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

Graduate Studies

by

Blaine Herbert Leslie Timlick

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

Department of Entomology

University of Manitoba

Winnipeg, Manitoba

February 1992

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Votre référence*

Our file *Notre référence*

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-77914-4

Canada

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

BY

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

© 1992

Permission has been granted to the LIBRARY OF THE UNIVERSITY OF MANITOBA to lend or sell copies of this thesis, to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film, and UNIVERSITY MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's permission.

ACKNOWLEDGEMENTS

I greatly appreciate Dr. N.J. Holliday for his supervision, support, encouragement and patience throughout this study. I thank Drs. P.A. MacKay and D. Punter for their participation as committee members. I also thank Dr. R. Currie for his friendship and time for resolving computer problems. I extend many Blue to Mr. D. Den Ouden for his time and help with computer graphics.

I am indebted to my family: my wife Marlene and daughter Lauren; my parents Warren and Doreen Timlick; and my father and mother in-law, Dr. Walter and Vera Willborn. Without their support this work would not have been possible.

To my friends, who make life so interesting.

Table of Contents

CHAPTER I 1
INTRODUCTION 1
Objectives 3
Thesis Organization 3
CHAPTER II 4
LITERATURE REVIEW 4
Distribution and Description 4
Phenology 5
Synchronization of Hatch to Host Bud Burst 6
Host Plant 7
Host Plant Defence 8
Host Selection by Females 10
CHAPTER III 12
The Effect of Leaf Maturity and Host Plant Species on the
Performance of Alsophila pometaria 12
(Lepidoptera: Geometridae) 12
Abstract 13
Introduction 14
Methods and Materials 15
Laboratory study 16
Field Study 17
Results 18
Larval Survival 19
Duration of Larval Feeding 20
Prepupal Weights 20
Pupal Duration 21
Fecundity 22
Prepupal weight / Fecundity Relationship 23
Discussion 23
Chapter III 48
Changes in quality of hybrid bog birch, Betula x sargentii,
defoliated by fall cankerworm, Alsophila pometaria 48
(Lepidoptera: Geometridae) 48
Abstract 49
Introduction 51
Methods and Materials 53
Laboratory Study 54
Field Study 55

Results 56
Larval Survival 56
Duration of Larval Feeding 57
Prepupal Weights 58
Pupal Duration 59
Fecundity 59
Prepupal weight - Fecundity Relationship 60
Discussion 60
Effect of phenology and defoliation intensity 61
Intertree Communication 65
CHAPTER III 80
Part iii 80
Orientation of Adult Fall Cankerworm, Alsophila pometaria (Lepidoptera: Geometridae) to visual cues 80
Abstract 81
Introduction 82
Methods and Materials 83
Results 85
Discussion 86
CHAPTER IV 94
GENERAL DISCUSSION 94
REFERENCES 101

List of Tables

pg.

Table 1. Effect of tree species and date of hatch on survival of *Alsophila pometaria* larvae. 30

Table 2. Effect of tree species and hatch date on duration of feeding period (days) of *Alsophila pometaria* larvae. 31

Table 3. Effect of tree species and date of hatch on the mean prepupal weight (±se) (mg) of *Alsophila pometaria.* 32

Table 4. Effect of tree species and date of hatch on the pupal duration of *Alsophila pometaria.* 33

Table 5. Effect of tree species and date of hatch on the fecundity of *Alsophila pometaria* females. 34

Table 6. Effect of tree species and date of hatch on egg production of *Alsophila pometaria.* 35

Table 7. Effect of defoliation intensity and date of hatch on survival of *Alsophila pometaria* larvae fed on foliage of *Betula x sargentii* 66

Table 8. Effect of defoliation intensity and date of hatch on feeding period (days ± se) of *Alsophila pometaria* larvae reared on *Betula x sargentii* 67

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.* 68

Table 10. Effect of defoliation intensity and date of hatch on on pupal duration of *Alsophila pometaria* larvae reared on *Betula x sargentii* 69

Table 11. Effect of defoliation intensity and date of hatch on fecundity of *Alsophila pometaria* females reared on *Betula x sargentii* 70

Table 12. Effect of defoliation intensity and date of hatch on egg production of *Alsophila pometaria* larvae fed on foliage of *Betula x sargentii* 71

List of Figures

pg

Fig. 1. *Alsophila pometaria* larva in 10 cm petri dish with fresh foliage 37

Fig. 2 Ten cm petri dishes in incubator. 39

Fig. 3 Cloth egg hatch cage over branch terminal of test tree. 41

Fig. 4 Nylon mesh sleeve cage 43

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. 45

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. 47

Fig. 7 Compartments of cage over *Betula x sargentii.* 73

Fig. 8 Low (left) versus high (right) defoliation intensity within compartments of caged *Betula x sargentii* 75

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. 77

Fig. 10 Relationship of prepupal weight and fecundity of female *Alsophila pometaria* reared on *Betula x sargentii* 1987: Fecundity = 3.1 prepupal weight - 42. The dashed lines represent the 95% confidence intervals. 79

Fig. 11 Top and side view of silhouette enclosure. 91

Fig. 12 Frequency of female and male *Alsophila pometaria* that are attracted to vertical silhouettes. 93

Abstract

Studies were conducted to examine the performance of the fall cankerworm, Alsophila pometaria (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 Betula x sargentii (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 Alsophila pometaria.

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, Betula x sargentii .

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, Alsophila pometaria (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, Acer negundo (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, Epirrita autumnata 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)

By Blaine Timlick,
Department of Entomology
University of Manitoba
Winnipeg, Canada
R3T 2N2

To be submitted to the Canadian Entomologist

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).