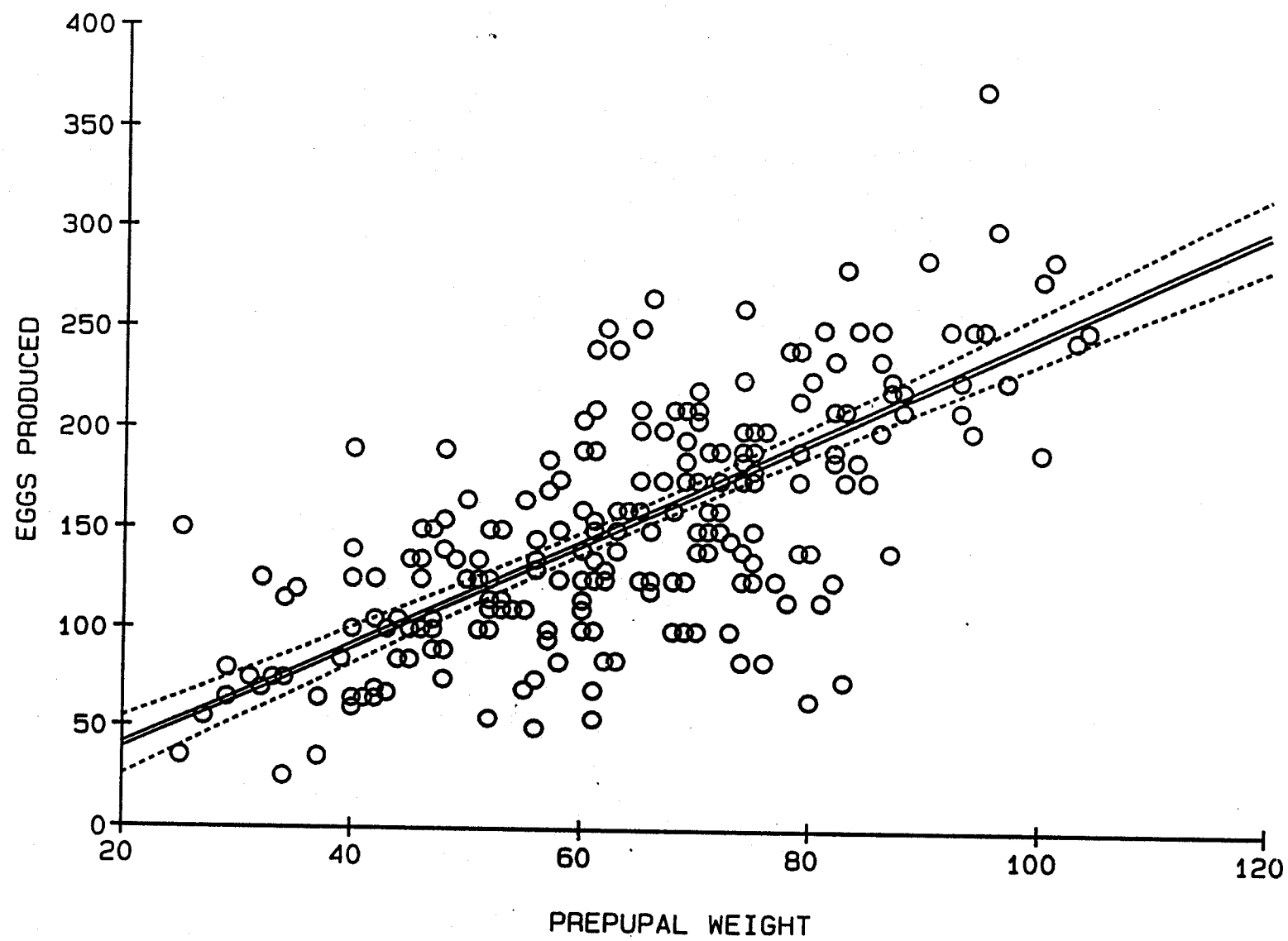
Chapter III

part ii

Changes in quality of hybrid bog birch, Betula x sargentii, defoliated by fall cankerworm, Alsophila pometaria

(Lepidoptera: Geometridae)

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Changes in quality of hybrid bog birch, <u>Betula x sargentii</u> defoliated by fall cankerworm, <u>Alsophila pometaria</u> (Lepidoptera: Geometridae).

Abstract

In 1986 and 1987, caged <u>Betula x sargentii</u> (Dugle 1966) were exposed to different levels of defoliation intensity by manipulating the densities of fall cankerworm larvae, <u>Alsophila pometaria</u> in the cages. The effect of these treatments on the quality of the foliage as food for fall cankerworm larvae was examined by determining insect performance when larvae were reared on the foliage. Indices of performance were larval survival, duration of larval feeding, prepupal weight and female fecundity. Performance was measured for larvae reared in sleeve cages on the trees, and for larvae reared on excised leaves in the laboratory. In both years, performance was measured for larvae that hatched at about the time of bud burst, and for larvae that hatched about two weeks after bud burst.

Cankerworms reared on young birch foliage performed better than those reared on mature foliage. In the laboratory experiment in 1986, increased defoliation was assoaciated with reduced performance of both early and late hatching fall cankerworms; this trend was also evident for late hatching larvae in the 1987 field experiment. Results of the field experiment in 1986, and the laboratory experiment in 1987, did not show significant effects of defoliation intensity. Both abiotic factors such as water stress and biotic factors such as host plant defences appears to affect insect

performance.

Introduction

Tree feeding insect herbivores may completely destroy their food resources. Repeated episodes of complete defoliation cause tree mortality and affect crown structure (Campbell and Valentine 1972), stand composition (Campbell and Sloan 1977) and forest growth and timber production (Mattson and Addy 1975). The chemical composition of leaves affects the quality of the tree foliage as food for insects and so can influence the intensity of defoliation to which trees are exposed. Drought (White 1974), nutrient availability (Mattson 1980), tree species (Werner 1979) and phenology (Feeny 1970) all affect leaf chemistry and so influence the survival, development rate and fecundity of the insect herbivore.

Trees may also produce secondary compounds in response to attack by insect herbivores. Such compounds may limit herbivore performance and so constitute induced defences against defoliating insects. Inducible defences of trees (Fowler and Lawton 1985) are defences which increase at or near the feeding site soon after the herbivore has fed. Claims have also been made that chemical changes can occur in adjacent, unattacked trees as a result of intertree communication (Baldwin and Schultz 1983). Rhoades (1983) suggested that this would result in detrimental effects on insect populations.

Experiments have been performed to investigate whether there are induced defences in Betula species in response to defoliation by lepidopterous larvae. Larvae of Apocheima pilosaria (D&S) feeding on

damaged _Betula pubescens_ (Ehrh.) exhibit lower larval weight and higher mortality than those feeding on undamaged leaves from undamaged controls (Fowler and MacGarvin 1986). _Coleophora serratella_ (L.) larvae reared on damaged _Betula pendula_ (Roth), take longer to develop than those reared on undamaged trees (Bergelson et al. 1987). Wallner and Walton (1979) found that, compared to performance on undamaged trees, prepupal weights, are lower, developmental time is longer and survival is reduced when larvae of _Lymantria dispar_ (L.) are fed on damaged _Betula populifolia_ (Marsh); these differences are greater in the season following that in which damaged occured. Werner (1979) found that _Rheumaptera hastata_ has greater survival and feeding intensity and produces more eggs when reared on _Betula papyifera_ that had not been previously defoliated, compared to those which were reared on foliage from trees that had been defoliated in previous years. Haukioja and Hanhimaki (1985) also demonstrated that damaged _Betula pubescens_ significantly retards growth, reduces prepupal weights and delays completion of larval development of _Epirrita autumnata_ L.These results suggest that insect feeding on many species of birch induces responses that affect the value of the host and thus influence the pest population.

The purpose of this study was to determine how the intensity of insect defoliation on a dwarf birch species affects the performance of fall cankerworm, _Alsophila pometaria_ (Harris).

Methods and Materials

Fall cankerworm, *Alsophila pometaria* (Harris) eggs used for this study were collected from *Acer negundo* L. and *Ulmus americana* L. in Winnipeg during the winter of 1985 - 1986 and 1986 - 1987. Eggs were kept outside until approximately 21 days before the anticipated date of bud burst of the host plants, after which they were placed in a cold room at 5° C. In the cold room, egg masses were kept in polyethylene bags and misted with water every two days until they were to be used.

In 1986 and 1987, experiments were performed in the laboratory and at The Plant Science Field Laboratory at "The Point" on the Fort Garry campus of the University of Manitoba. At The Point, a row of eight birch trees was enclosed in a 3 m x 3 m x 6 m cage (Fig. 7). The trees were a hybrid bog birch, *Betula x sargentii* Dugle. These trees are a dwarf variety similar to many other mountain birch species found in northern tundra environments and were transplanted from the region of Churchill, Manitoba (L. Lenz, personal communication). Aspenite sheets were used to partition the cage into six compartments, so that two replicates of three treatments could be established. Because of the difficulties in separating the trees, two compartments contained two trees each and the other four compartments contained one tree each. The cage was erected over the trees when the trees had reached approximately 50% bud burst (8 May in 1986 and 12 May in 1987).

To establish different intensities of defoliation, different numbers of egg masses of fall cankerworm were placed in each

compartment of the cage shortly after it was erected. There were two replicates of 'Low', 'Medium', and 'High' defoliation intensity with 0, 35, and 70 egg masses respectively. In 1986, low, medium and high intensity treatments were assigned randomly; assignments were the same in 1986 and 1987 (Fig. 8). Approximately 1 week after the eggs hatched, cankerworm densities in each compartment were estimated by sampling larvae on five 30 cm twigs from each of the upper, middle and lower portions of the canopy . Larvae were then culled from compartments so that the two 'High' and two 'Medium' compartments had similar densities, and thus defoliation intensities. Densities were 0.19 and 0.15 larvae / cm of twig for medium pressure in 1986 and 1987 respectively, and 0.30 and 0.25 larvae / cm of twig for high density in 1986 and 1987 respectively.

Laboratory Study

In both years, performance of fall cankerworm was estimated for larvae that hatched at about the same time as the bud burst of the host and the experiment was repeated with larvae that hatched approximately 2 weeks later. Newly hatched larvae were placed in groups of five in 2.5 cm x 8 cm cylindrical clear plastic tubes and fed excised leaves from one of the compartments. The first tube was assigned leaves from the first 'Low' compartment, the second from the first 'Medium' compartment, and the third tube received leaves from the first 'High' compartment. This was repeated for the the second set of compartments, after which the process was repeated until all of the tubes were assigned a diet. Larvae in the tubes were then placed in incubators at 17.5° C and a photoperiod of 16:8 h L:D.

Each day, the larvae were monitored for survival and fed fresh excised leaves. After 5 - 7 days, larvae from the tubes were placed individually into 10 cm petri dishes with moistened filter paper and fresh foliage (Fig. 1). Daily monitoring and feeding took place as before.

Before pupation, larvae cease feeding and enter a prepupal phase; prepupae are shorter and fatter and less mobile than feeding larvae. Prepupae were weighed and placed individually in 10 cm petri dishes with moistened vermiculite. These dishes were then placed in a dark container at 20° C, and monitored weekly until adults began to emerge, and then daily until emergence was complete. To estimate fecundity, one newly emerged male and one newly emerged female were placed into a 25 x 10 x 10 cm clear plastic box containing twigs for oviposition. Boxes were placed in incubators at 17.5° C at 16:8 h L:D. After the females had died, eggs which had been laid were counted, and the females were dissected and unlaid eggs counted.

Field Study

In the field study, larvae were reared on growing foliage in sleeve cages, and performance was measured for larvae hatching at bud burst and again for larvae hatching about 2 weeks after bud burst. Fall cankerworm larvae for the field study were hatched from eggs placed in egg hatch cages within each compartment of the 3 x 3 x 6 m cage on 7 and 22 May in 1986 and on 10 and 25 May in 1987 for the early and late hatchings respectively. Two egg masses, each of about 150 eggs, were placed into a 50 cm (long) x 30 cm (diameter)

egg hatch cage placed over a branch terminal (Fig. 3). These cages were green cotton with a 15 cm x 30 cm clear plastic window and a zipper to allow entry. Approximately 7 days after hatching, larvae were transfered to 50 cm (long) x 20 cm (diameter) nylon mesh (10 mesh / cm) sleeve cages (Fig. 8). There were two of these cages mounted over branches in each compartment of the field cage. Five larvae, taken from the egg hatch cage in the same compartment, were introduced into each mesh sleeve cage. Larvae in these sleeve cages were monitored every second day until they died or became prepupae. Prepupae were removed from the cages, weighed, and placed in 10 cm petri dishes containing moistened vermiculite. Duration of the pupal period and fecundity of the females was estimated in the laboratory as previously described.

Effects of treatments and hatch date on the duration of feeding, prepupal weights and fecundity were examined by analysis of variance (Proc GLM, SAS Institute 1985). Insect survival was subjected to chi-square analysis (Sokal and Rolf 1981). The relationship between prepupal weight and egg numbers was analysed by regression.

Results

Larval Survival

Except in the early hatch group in 1986, survival was much lower in the laboratory experiments than in the field experiments (Table 1). Survival in the laboratory was much better in 1986 than in 1987. In the laboratory in 1986 and 1987, and in the field in 1987, larvae which hatched at the same time as bud burst had significantly

higher survival than those which hatched later (Table 7). Although a similar trend is evident in the 1986 field experiment, it was not significant.

Differences in survival among defoliation intensity treatments was significant only in 1986 in the laboratory (Table 7). In 1986 in the laboratory, larval survival decreased as defoliation intensity increased in both the early and late hatches; there was no significant interaction between time of hatch and defoliation intensity.

Late season foliage affected the survival of the larvae in the laboratory quickly. Of the larvae that died from the delayed hatch groups, 90% died in less than 5 days after hatching in 1986 and 98% died in less than 4 days in 1987. Significantly more larvae died within 5 days of hatch from the late hatch group than from the early hatch group in both years (1986: $\chi^2 = 128.5$; df=1; P< 0.001; 1987; $\chi^2 = 166.3$; df=1; P< 0.001).

Duration of Larval Feeding

In the 1986 laboratory experiment, the feeding period was significantly shorter in the early hatch group than when hatch was delayed (F= 208.5; df= 1,4; P< 0.01) (Table 8). No differences in the length of feeding period were observed between early and late hatch groups in either year's field experiments (1986: F= 2.8; df= 1,4; 1987: F= 01.7; df=1,4).

Although there was a trend for larval feeding period to increase as the defoliation intensity increased (Table 8), there was no significant difference in either years' laboratory or field experiments (Lab. 1986: F= 1.1; df= 2,3; Lab. 1987: F= 2.2; df= 2,3; Field 1986: F=

2.8; df= 2,3; Field 1987: F= 1.1; df= 2,3). However, in both early and late hatch groups of the 1986 laboratory study, fall cankerworm reared on birch leaves under low defoliation intensity had shorter feeding periods than did those that were reared on foliage from highly defoliated trees (Early: F= 5.5; df= 2,146; P< 0.01; Late: F= 5.4; df= 2,166; P< 0.01).

Prepupal Weights

In 1986 in the laboratory, prepupae from the early hatch were significantly heavier than were their counterparts from the late hatch (F= 39.1; df= 1,4; P< 0.001) (Table 9). In both years', prepupal weight in the field was not significantly affected by the time of hatch (1986: F= 0.24; df= 1,4; 1987: F= 0.7; df= 1,4).

In 1986 in the laboratory, prepupal weight was significantly affected by defoliation intensity (F= 19.4; df= 2,3; P< 0.05); as the defoliation intensity increased, prepupal weight decreased (F= 5.4; df= 1,3; P< 0.05) (Table 9). In the laboratory in 1987, and in both years' field experiments, prepupal weight was not significantly affected by defoliation intensity (Lab 1987: F= 0.6; df= 2,3; Field 1986: F= 0.02; df= 2,3; Field 1987: F= 1.3, df= 2,3). There was no significant interaction between the hatch and defoliation intensity in any of the experiments (Lab 1986: F= 0.2; df= 2,3; Field 1986: F=0.02; df= 2,3; Field 1987: F= 2.1; df=2,3).

Pupal Duration

The mean pupal duration showed little difference between hatch groups or among defoliation treatments (Table 10). Generally, the pupal duration was greater for those reared in the field than for those reared in the laboratory (1986: F= 12.9; df= 1,131; P<0.001; 1987: F= 54.8; df= 1,137; P< 0.001). No difference in pupal duration was observed in the 1986 field experiment, however, in the 1987 field experiment, those in the early group were pupae for a significantly longer time than did those in the late hatch group (F= 6.1; df= 1,48; P< 0.05). The increase in defoliation intensity did not affect the pupal duration in either years laboratory or field experiments.

Fecundity

Little difference was found between the mean number of eggs produced from females previously reared on any of the foliage groups, or between hatch groups for laboratory or field experiments (Table 11). No significant difference was found between the early or late hatch groups in the laboratory in 1986 (F= 1.5; df=1,71), the field in 1986 (F= 0.55; df= 1,3) or the field group in 1987 (F= 0.01, df= 1,8).

While the mean egg production was not significantly different, there was a trend for eggs/egg hatched to decline from those produced on low defoliation intensity foliage to those reared on highly defoliated trees, as well as decline from the early to the late hatch (Table 12).

Prepupal weight - Fecundity Relationship

The relationship between prepupal weights and fecundity of emerging fall cankerworm females was estimated only from the laboratory results, because there were insufficient emerging females from the field experiments. In both years the results were positive and significant (1986: $F= 63.8$; $df= 1,49$; $P< 0.01$; 1987: $F= 16.2$; $df= 1,30$; $P< 0.01$) (Figs. 9 and 10).

Discussion

There are a number of possible artifactual reasons for differences among the four series of experiments. In the laboratory, these include the effect of drought, and the relative phenology of the insects and the test trees in 1986 and 1987. In the field, these include the aforementioned as well as an improved technique, using more eggs in 1987.

These birch trees are of a dwarf variety which is found naturally in moist tundra environments. The birch trees tested were exposed to drought-like conditions over the course of the two years. In 1987, leaves at the time of bud burst were fewer than in 1986, and were small and became tough and brittle quickly. These tougher and more brittle leaves seemed detrimental to the fall cankerworm. Trees under moisture stress have been shown to have deleterious effects on lepidopteran larvae which feed on them (Watt 1986). However, White (1974) states that tree foliage can become a richer

source of nitrogen when the trees are stressed by factors such as drought. In my experiments, it is very probable that the effect of drought on the birch trees had a negative impact on the fall cankerworm.

The relative phenology of the insects and the trees was somewhat different between the years. In 1987, spring was very warm and the trees flushed earlier than the emergence of the cankerworms. Generally, insects like the fall cankerworm hatch at about the time of bud burst. In the field in 1987, by starting with more eggs, I was able to obtain more surviving larvae, and therefore, more insects to evaluate throughout the experiment.

Effect of phenology and defoliation intensity

The results from this study indicate that the maintenance of phenology is an important factor for the success of fall cankerworm. Larvae hatching at about the time of bud burst have greater survival than do those hatching later. This decline in survival is likely due to a decline in available foliar nitrogen and water (Scriber 1977, Scriber and Feeny 1979), as well as increases in leaf toughness (Feeny 1970) and secondary metabolites in birch (Tuomi et al. 1984; Haukioja et al. 1985) as the foliage matures. Fall cankerworm is an early season feeder with high consumption rates of food, but has a relatively low efficiency of food conversion (Lawson et al. 1984). Thus, as birch foliage matures, it likely becomes less succulent, and late hatching larvae may not be able to consume enough foliage to satisfy their needs.

Many of the larvae in the laboratory experiments died shortly after hatch; this may indicate that the larvae starved because of an inability to consume enough foliage. Schneider (1979) indicated that fall cankerworm larvae could survive for 3 to 4 days when starved, and Cuming (1961) stated that newly hatched winter moth could survive for up to 5 days without a source of food. Wint (1983) demonstrated that the duration of survival of first instar winter moth larvae declined with an increase in temperature. Wint showed that first instar larvae would last only 3 days at 20° C. The cankerworms were incubated at 17.5° C, and therefore, death after 4 to 5 days would parallel that found for winter moth. Laboratory reared cankerworms were always in contact with food, therefore, I conclude that they either found the food unpalatable or they were unable to consume enough to sustain themselves.

Laboratory studies show differences in larval survival: survival declined from early to late hatch in 1986; survival was similar in the late hatch in 1986 and the early hatch in 1987; survival was lower from the early to the late hatch in 1987. Also, the effect of defoliation intensity on survival was significant only in the 1986 laboratory study. I suggest two reasons for this. Firstly, the birch may be exhibiting an induced defence mechanism to the defoliation intensity, and there is a continued resistance in the years after defoliation as described by Haukioja (1982). Phenology (Holliday 1985) and the amount of defoliation (Haukioja et al. 1985) have previously been implicated as evidence for low survival of other geometrids. Secondly, water stressed trees are likely to produce fewer and tougher leaves. Leaf water content is important to larval

growth (Scriber and Feeny 1979), and damaging water stressed trees likely causes the leaves to expel more water causing the leaves to become tougher more quickly.

Results of survival studies in the field did not parallel those found in the laboratory. This is likely partially due to an artifact of the methodology. Those larvae placed in the mesh sleeve cages were already survivors of the egg hatch cages, therefore the effects were not as obvious.

Obviously, performance could only be measured for those that survived. Performance, based on the indices mentioned above, was significantly affected by hatching time and defoliation intensity only in the 1986 laboratory study. In this experiment, larval feeding period was shorter and prepupal weight was greater in the early hatch than in the late hatch. Prepupal weight was also greater for larvae reared on foliage under low defoliation intensity, than for those on intensely defoliated foliage. These results are also evidence for induced defence mechanisms occuring in the birch trees. The fact that the prepupal weights in the 1986 late hatch are similar to those in the 1987 early hatch coupled with the survival results, may be an indication that long term defences are at work. Other geometrid larvae that encounter foliage from intensely, or previously defoliated birch trees perform poorly compared to those reared on trees not under defoliation pressure (Haukioja and Niemela 1977; Haukioja et al. 1985; Fowler and MacGarvin 1986).

While the field studies show no significant differences in performance, they do show a continual decline over the course of the study, and there is a trend for prepupal weights to decline as

defoliation intensity increases (1987 early and late). This may be not only an indication of induced defence, but of drought stress as well. Those larvae that survive must feed on tough foliage. Therefore, their consumption is likely limited compared to larvae feeding on suitable foliage.

The duration of feeding was similar in the early hatch in the laboratory in both years. Larvae in the 1987 field experiments had much longer feeding period. Those in the laboratory were given fresh foliage daily and it was placed on moistened filter paper. This additional moisture coupled with a consistent temperature may have helped the larvae to consume their necessary compliment of food in a shorter time than did those that fed directly on the drought stressed trees.

Egg production is also greatly affected by hatching and defoliation intensity. The numbers of eggs / egg hatched from the low defoliation intensity were 3 times that of high defoliation intensity in the laboratory in the early hatch. In the 1986 late hatch group, all values were much lower, but there is little difference between the defoliation intensities. Eggs / egg hatched from the 1987 early hatch are only slightly greater than those in the 1986 late hatch. This also seems to indicate the presence of induced defences. This evidence might also support theories of long term defences. However, I believe that water stress was a limiting factor in 1987. Egg production from the field was difficult to assess, as the initial number of eggs hatched is not known and since the numbers of observations are low.

Intertree Communication

Intertree communication has been postulated where induced chemical changes occur in undamaged trees when defoliation occurs in adjacent trees; the communication mechanism may be airborne chemicals released by the damaged trees (Baldwin and Schultz 1983; Rhoades 1985; Haukioja et al. 1985). This idea certainly 'captures the imagination' (Fowler and Lawton 1985) and is brought forward only because intertree communication is thought to occur in birch (Haukioja et al. 1985). This idea cannot be proved or disproved here since I have no evidence to show that the trees root systems were not connected. However, if the roots were connected, one might question whether it would negate the idea of communicable induction of defences. Baldwin and Schultz (1983) indicated that intertree communication was rapid. The changes occuring in my experiments were long term. If communicable defence exists within these birch trees, then my data from the 1986 laboratory suggest that it does not happen quick enough to affect those larvae hatching synchronous to the bud burst. A more likely explanation for the results in 1987 is that the water stress which was probably similar in all the trees, was the limiting factor and therefore all trees were poor quality hosts for the cankerworm larvae.

Table 7. Effect of defoliation intensity and date of hatch on survival of *Alsophila pometaria* larvae fed on foliage of *Betula x sargentii*.

EXPERIMENT	DATA				ANALYSIS		
DEFOLIATION INTENSITY	EARLY HATCH		LATE HATCH		SOURCE	d.f.	χ^2
	N	SURVIVAL (%)	N	SURVIVAL (%)			
LABORATORY							
1986 LOW	152	73	317	28	HATCH	1	148 ***
MEDIUM	91	66	253	23	INTENSITY	2	19 **
HIGH	91	55	229	9	INTER-		
					ACTION	2	0.1 n.s.
LABORATORY							
1987 LOW	218	20	153	0	HATCH	1	177 ***
MEDIUM	221	24	184	0	INTENSITY	2	1 n.s.
HIGH	203	24	109	0	INTER-		
					ACTION	2	1 n.s.
FIELD							
1986 LOW	10	50	10	40	HATCH	1	2 n.s.
MEDIUM	10	50	10	40	INTENSITY	2	0.9 n.s.
HIGH	10	70	10	40	INTER-		
					ACTION	2	0.9 n.s.
FIELD							
1987 LOW	10	100	10	90	HATCH	1	5 *
MEDIUM	10	100	10	80	INTENSITY	2	0.9 n.s.
HIGH	10	100	10	70	INTER-		
					ACTION	2	0.9 n.s.

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; n.s = not significant

Table   8   Effect of defoliation intensity and date of hatch on feeding life (days ± se) of *Alsophila pometaria* larvae reared on *Betula x sargentii*.

EXPERIMENT	DEFOLIATION INTENSITY	EARLY HATCH		LATE HATCH	
		N	LIFE	N	LIFE
LABORATORY 1986	LOW	81	24±1	89	32±1
	MEDIUM	39	27±1	58	32±1
	HIGH	27	26±1	20	36±1
LABORATORY 1987	LOW	43	26±1		
	MEDIUM	52	24±1		
	HIGH	48	28±2		
FIELD 1986	LOW	5	28±0.1	4	26±1
	MEDIUM	5	23±2	4	26±2
	HIGH	7	28±2	4	25±3
FIELD 1987	LOW	10	36±0.3	9	32±2
	MEDIUM	10	37±0.3	8	37±2
	HIGH	10	37±0.4	7	42±1

Table 9. Effect of defoliation intensity and date of hatch on mean prepupal weight ± se (mg) of *Alsophila pometaria* reared on foliage of *Betula x sargentii*.

EXPERIMENT

	DEFOLIATION	EARLY HATCH		LATE HATCH	
	INTENSITY	N	WEIGHT	N	WEIGHT
LABORATORY 1986					
	LOW	81	57±2	89	40±6
	MEDIUM	39	49±2	58	36±1
	HIGH	27	47±2	20	34±2
LABORATORY 1987					
	LOW	43	36±2		
	MEDIUM	52	37±1		
	HIGH	48	36±2		
FIELD 1986					
	LOW	5	41±3	4	49±7
	MEDIUM	5	46±11	4	44±9
	HIGH	7	45±7	4	47±9
FIELD 1987					
	LOW	10	36±2	9	30±4
	MEDIUM	10	27±3	8	26±5
	HIGH	10	26±3	7	19±1

Table 10. Effect of defoliation intensity and date of hatch on pupal duration (days) of *Alsophila pometaria* larvae reared on *Betula x sargentii*.

EXPERIMENT	DEFOLIATION INTENSITY	EARLY HATCH N	PUPATION	LATE HATCH N	PUPATION
LABORATORY 1986	LOW	81	122±3	89	124±4
	MEDIUM	39	120±3	58	125±3
	HIGH	27	119±4	20	115±4
LABORATORY 1987	LOW	43	125±1		
	MEDIUM	52	128±2		
	HIGH	48	131±2		
FIELD 1986	LOW	5	142±9	4	129±17
	MEDIUM	5	152±9	4	135±7
	HIGH	7	142±7	4	136±6
FIELD 1987	LOW	10	157±7	9	139±10
	MEDIUM	10	160±7	8	147±9
	HIGH	10	155±7	7	136±9

Table 11. Effect of defoliation intensity and date of hatch on fecundity of *Alsophila pometaria* females reared on *Betula x sargentii*.

EXPERIMENT

	DEFOLIATION INTENSITY	EARLY HATCH		LATE HATCH	
		N	FECUNDITY	N	FECUNDITY
LABORATORY 1986	LOW	35	110±14	7	82±21
	MEDIUM	14	83±24	5	35±18
	HIGH	12	66±23	3	80±19
LABORATORY 1987	LOW	10	94±12		
	MEDIUM	11	75±7		
	HIGH	11	87±12		
FIELD 1986	LOW	1	90	1	141
	MEDIUM	1	183	1	175
	HIGH				
FIELD 1987	LOW	1	131	4	94±25
	MEDIUM	2	89±26		
	HIGH	2	54±10	1	26

Table 12. Effect of defoliation intensity and date of hatch on egg
production of *Alsophila pometaria* reared on *Betula x
sargentii*. Numbers represent the number of eggs per egg
that hatched.

EXPERIMENT	DEFOLIATION INTENSITY	N	EARLY HATCH	N	LATE HATCH
LABORATORY 1986					
	LOW	152	34.7	317	1.8
	MEDIUM	91	12.8	253	0.7
	HIGH	91	8.7	229	1.0
TOTAL EGGS PRODUCED			6170		802
LABORATORY 1987					
	LOW	218	4.3	153	0
	MEDIUM	221	3.7	184	0
	HIGH	203	4.7	109	0
TOTAL EGGS PRODUCED			2709		0

Fig. 7 Compartments of cage over *Betula x sargentii*..
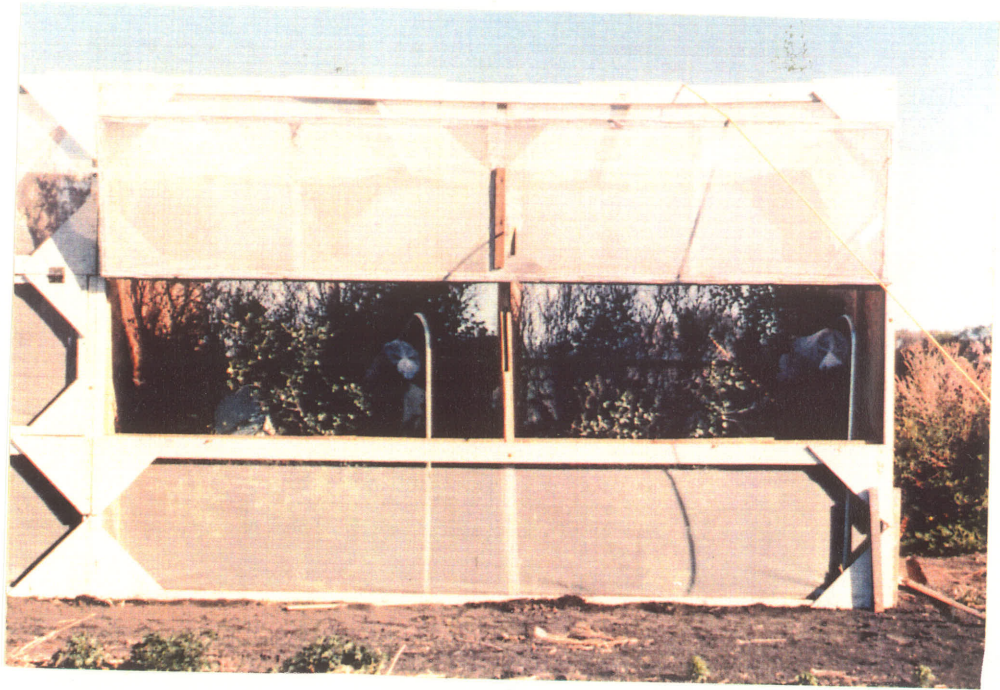
Fig. 8 Low (left) versus high (right) defoliation intensity within compartments of caged *Betula x sargentii*.

Fig. 9   Relationship of prepupal weight and fecundity of *Alsophila*

pometaria reared on *Betula x sargentii* 1986: Fecundity =

3.6 prepupal weight - 65. The dashed lines represent the 95%

confidence intervals.

Eggs Produced (y-axis)

Prepupal Weight (x-axis)

Fig. 10 Relationship of prepupal weight and fecundity of female *Alsophila pometaria* reared on *B.etula x sargentii* 1987: Fecundity = 3.1 prepupal weight - 42. The dashed lines represent the 95% confidence intervals.

Eggs Produced (y-axis)

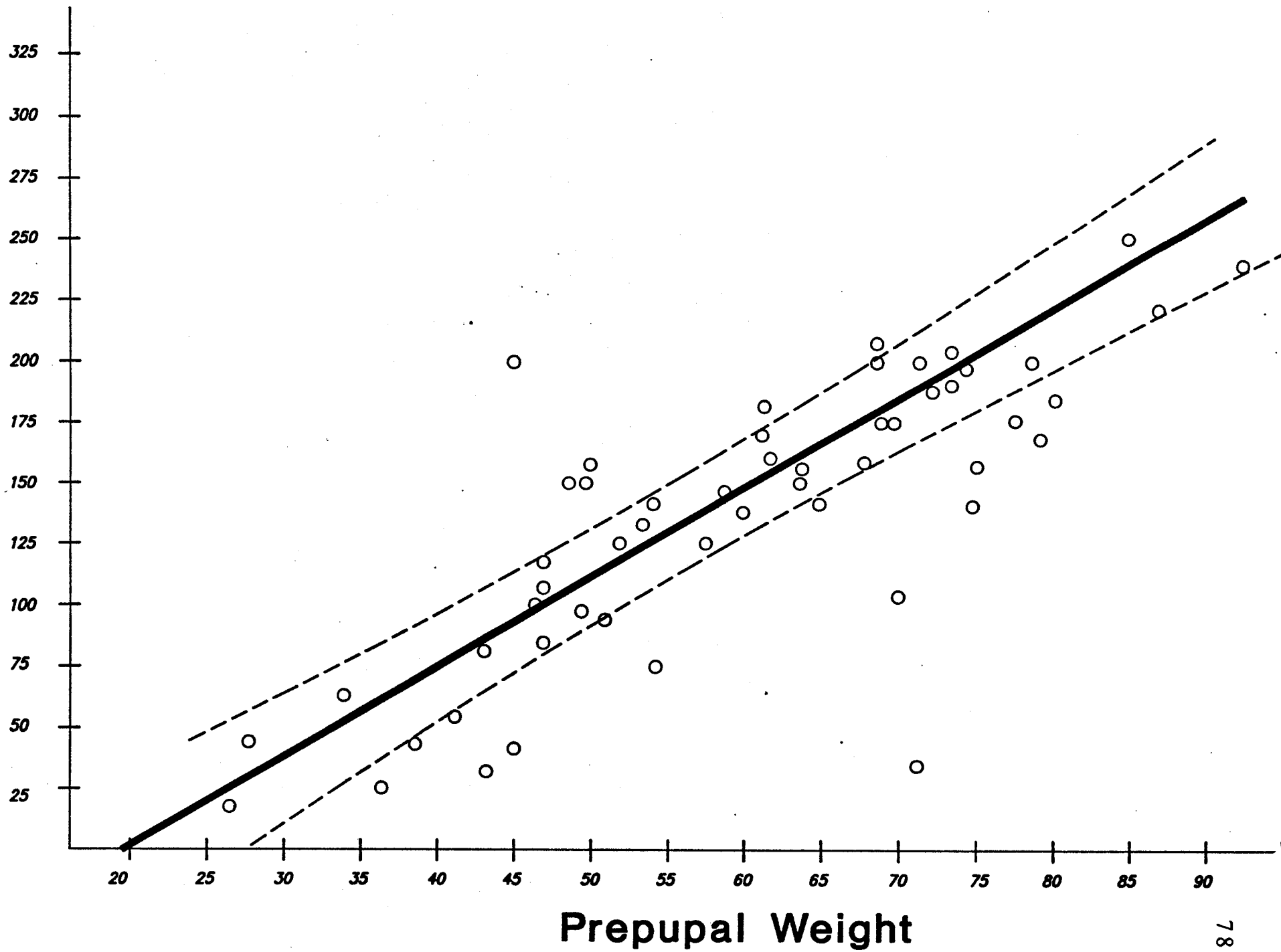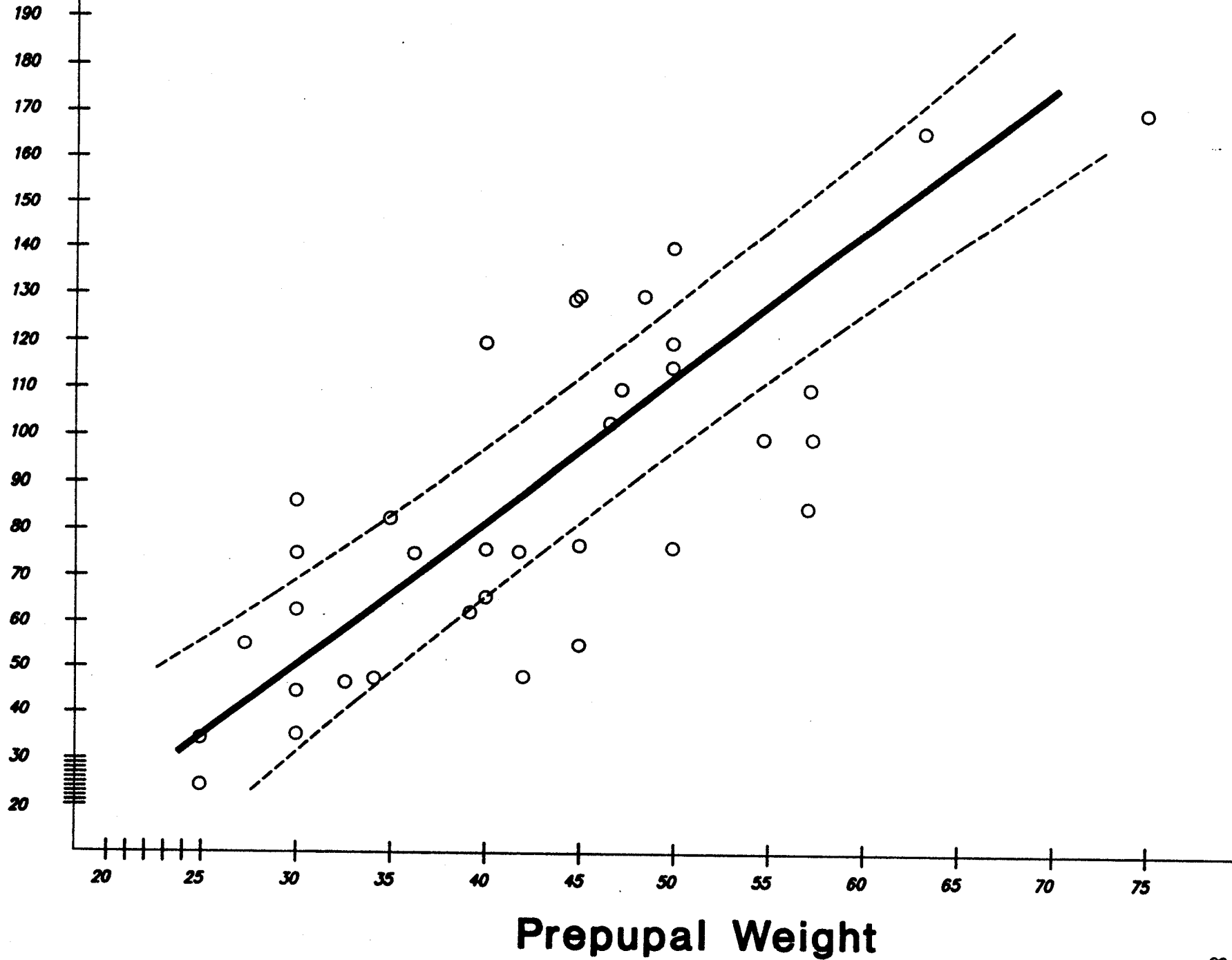**Prepupal Weight** (x-axis)

CHAPTER III

Part III

Orientation of Adult Fall Cankerworm, *Alsophila pometaria* (Lepidoptera: Geometridae) to visual cues

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Orientation of Adult Fall Cankerworm, *Alsophila pometaria* (Lepidoptera: Geometridae) to visual cues.

Abstract

Tests to determine if fall cankerworm, <u>Alsophila pometaria</u> (Harris), adults are attracted to vertical silhouettes were conducted in an enclosure with controlled lighting and temperature. Adults of the two sexes were released at separate times to avoid the influence of pheromonal attraction. Of those adults that were introduced into the enclosure, between 64% and 94% were attracted to dark silhouettes which occupied only 4.8% of the enclosure's vertical surface area. Males and females were equally attracted, and attraction to two different types of silhouettes was equal.

Introduction

In southern Manitoba, adult fall cankerworms, <u>Alsophila</u> <u>pometaria</u> (Harris), emerge from pupation from late September to early October (Hildahl and Peterson 1974). Females usually deposit their eggs on the branches of trees (McGuffin 1988). Females are apterous and disperse only by walking (Palaniswamy et al. 1986). Thus location of oviposition is limited to trees in close proximity to the site of adult female emergence. Baker (1972) describes the life histories of geometrids in the eastern United States and Schneider (1979) notes that six of these species are flightless, concluding that flightlessness is correlated with numerical abundance. These species all emerge in early spring and are all highly polyphagous.

The adult female fall cankerworm chooses the host that the larvae hatch on. Therefore, the role of cues in the selection of the oviposition site is important because it greatly influences future larval feeding site. Male and female fall cankerworm have been observed on the lower portions of tree trunks prior to mating. The winter moth, <u>Operophtera</u> <u>brumata</u> (L.), like the fall cankerworm, is a geometrid moth in which the female is flightless and has restricted dispersal. Grison and De Sacy (1954) conducted experiments with winter moth in apple orchards and discovered that females orient themselves to tree trunks or wooden posts, indicating that within a certain distance, the eclosing adult females perceive, and orient towards, vertical shapes. Grison and De Sacy observed that, without

exception, females in an experimental arena were located on tree trunks or painted silhouettes and none were found on the light colored perimeter of the test arena.

Richerson et al. (1976) observed that 9.5% of male gypsy moth, Lymantria dispar (L.), males orient to vertical silhouettes when no females were in the vicinity and these numbers rose dramatically when females were tethered to the trees, suggesting that both visual cues and pheromones are responsible for male orientation. Like the winter moth, the sex pheromone of fall cankerworm females has been identified (Wong et al. 1984); Palaniswamy et al. (1986) observed that fall cankerworm males are attracted strongly to this pheromone and it was suggested orientation of male cankerworms to trees is in response to visual cues and sex pheromone.

This study was designed to determine if male and female fall cankerworm adults orient themselves to vertical silhouettes in the absence of the opposite sex.

Methods and Materials

Fall cankerworm adults were released into a 2 m diameter cylindrical arena (Fig. 1) in which vertical silhouettes were placed. The frame of the arena was made of 2 cm diameter aluminum conduit pipe, which was bent into circles to form the base and top. Four vertical straight pieces of pipe connected the circular frames. The wall of the arena was 2 m high and was made of white nylon cloth wrapped around the outside of the frame. The floor of the arena was made of burlap and the roof was made of plywood. Access

was through a velcro-fastened slit in the side of the arena. The enclosure was erected in a storage building located on the Fort Garry campus of the University of Manitoba so that light and temperature could be controlled.

Two light systems were attached to the roof inside the arena. Firstly a 60 w incandescent bulb, attached to a dimmer switch was left on constantly at very low amperage to simulate evening light conditions and to illuminate test silhouettes. Daytime light conditions were simulated using a bank of two 1.2 m long 'cool white' fluorescent lights controlled by a timer that switched the lights on at 07:00 and off at 20:30 CST. Light intensity on the floor of the arena was 6000 lx. when both light systems were on; with the incandescent bulb alone, the intensity was 30 lx. Mean temperature was 15° C (range 14°- 16.5° C).

The vertical silhouettes placed in the arena were of two types. In 1986, 10 cm wide black nylon cloth strips were attached to the inner wall of the arena at four locations at 90° intervals. These strips extended vertically from the floor to the roof and covered the four 2 cm pipe supports. In 1987, two 10 cm wide cloth strips and two 5 cm diameter tree branches were placed at 90° intervals. The tree branches also reached from the floor to the roof and were alternated with the cloth strips. A 10 cm wide band of Tanglefoot ™ sticky spray was applied 1 m above the floor around the inside wall of the arena and the silhouettes.

Moths were released into the arena in single sex groups within 24 h of emergence. In each year, all experiments with males were done first so that the female sex attractant (Wong et al. 1984) would

not influence male activity. Groups of moths were released at the center of the floor of the enclosure and observations were made daily. Moths were considered to be attracted to silhouettes if they were on a silhouette or within 15 cm arc of a silhouette on the ground. After several days, moths were counted. Chi square analysis was used to determine if more moths were attracted to the silhouettes than expected if they had distributed themselves randomly around the circumference of the cylindrical arena.

Results

In 1986, 23 males and 16 females were released into the enclosure. Of the 23 males released, 20 were found on a silhouette or on the floor within 15 cm of a silhouette, while 3 were found elsewhere (Fig 2). Females released in 1986 showed a similar response. Fifteen of 16 females were found on a silhouette or on the floor near a silhouette. Thus, 87% of the males and 94% of the females oriented themselves to the vertical objects which make up only 6.4% of the wall surface area. Chi-square results show that both males (N=23; df=1; χ^2=204.7; P<0.001) and females (N=16; df=1; χ^2=51.4; P<0.001) were significantly attracted to the silhouettes.

In 1987, 53 of 86 released males were attracted to the silhouettes, while 70 of 110 females were attracted. Therefore, 67% of males and 64% of females were attracted to silhouettes occupying 4.8% of the wall surface area. Results from the chi-square analysis show again that both males (N=86; df=1; χ^2=702.2; P<0.001) and females (N=110; df=1; χ^2=511.4; P<0.001) were attracted to the

silhouettes to a significant degree. In 1987, there was no difference in attraction between the 5 cm tree branches and the cloth silhouettes (N=123; df=1; χ^2=0.001).

There was no significant difference between the sexes attraction to the silhouettes (N=235; df=1; χ^2=0.017). There was a significant difference of attraction between the years (N=235; df=1; χ^2=10.3; P<0.001).

Discussion

Outside the building, light measurements were 90000 lx during the daytime (clear sky at 13:00 hr) and 30 lx at night (quarter moon at 24:00 hr). Since the moths are nocturnal, it is the lower evening light conditions which are most important. The daily mean temperature in the area of study at the end of September (Environment Canada Monthly Meteorological Summary. Sept. - Oct. 1988) was similar to those produced within the arena.

The data show that both male and female fall cankerworm adults were strongly attracted to vertical silhouettes. This suggests that emerging males may orient themselves visually to vertical objects and then become attracted to the sex pheromone released by the females (Palaniswamy et al. 1986) when they are close enough. In these experiments, males were released into the enclosure before females for two reasons. First, males eclosed before females and secondly, residues of the females sex pheromone may otherwise have influenced the results for the males.

Many of the moths tested were quickly aware of the presence of the silhouette no matter what time of day the groups of moths were released. Moths when initially released, were observed moving toward the observer, who was standing still in the middle of the floor at the time of release. No doubt the observer represented a more obvious silhouette than those presented because of proximity to the moths.

The finding that female fall cankerworm adults orient to the vertical silhouettes, regardless of whether or not they are tree branches, suggests that the choice of oviposition site is not made on the basis of the quality of the foliage that the host would produce. Newly hatched larvae have a choice of consuming the foliage from the tree on which they hatch, or spinning a silken thread and dispersing. However, each female is most likely to pupate beneath the canopy of the tree on which she has fed, and is likely to respond to its silhouette when she emerges. Thus the tree on which her progeny hatch is likely to be suitable for larval feeding, and so, sophisticated methods of locating oviposition sites may be unnecessary.

The frequency of attraction to the silhouettes in this experiment is similar to that for winter moth (Grison and De Sacy 1954). The threshold of discriminating the silhouette was not determined in my experiment; however, similar numbers were found on the 5 cm branches and the 10 cm cloth silhouettes. Therefore, I conclude that cankerworms in the described arena perceive the 5 cm branch and 10 cm wide cloth silhouettes as equally acceptable. One would think that the cankerworms would find the 5 cm silhouette

half as attractive as the 10 cm. It might be that the thickness of the silhouette has some bearing on the attractiveness. A flat 10 cm silhouette might not be as readily perceived from the side, whereas a tree branch would be equally visible from the side as it is from the front.

Both male and female cankerworm adults have relatively large bulbous eyes with many omatidia which help visual perception for nocturnal insects (Dreisig 1980). The eyes of male fall cankerworm adults are larger than those of females. While both sexes perceive the silhouettes similarly, males may have larger eyes because they fly and so move in three dimensions, whereas walking females move in only two dimensions on a surface. Palaniswamy et al. (1986) noted that fall cankerworm males appear to orient themselves to vertical objects and suggested that the presence of females on the vertical objects would enhance this. In experimental studies gypsy moth males orient to trees with and without females on them, however, more males search in the area where the greatest number of females are tethered (Richerson et al. 1976). This suggests that the visual cues that adults perceive are as important as pheromone cues. Evidence for this is that males are observed eclosing first and by themselves orient to the vertical silhouette. Females migrate to the vertical silhouette in the absence of males; this suggests that females do not wait to be found by males on the ground.

Visually orientation to vertical objects probably maximizes energetic efficiency. Cankerworm adults do not feed and are therefore limited in the amount of energy they can spend in host location. Females must spend energy on host location, mating and egg

deposition, while males spend energy on multiple mating which may require much flight. By moving to vertical silhouettes, females are moving to oviposition sites, and male behavior enhances the probability of finding a female which has not mated. The behavior patterns of both sexes are likely to be more energetically efficient than random movement or movement following pheromone perception.

It seems that the orienting to visual cues is an adaptive strategy for the fall cankerworm. The closest vertical silhouette to an emerging female is likely to be the original host tree, so females place progeny on a source of food on which their mother survived. This not only gives the progeny a potentially acceptable source of food, but reduces the risk of the female being eaten by ground dwelling predators.

Fig. 11. Top and side view of silhouette enclosure.

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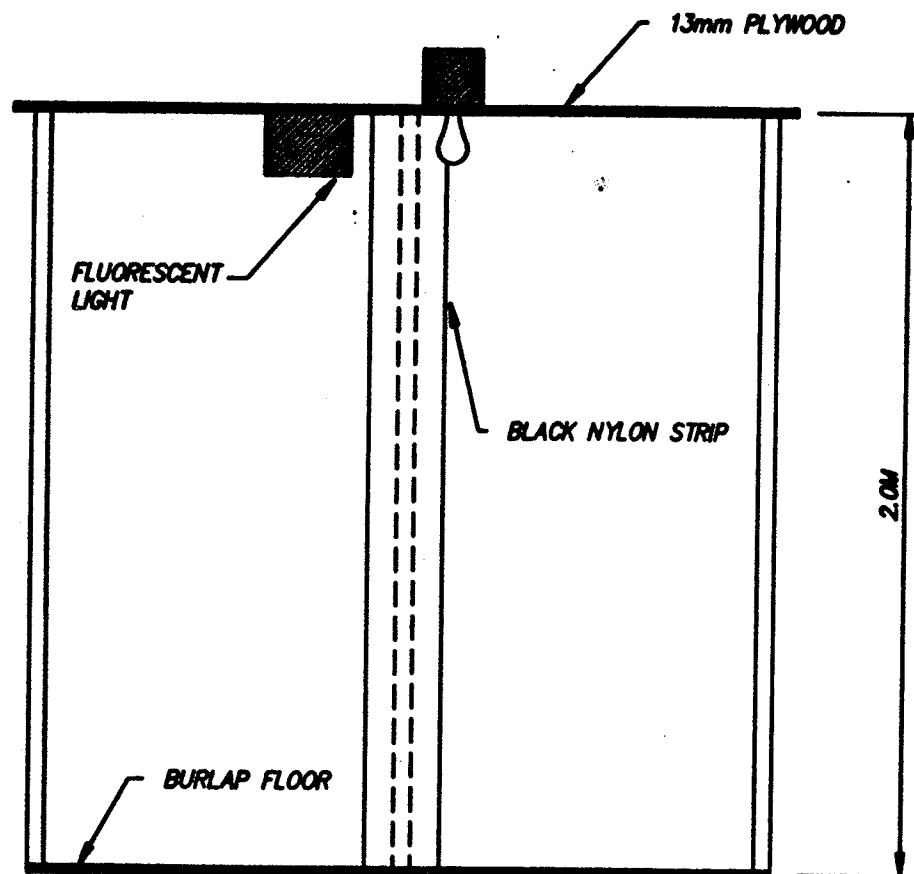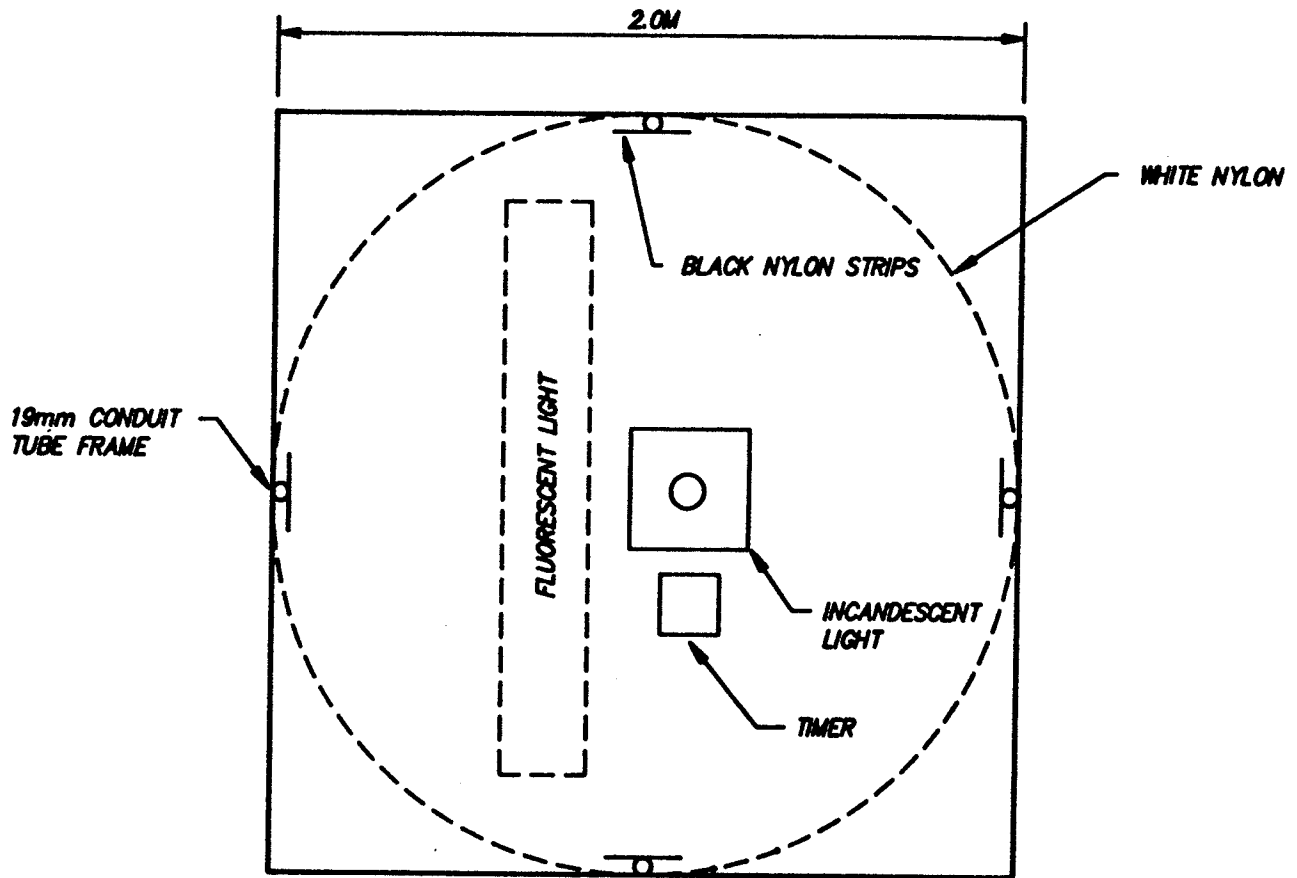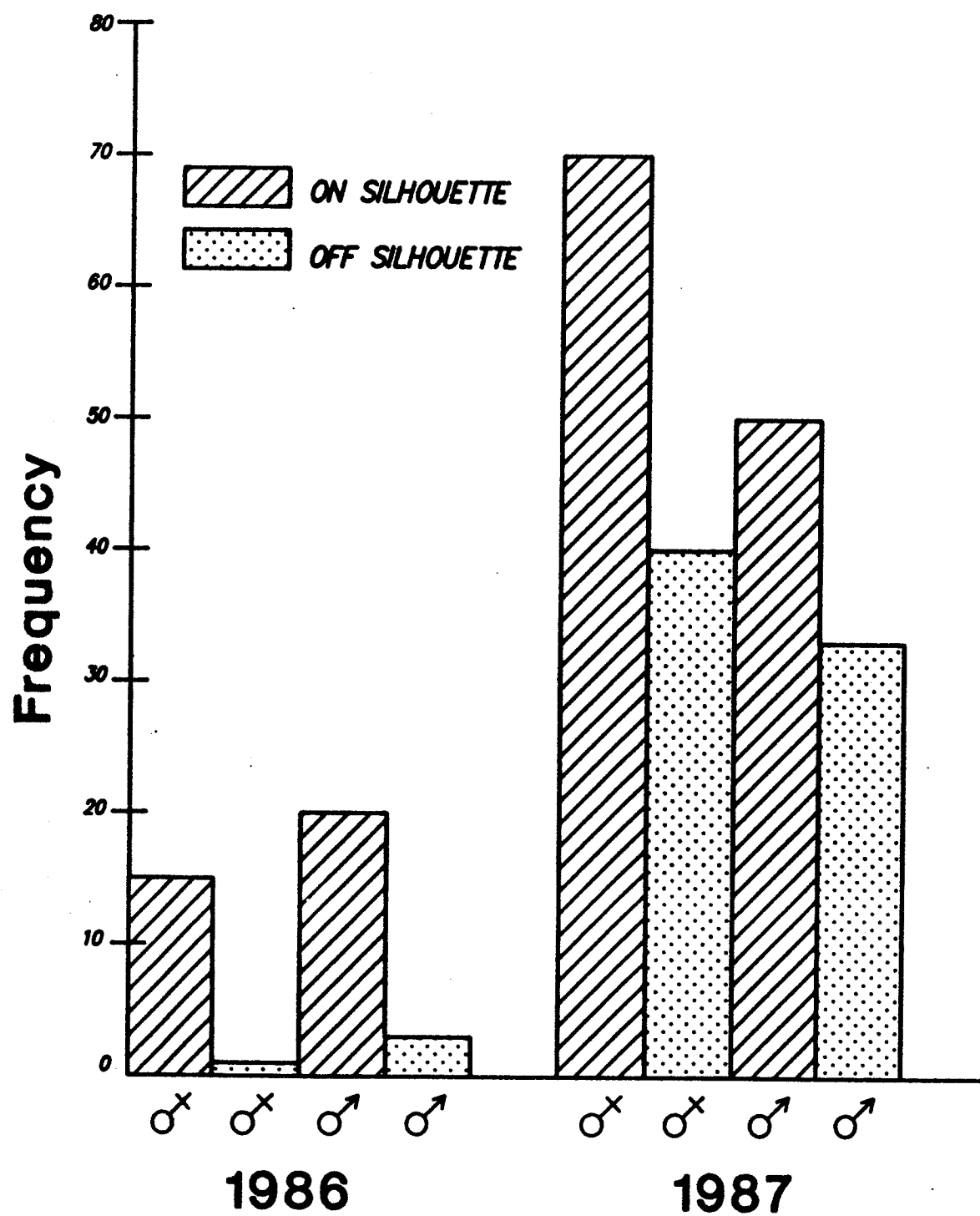
Fig. 12. Frequency of female and male *A. pometaria* that are
attracted to vertical silhouettes.

CHAPTER IV

GENERAL DISCUSSION

Literature on the development and performance of fall cankerworm in the past was limited to eastern regions (Schneider 1979) with only basic biology and phenology information available for the cankerworm in the prairies (Hildahl and Peterson 1974); although work on pheromones has taken place in Manitoba and Saskatchewan (Wong et al. 1984; Palaniswamy et al. 1986).

My studies demonstrate that spring feeding is an important mechanism by which the cankerworm succeeds. Performance, measured by survival, duration of feeding, prepupal weight and fecundity, is much better when the cankerworm hatches close to the time of host bud burst than if hatch is later. Changes in foliage toughness, water and nitrogen content along with the production of host plant defensive chemicals occur as leaves mature, and these affect leaf suitability for herbivores. Reduction in foliage succulence and increases in host plant defences are suggested as the main reasons for spring feeding of the winter moth (Feeny 1970; Wint 1983; Holliday 1985). Lawson et al. (1984) suggest that access to leaves with succulent, high nitrogen levels is the major benefit of spring feeding for the cankerworm.

Insects like the fall cankerworm are generalist spring feeders that avoid late season foliage, rather than specialists that have mechanisms which allow them to deal with more mature foliage. Generalists are usually opportunists which go through fluctuations in

their population density. Survival and performance of opportunists is high in the presence of high quality food resulting in population increase.

The polyphagy of the fall cankerworm is likely what drives the selection of spring feeding, and it is female aptery which likely drives polyphagous feeding. Specialist Lepidoptera make choices of oviposition and feeding sites based on many factors. However, adult female cankerworms choose oviposition sites through visual cues and larvae may be forced to balloon to find suitable hosts, so the advantage for the cankerworm being polyphagous is evident. Polyphagous feeders attack a greater and more chemically diverse range of host plants, and therefore, are more inefficient in food consumption and digestion (Scriber and Feeny 1979). Thus, these polyphagous opportunists evolve to feed when the food is least detrimental.

Female aptery likely drives polyphagy because it is a mechanism by which the cankerworm can track the interstand variation of bud burst within a given area (Feeny 1976). Schneider (1979) discovered that there was a relationship of foliation time of individual trees relative to the mean foliation in a given area.

Female aptery probably evolved in a cold climate to help maximize egg production (Dierl and Reichholf 1977; Holliday 1985). Adult fall cankerworm females are flightless and eclose with non functioning mouthparts which do not allow for feeding. Females eclose with fully formed eggs and walk to their hosts using visual cues (Chapter III, part iii of these studies). Therefore, walking to the nearest vertical silhouette allows females to spend a minimal amount

of energy for host and mate finding, and allocate most of their resources to egg production.

The female's oviposition site is therefore dependent on the prepupation site, also, the oviposition site strongly influences the host plant consumed by her offspring. If the host plant's defences are non-inducible, then returning to the same tree seems to be a good strategy. However, if the defences are inducible and lingering, then then this force may help to control performance of returning cankerworms.

The fecundity of female cankerworms is dependent upon the female weight at pupation which is dependent on the efficiency of consumption and digestion of the foliage by the larvae. My studies show that cankerworms feeding on early season foliage of any of the four hosts tested had greater prepupal weights and therefore greater fecundity. Different host foliage also causes differences in survival and this also influences greater total egg production.

There have been suggestions that even polyphagous feeders have preferred host plants. Wint (1983), feels that oak, Quercus, is the preferred host for winter moth, but other species such as Crataegus, Prunus, or Fagus are acceptable alternative host plants. He supports this conclusion by demonstrating better performance on, preference for, and higher densities on oak. If oak is unavailable, or larvae find themselves on an unsuitable host, then dispersal takes place to find oak or another suitable host. If one follows Wints' arguments, then my experiments show that birch and willow are the fall cankerworm's preferred hosts, while oak and elm are acceptable alternatives. Bog birch and willow are the likely preferred hosts for

the fall cankerworm because at the cessation of glaciation they were probably the only tree species available (Pennington 1969). These tree species are still the only tree like vegetation available in various upland and tundra areas (Ritchie 1984) Female aptery is a likely reason why the cankerworm was not able to follow the northward migration of the preferred hosts. If eclosing flightless females had already evolved their orientation behavior towards silhouettes, the larger silhouettes of the alternative hosts would tend to divert insects towards these trees. If progeny of these diverted insects could survive, then this would interfere with selection favoring tracking the preferred host. Bigger trees with more apparent silhouettes, along with the scarcity of the preferred hosts are probable reasons why fall cankerworm is currently found primarily on these alternative hosts.

Futuyma et al. (1984) found cankerworms on Long Island to be parthenogenetic and to have varying genotypes depending on the preferred host. This would seem to support the idea that the females moving back up the same tree would have an advantage. In Manitoba, there are no records of the existence of parthenogenesis or gynogeny in cankerworm populations.

The transfer of fall cankerworm to oak, elm and other large trees in which mature foliage is unsuitable would result in selection pressure favoring spring feeding to maximize fecundity. Results of performance indices indicate that fall cankerworm feeding on early spring foliage will have a greater reproductive capacity on more different types of foliage. Wint (1983) felt that polyphagy resulted in a selection pressure favoring spring feeding of the winter moth and

that preferred, but unpredictable food resources could be substituted by other types of foliage resulting in successful performance. This suggests that fall cankerworm, hatching before the bud burst of the initial host, may disperse and be equally successful and produce a large number of eggs on a number of host species.

Cankerworms able to consume and digest their host's foliage efficiently, should produce a greater number of heavy pupae; these will probably be more numerous in the soil near the base of that host than around a host on which cankerworms performed poorly. The resulting apterous females emerge and move towards the most apparent silhouette. This silhouette is likely to be the same host that the female fed on as a larvae. This means that large numbers of egg laden females should return to the same host. The potential increase in the population is governed by the population density, which is limited by the host, host defenses and the density of similar or alternative hosts in the vicinity.

Increasing defoliation intensity by cankerworm on birch trees may result in a decline in insect performance. In nature, as the intensity of defoliation increases, the availability of the 'best' foliage declines, forcing the larvae not only to feed on the leaves of lower quality but to also forage more to seek adequate resources. This increased foraging decreases the amount of time spent feeding and results in an increased amount of time to ingest the food necessary to achieve the mature larval state. Previously damaged foliage is a lower quality food resource (Bergelson et al. 1986, Wallner and Walton 1978, Haukioja and Niemela 1977) and browsing larvae feeding on previously damaged foliage have longer feeding periods

and decreased prepupal weights, which results in lower survival and fewer eggs.

It is suggested that the general decline in survival and performance of many herbivorous insects is partially due to an induced defensive response by the trees against attack. This response is likely not specific against just cankerworms, but against herbivores in general and is also to protect against disease infection. It has also been suggested that delayed response, or response which has a slow relaxation time affects successive generations (Haukioja et al. 1988). Werner (1979) found that spear-marked black moth, Rheumaptera hastata performance declined when fed foliage from birch trees that were repeatedly defoliated for 2 and 3 years. The birch in my experiments may also have had this delayed response but abiotic factors made it impossible to determine.

These host plant defences may also be mechanisms which maintain spring feeding and polyphagy. Larvae hatching early will have a longer period of time to feed before the plant defenses make it difficult, if not impossible to feed. The delayed host defences which affect the performance of insects feeding on them may also cause dispersal which may help to maintain polyphagy.

Host plant defences are also proposed to be communicated from a damaged host to an adjacent undamaged host whereby the undamaged host is able to defend itself against attack (Baldwin and Schultz 1983; Rhoades 1983; Haukioja et al. 1985). Inter-tree communication cannot be used here to explain declining performance of the fall cankerworm reared in the defoliation intensity experiment

because of water stress. However, it also cannot be ruled out as a possible explanation.

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