LABORATORY AND FIELD STUDIES ON *LYMANTRIA DISPAR* L. (LEPIDOPTERA: LYMANTRIIDAE) IN QUEBEC

by

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MADRID

ABSTRACT

Ph.D. Francisco J. Madrid Entomology

LABORATORY AND FIELD STUDIES ON *LYMANTRIA DISPAR* L. (LEPIDOPTERA: LYMANTRIIDAE) IN QUEBEC

Lymantria dispar L. is well adapted to Quebec conditions. Development time was shorter than for populations in the United States. Older larvae from Quebec, preferred birch leaves to oak and maple, in contrast to Massachusetts specimens, which prefer oak.

Overwintering eggs supercooled to -30°C and the ability to supercool was correlated with the content of glycerol and glycoproteins in the eggs. Glycerol was confined mainly to the embryo and the glycoproteins were in the external yolk.

68% of eggs above snow cover and 92% of those beneath snow cover survived the winter.

Larvae and pupae were parasitized by *Sarcophaga aldrichi* (Park.)(Diptera: Sarcophagidae), *Blepharipa pratensis* (Meig.), *Compsilura concinnata* (Meig.), *Exorista larvarum* (L.), *Parasetigena silvestris* (R.-D.)(Diptera: Tachinidae), *Apanteles melanoscelus* (Ratz.)(Hymenoptera: Braconidae), *Brachymeria intermedia* (Nees)(Hymenoptera: Chalcididae), *Phobocampe disparis* (Vier.), *Pimpla pedalis* (Cress.), *Theronia atalantae fulvescens* (Cress.) (Hymenoptera: Ichneumonidae), and preyed upon by *Calosoma frigidum* (Kirby)(Coleoptera: Carabidae), *Podisus maculiventris* Say (Hemiptera: Pentatomidae) and *Lygaeus kalmii* Stal(Hemiptera: Lygaeidae).

RESUME

Ph.D. Francisco J. Madrid Entomologie

ETUDE DE TERRAIN ET DE LABORATOIRE DE LYMANTRIA DISPAR L. (LEPIDOPTERA: LYMANTRIIDAE) AU QUEBEC

Lymantria dispar L. se trouve bien adaptée aux conditions du Québec. Le temps de developpement des larves est plus court que celui des populations aux Etat-Unis. Les larves plus agees préférent les feuilles de bouleau à celles de chêne et d'érable au Québec. Ceci contraste avec les populations plus méridionales du Massachusetts où le chêne est l'hôte.

La survie des oeufs a l'hiver sur-congeles jusqu'a -30°C et la capacité de sur-congelation ont été relié avec leur contenu en glycérol et en glycoprotéines. Le glycérol fût principalement trouvé dans l'embryon, les glycoprotéines dans le jaune d'oeuf externe.

68% des oeufs au-dessus de la couverture de neige, le meme que 92% des oeufs au-dessous de la couverture de neige survécurent a l'hiver.

Les larves et les pupes ont été parasités par Sarcophaga aldrichi (Park.)(Diptera: Sarcophagidae),Blepharipa pratensis(Meig.), Compsilura concinnata (Meig.), Exorista larvarum(L.), Parasetigena silvestris (R.-D.)(Diptera: Tachinidae), Apanteles melanoscelus (Ratz.)(Hymenoptera: Braconidae), Brachimeria intermedia (Nees)(Hymenoptera: Chalcididae), Phobocampe disparis (Vier.), Pimpla pedalis (Cress.), Theronia atalantae fulvescens (Cress.)(Hymenoptera: Ichneumonidae).

Trois espèces d'insectes, Calosoma frigidum Kirby (Coleoptera: Carabidae), Podisus maculiventris Say (Hemiptera: Pentatomidae) and Lygaeus kalmii Stal (Hemiptera: Lygaeidae), sont prédateurs de la spongieuse.

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CLAIM TO ORIGINALITY

The research in this thesis is considered to be an original contribution to knowledge in the following respects.

1. It is the first comprehensive study of the relationship between Lymantria dispar and its new ecological niche in Quebec.

2. The length of the life cycle in Quebec was measured, hatching period was established and the influence of temperature and relative humidity on starving newly hatched caterpillars is largely new information.

3. Amount of food consumed by instar IV, V, VI larvae was determined and compared. Food preference, calculated by examining leaf area consumed, when offered birch, oak, maple and horse chestnut, was measured.

4. Winter mortality of eggs was measured and related to snow cover, and used to indicate success of oviposition sites.

5. The presence of glycerol and glycoprotein in the whole egg (overwintering embryo and external yolk) was determined and measured. The relationship between supercooling points and levels of glycerol and glycoprotein was established.

6. Five exotic species and one native species of parasitoids

are reported for the first time in Canada. Two species of predators are recorded also for the first time.

7. Larval and pupal parasitism was measured systematically for the first time in Quebec.

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I. GENERAL INTRODUCTION

Periodic outbreaks, defoliating large areas of hardwood forest in New England and Southeastern Canada have placed the gypsy moth among the most injurious insects in North America. Enormous sums of money have been expended since the last century with the intent of suppressing high populations and the associated economic losses and reduced aesthetic and recreational values of forest.

Intensive eradication efforts have led to extensive research activities, making the gypsy moth one of the most studied insects. It was even part of a project in Skylab. Nevertheless, the pest is expanding its range inexorably in all directions. Man has contributed to this expansion, carrying the egg-masses to uncontaminated places on tools and vehicles.

Dispersal into Canada has been successful and there are established populations in Quebec, Ontario and very recently in British Columbia. Factors that could help to arrest this dispersal are the colder climate of Canada, which reduces the availability of suitable favored food plant species. Another important possible regulatory factor, natural enemies, needed to be assessed, since these could have become established by spreading from southern populations in the United States.

The aims of this study were to assess the impact of these new conditions upon the Quebec gypsy moth populations. The extent of its cold-hardiness, physiological response to winter

cold and short growing season, adaptability to new host plants, the array of natural enemies; all factors that could play a role in determining gypsy moth population levels were investigated in the field and supported with laboratory studies.

This thesis is arranged in the form of individual papers designed for journal publication, a format previously approved by the Faculty of Graduate Studies and Research, McGill University. Some of the papers have been submitted for publication.

II. LITERATURE REVIEW

TAXONOMY AND HISTORICAL BACKGROUND

The gypsy moth was first described by Linnaeus (1758) in his "Systema Naturae", under the name of Phalaena (Bombyx) dispar. Schrank (1801) placed it in his genus Laria, but this name was preoccupied and could not be used for the moth (Forbush and Fernald, 1896). Ochsenheimer in 1810 established the genus Liparis and put dispar in it, but Liparis was also preoccupied and had to be eliminated (Ferguson, 1976).

Hübner (1819) published both names, Lymantria and Porthetria, on the same page and in the same work he also published the name Ocneria, all of them as separate genera, so neither has clear priority. Stephens (1829) finally gave it another generic name, Hypogymna, a name also used by many subsequent authors.

Kirby (1892) designated the gypsy moth under the genus Porthetria, with dispar as the type and this nomenclature was adopted by Dyar (1893) and Comstock (1895) in North America.

Recently, the name of the gypsy moth has been reviewed by Ferguson (1976,1978). He states that under the International Code of Zoological Nomenclature, Article 24, which specifies "If more than one name for a single taxon, or identical names for different taxa, are published simultaneously whether in

the same or different works, their relative priority is determined by the action of the first reviser," the correct generic name for the gypsy moth is Lymantria. Walker (1855) is considered the first reviser and Ferguson (op. cit.) following Walker's adoption of Lymantria over Porthetria, with this last name listed in the synonymy, has chosen the name Lymantria dispar (L.). This name has been widely used in Europe, Africa and Asia during this century. In Russia the most common name for the gypsy moth is Ocneria dispar.

The classification of the gypsy moth then is as follows:

Order Lepidoptera

Sub Order Frenatae

Division Macrolepidoptera

Super-family Noctuoidea

Family Lymantriidae

Sub-family Lymantriinae

Tribe Lymantriini

Genus Lymantria

Species L. dispar

The gypsy moth, a notorious pest of forest and shade trees, was introduced from Europe to Medford, Massachusetts in 1869 (Forbush and Fernald, 1896). Since then, it has spread north, east and westward to most of the New England States and into Canada where it is already well established, near the

border between Quebec and New York State (Leonard, 1974; Burgess, 1915) and in a few localities in Ontario (Brown, 1968, 1969).

In the United States recently new populations have become established in Maryland, Southern Virginia, Central North Carolina, Ohio and Lower Michigan. Males have been trapped as far west as California, Washington and Oregon States, and to the south at Georgia, South Carolina, Kentucky and Florida (Ferguson, 1978).

In Canada, new infestations have been found in Belleville, Ontario (Schmidt, 1977), Contrecoeur, Quebec (McArthur, pers. comm.)[a] and in Vancouver, British Columbia (Canadian Pest Manag. Society, Newsletter, Oct. 1978) and flying males were captured as far as Yarmouth County, Nova Scotia in the period 1971-73 (Forbes et al., 1974).

LIFE HISTORY, GENERAL BIOLOGY AND CONCEPTS OF CONTROL

The life history and general biology of the gypsy moth has been reviewed by Forbush and Fernald (1896), Burgess and Crossman (1929), Britton (1935), Burgess and Baker (1938), Bess (1961).

Johnson and Lyon (1976) gave a life cycle description with several photographic plates.

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[a] J.D. McArthur. Faculty of Agriculture, McGill University.

The gypsy moth has a single generation each year and overwinters as a fully mature embryo. Egg-masses are tan-coloured and hair-covered. Each egg-mass contains 50 to 1000 eggs with larger egg-masses being produced by larger females. Female size, in turn, is closely related to the density of the larval population from which they were produced, smaller females result from denser populations (Campbell, 1975).

According to Leonard (1970) gypsy moth eggs vary in size not only between egg-masses, but also within the egg-mass. The first eggs laid are larger than the last laid eggs. There is a size gradient in eggs from the front to the rear of the egg-mass, the largest eggs being those first produced in the ovaries and then laid first (Leonard, 1971b). Moreover, the larvae hatching from smaller eggs showed a higher percentage of individuals with an additional instar. Leonard (op. cit.) has suggested that nutritively deficient eggs (from a high density population) of gypsy moths result in active larvae which do not feed immediately and are more readily dispersed by wind.

Capinera et al. (1977) have found egg size and amount of yolk to be positively related. Egg yolk, they found, is enclosed within the mesenteron and stomodeum in the embryo and there is also an external yolk reserve surrounding the embryo.

Embryonation occurs during late summer (Capinera et al., op. cit.) and the embryos are fully developed by week four after

oviposition (Leonard, 1968).

Diapause of the gypsy moth is obligatory (Leonard, op. cit.). From 67 species of Lepidoptera listed by Danilevskii (1965) in relation to the influence of photoperiod on diapause, 8 species were photoperiodically neutral. The gypsy moth was found to be among those 8 species. Hoy (1978), however, found a non-diapausing gypsy moth laboratory strain.

Normally, hatching takes place in May and newly hatched larvae remain on the egg-mass for a few hours (Leonard, 1966a; Campbell, 1974). Afterward, they crawl upward towards light and food, reaching the top of the tree. Before feeding, many of these larvae will spin down on silken threads, and large numbers can be dispersed by wind movements.

High population densities seem to influence larval behaviour so as to favor dispersal (Leonard, 1969). He found first instar larvae from a dense population left the egg-mass sooner and responded to air movements by arching their bodies and releasing their attachment to the substrate (Leonard, 1971a).

First-instar larvae are well equipped for air-borne dispersal weighing less than 1 mg at hatching, with the production of silk and the long setae covering their bodies (Leonard, op. cit.).

Dispersal may continue for a period of about two weeks and results, very often, in new outbreaks, but ceases after the

insects find suitable foliage. The young caterpillars remain on the foliage until they have molted twice. The larval feeding period lasts 6 to 8 weeks, usually terminating by mid-July. Male larvae have five instars; female larvae pass through six instars. After instar III, there is a change in larval behaviour. In the first three stages, larvae feed during daylight. Half way through the third instar, larvae start resting in dry, dark places during daylight and feeding at night (Leonard, 1970, 1974). Under certain conditions, the larvae will remain on the foliage during the day. In fact, at very high densities, virtually all of the older caterpillars feed almost continually, day and night (Campbell, 1974).

Larvae ready to pupate begin spinning a silk mat that holds the pupa to the substrate, which most of the time is an old branch hole, bark crevices, or other niches on tree trunks, beneath branches, or on stumps, rocks and leaf litter (Smith and Campbell, 1978). Male pupae are generally smaller than the female. The insects spend about two weeks as pupae with the females taking 1 to 3 days longer than the males.

Males emerge usually first before females. The strong-flying males are attracted by the potent olfactory sex attractant emitted by the heavy-bodied female, who although winged, does not fly (Leonard, 1974; Doane, 1976b). Forbush and Fernald (1896) used virgin females as bait for trapping males. The

same principle was used in survey work as early as 1913 (Collins and Potts, 1932). Later, extracts of the female pheromone gland were obtained and treated for greater effectivity (Burgess, 1950).

Two compounds, gyplure and gyptol, have been the subject of abundant research (Jacobsen, 1960; Doane, 1961; Godwin and Hastings, 1961; Beroza, 1971) but proved to be very poor or inactive. Bierl *et al.* (1970) succeeded in isolating a new compound, cis-7,8-epoxy-2-methyloctadecane, and proposed the name disparlure for it.

Behavioural aspects of the attractiveness to males of this pheromone have been studied by Doane (1968), Doane and Cardé (1973), Cardé *et al.* (1973) and Doane (1976).

Virgin females are very attractive to males but after mating takes place, their attractiveness fades rapidly. Each female normally lays one egg-mass.

The gypsy moth has now been spreading over the north-eastern United States for well over 100 years and has defoliated hundreds of thousands of acres of forested lands. The variety of plants that the gypsy moth larvae are known to feed on is very wide. Forbush and Fernald (1896) found 458 acceptable hosts from 477 species tested. Mosher (1915) developed four categories of acceptability and tested and classified about 152 species. *Quercus* is the most favored food species together with *Fagus*, *Betula*, and *Pyrus*, but when population density increases,

few species escape the attack of the caterpillars, especially if good silvicultural practices are lacking (Bess et al., 1947; Leonard, 1974; Barbosa, 1973). The amount of food that larvae consume is considerable and always increasing as the larvae get older, with 60 to 70% of the total amount consumed during larval life being consumed in the last larval stadium (Furuno, 1964; Leonard, 1966).

The influence of food quality upon development of the gypsy moth have been studied by Maksimovic (1958), Leonard (1970a,b,1971a,b), Barbosa and Capinera (1977), Capinera and Barbosa (1977). Defoliation can cause reduced growth of the trees and even death if severe defoliation happens more than one year (Kulman, 1971). Certain silvicultural practices can reduce the possibility of defoliation and damage (Bess et al., 1947). Less preferred hosts will diminish the chances of infestation in mixed stands.

The control of the gypsy moth in the past relied considerably on the use of DDT, but it has been abandoned (Brown, 1961; Turner, 1963; Hinckley, 1972). Carbaryl has also been widely used (Connola et al., 1966; Doane and Schaefer, 1971) as well as Trichlorfon, Gardona and Pyrethrins (Leonard, 1974). Recently, a new chemical, Dimilin (1-(4-chlorophenyl)-3-(2,6 difluo robenzoyl)-urea), which is a potent insect growth regulator, has been tested (Granett and Dunbar, 1975; Stewart and

Madrid, 1978), and proved useful, but more research on the impact on parasites and the environment is needed (Granett and Weseloh, 1975).

Pathogens have also been used in the control programs of the gypsy moth with some success. When first brought into North America the gypsy moth appears to have been introduced without the nuclear polyhedrosis virus (NPV), causal agent of polyhedrosis or wilt disease (Doane, 1976a). First records of disease were given by Howard and Fiske (1911). Glaser (1915) stated the possibility of using diseases of the gypsy moth as natural control agents. Wallis (1957,1962), studying the incidence of polyhedrosis on gypsy moths in Connecticut, found a direct correlation between high humidity and the occurrence of disease outbreaks in gypsy moth.

Doane (1967,1969,1970,1971a,b,1975) has worked extensively on gypsy moth pathogens specially nuclear polyhedrosis virus and Streptococcus faecalis. Nuclear polyhedrosis virus major source of infection for the hatching larvae seems to be the egg surface and hair of the egg-mass. The longer the larvae remain on the egg-mass after hatching, the more likely these larvae will become infested, die and serve as a primary inoculum for transmission to other larvae (Doane, 1975). This virus, under natural conditions, reaches epizootic proportions as the host population density increases (Campbell, 1963). Nuclear

polyhedrosis virus has been tested as a control agent against the gypsy moth (Rollinson et al., 1965; Magnoler, 1967,1968, 1970; Cardinal and Smirnoff, 1973) with some success.

Bacillus thuringiensis thuringiensis (Doane and Hitchcock, 1964) and Streptococcus faecalis (Doane, 1971a) have also been tested against the gypsy moth.Weisser (1961) discusses the role of microsporidia as a mortality factor of gypsy moth population and Kerner (1959) reported the use of the entomogenous fungus Paecilomyces farinosus against the gypsy moth.

Another substance that is being tested as a possible control tool is the sex pheromone, disparlure (Granett, 1976). Beroza and Knipling (1972) suggested a method that would disrupt normal finding and mating between female and male. Disparlure has proved to be an extremely effective bait in survey work.

INFLUENCE OF LOW TEMPERATURE UPON SURVIVAL OF THE GYPSY MOTH

General Review of Insect Winter Survival

The gypsy moth, Lymantria dispar (L.) is a univoltine species distributed in a wide range of temperate areas in the world, most of them with extremely low winter temperatures.

An essential part of winter survival of gypsy moth eggs is the ability to avoid freezing (Sullivan and Wallace, 1972). Bachmetjew (1901) made one of the earliest comprehensive studies

on body temperature and freezing point in insects, although his work was criticized later because he extrapolated his results from the species he studied to all insects.

Carter (1925) working on Bruchus obtectus found that injuring (piercing) an insect with a thermocouple affected not only survival but supercooling points. Payne (1926,1927a,1927b) did extensive and thorough studies on insect cold resistance. Supercooling and freezing points of various insects exposed to varying environmental conditions were determined seasonally. They were found to oscillate periodically, being lowest in winter and highest in summer. She found that starvation or dehydration may facilitate cold hardiness.

Ludwig (1928) researching on the Japanese beetle demonstrated that variations during the individual's development was important in determining the response to low temperature.

The works of some of these former researchers (Payne, Bachmetjew and others) provided material for the comprehensive review of Uvarov (1931). He tried to integrate the prior knowledge and formulate a theory of low temperature survival, but concluded only that obviously the problem was intimately connected with the most obscure phenomena of the biochemistry and biophysics of metabolic water in the living organism and it had to be attacked with corresponding methods instead of crude qualitative experiments.

The next twenty years saw a few studies, primarily concerned with different techniques and its betterment (Ditman, Vought and Smith, 1942, 1943).

A fresh approach in the development and utilization of new procedures came from Scholander et al. in the early fifties (1953), working with the Alaskan midge Chironomus. This insect overwinters in ice or frozen mud in the arctic pools and was found to survive at temperatures as low as -40°C.

Studying the pupa of the slug caterpillar Monema flavescens (Lepidoptera, Lymacodidae), Asahina et al. (1954) reported that the overwintering stage survived freezing at -30°C following acclimation at -20°C. The summer larvae did not survive freezing at -10°C. They found, after microscopic studies, that freezing in the summer stage was intracellular and extracellular in the overwintering stage.

Asahina and Aoki (1958), working with the same species, reported that slow cooling rates enhanced survival at extremely low temperatures; with cooling rates of approximately 1°C per minute, there was survival after 45 minutes at -90°C.

Smith (1961) and Salt (1961) both reviewed the existing information on cold hardiness. Salt (1961) identified three mechanisms by which insects could acquire cold-hardiness.

(1) Acclimation to cold but not freezing temperatures

(2) Avoid freezing by supercooling

(3) Withstand freezing

Exposure to low temperatures, without freezing, has been named chilling, specially when temperatures are just above 0°C. All insects develop supercooling to a certain extent, need it or not. Actually, most hibernating insects do need to supercool, to avoid freezing and hence death.

Most of the research done up to this point on poikilotherms was from the viewpoint of changes in activity of the insect before and after acclimation. This is the viewpoint of Bullock (1955) in his review of temperature compensation in poikilotherms.

Few studies were made on the aspects of survival in relation to acclimation to low temperatures. Atwal (1960), working in pupae of Anagasta kuehniella (Zeller) found that cold-acclimation increases with exposure to non-lethal low temperatures, but after an extended period of exposure to these temperatures, the advantages of acclimation begin to be offset by the injurious effects of chilling.

Salt (1961) states that acclimation is a potential advantage that may or may not be used, depending if the insect is exposed or not to a lower temperature.

The most common mechanism used by insects to avoid freezing is supercooling. Supercooling per se is harmless to the insect and is chiefly a matter of prevention of freezing. Some

insects can survive freezing but most of them cannot. The supercooling points then represent the lethal limit of low temperature for all frost-susceptible insects but they can be different for every insect, depending on individual differences and several factors. Metabolically, supercooling represents just an extension of activity to below freezing temperatures (Scholander et al., 1953; Salt, 1961), and does not imply any danger to the insects; the real concern is with the freezing injury that results after freezing takes place.

Since the gypsy moth is not a freezing-tolerant species, I will not attempt to review literature concerning actual freezing but only its consequences as well as the function of the cryoprotectans in lowering the supercooling points.

There is still very few agreements on the nature of the injury caused by freezing. Several theories have attempted to explain it, but there is still much contradiction.

Robinson (1927) postulated his theory of bound water correlated with cold-hardiness. Later Ditman et al. (1943) found no correlation between the percentage of water that remained unfrozen and cold-hardiness degree in seven species of insects studied.

Karow and Webb (1965) believed that freezing damage would be the result from denaturation when bound water is lost from the protein surface or that cellular dehydration causes a

reduction in the distance between individual proteins. This distance reduction would give place to the formation of abnormal disulfide bonds (Levitt, 1962).

Lovelock (1953) postulated the theory of the electrolyte-concentration. Electrolyte levels would increase proportionally with the amount of extracellular water freezing out, and at the same time intracellular water would diffuse out as a result of the new osmotic gradient, then both electrolyte concentration and dehydration would reach lethal levels.

Meryman (1971), working with red blood cells and mollusks, concluded that as freezing progresses and cell water is lost, cells shrink and reach a "minimum critical cell volume", after which membrane rupture would occur.

One of the most obvious theories about freezing damage is the so called "mechanical theory". It refers to the mechanical stress and distorsion that apparently the cell would suffer during freezing. Salt (1961) states that mechanical damage would be quite expected especially in plant cells, but not so evident in the more flexible animal cells. He criticizes this theory for lack of specificity.

Asahina (1966) has developed the "site of freezing" theory, which states that extracellular ice is tolerable but intracellular ice is lethal. He also suggested that one of the most probable factors of increased resistance to fatal

dehydration may be changes in the structure of protoplasm (Asahina, 1969).

The mechanisms involved in survival, nevertheless, were unknown. In 1957, Chino, working with diapausing eggs of the silkwork Bombyx mori and Wyatt and Kalf (1957), working independently in pupae of Hyalophora cecropia, found glycerol to be present in considerable amounts in the overwintering stage.

Salt (1957) reported 2 to 4% glycerol content in the overwintering form of the gall fly Eurosta solidaginis and the webworm Loxostege sticticalis. In a following paper, Salt (1959) reported a glycerol concentration as high as 25% in the overwintering stage of Bracon cephi with the melting points lowered to -17.5°C and the supercooling points depressed as low as -47°C. The factor or factors influencing the build-up and decrement in glycerol content were found to be related to the season.

Glycogen is not involved in glycerol synthesis, at least in B. cephi (op. cit.). Undoubtedly, an increased content of glycerol in B. cephi increases cold-hardiness by decreasing the supercooling point, thus lowering the risk of freezing and/or protecting the tissues if freezing actually occurs.

The role of glycerol and other polyols, mannitol and sorbitol in the development of cold-resistance, is still very much controversial. Somme (1964), working in several species,

found that high concentrations of glycerol in some species (15%) did not protect against freezing injury, whereas other species with a much lower level (< 3%) or no glycerol presence, were freezing-tolerant. He suggested for the first time that other substances besides glycerol are responsible for the development of insect freezing tolerance.

The process of glycerol accumulation in overwintering insects has been the subject of several studies besides those already mentioned. Dubach et al. (1959), Somme (1965a,1965b) Asahina (1969), all of them concerned with glycerol or other polyhydric alcohols as single cryoprotectants. Dual cryoprotectants, glycerol and sorbitol together and related with diapause were found by Chino (1957,1958) in Bombyx mori. Mansingh and Smallman (1972) reported the same two polyols and a correlation between cold-hardiness and diapause.

The regulatory mechanism of glycerol accumulation is not known yet. In some species glycerol forms immediately after diapause initiation (Wyatt and Meyer, 1959), whereas in others, its accumulation takes place only after prolonged chilling or exposure to very low temperatures (Mansingh and Smallman, 1972).

As for the source of glycerol, during overwintering, there is still a need for research; Chino (1957) reported glycogen as the source of glycerol in B. mori. Salt (1958) stated that glycogen was not providing for the synthesis of glycerol

in B. cephi. Recently, Wood and Nordin (1976) suggested that glycerol could be biosynthesized from one or both of the two most probable precursors, hexosil units derived from glycogen and/or acyl glyceride glycerol (in fat body tissue).

It is very important to identify precursor(s) of glycerol as a first step to understanding the enzymic mechanism controlling its accumulation (Wood and Nordin, op. cit.).

Lately, besides the studies on the relationship between cold resistance and glycerol or other low molecular weight polyols, research began on the correlation of cold hardiness to solutes of high molecular weight in antarctic fish (Komatsu et al., 1970; DeVries, 1971), and in an insect species, Meracantha contracta (Duman, 1977). DeVries and Wohlschlag (1969) found three glycoproteins which depress the freezing point in the antarctic fish Trematomus borchgrevinki.

Duman (1977a) suggested that macromolecular antifreeze solutes (glycoprotein) present in the insect hemolymph (overwintering larvae of M. contracta) produce a difference between the freezing and melting points of the hemolymph, phenomenon called thermal hysteresis. This thermal hysteresis contributed to lower significantly the supercooling points of the larvae, preventing ice formation down to temperatures as low as -11°C (Duman, 1977b).

A proteinaceous substance has also been found in the

overwintering queen of the bald faced hornet Vespula maculata, which also presents high levels of glycerol in the haemolymph (Duman and Patterson, 1978).

Winter Survival of the Gypsy Moth

Gypsy moth eggs containing fully formed embryos pass the winter in obligatory diapause (Danilevskii, 1965). The survival rate for the next spring depends upon various factors but low winter temperatures are important. Leonard (1972), studying survival of gypsy moth populations in Maine, during a very severe winter (1970-1971) when the minimum temperature was -32.2°C found that only 15% hatched.

In 1922, Summers reported 100% mortality for Maine and New Hampshire populations exposed to a winter low of -31.7°C. Sullivan and Wallace (1972) showed that the supercooling points (minimum temperature below 0°C at which sudden freezing occurs) of Quebec and Massachusetts eggs did not differ between the two populations but eggs from Quebec withstood low temperatures longer than eggs from Massachusetts.

In the Soviet Union eggs from far Eastern Russia survived longer exposures to low temperature (-20.8°C to -21°C) than eggs from the milder North Caucasus (Pantyukhov, 1964) but eggs from the same Caucasus stock had a higher survival rate than eggs from far Eastern Russia, after being exposed to temperatures

between -25.3°C to -30.5°C for five days. At -15°C egg mortality was 30% and 100% for eggs from Eastern Russia and North Caucasus respectively after 100 days exposure and the mortality for the same population after exposures of 22/24 and 12/14 hrs at temperatures between -45°C to -48°C was about 100%.

Another factor affecting winter survival is the vertical distribution of the egg-masses on tree trunks, in relation to snow cover. Some populations apparently are more likely to lay eggs lower in the habitat. Leonard (1972) found 81% of egg masses below 1.5 m in Maine, in contrast with the Summers report of 30% in Maine, New Hampshire and Massachusetts (Summers, 1922).

In mountainous regions of Yugoslavia, Jankovic (1958) found 85% of egg masses on the trees, laid below 0.5 m (snow line).

The protection afforded by the insulating property of the snow cover is considerable, shown by the air temperatures needed to freeze 50% of supercooled eggs at depths of 2, 4, 6 and 8 inches below the snow line; these are air temperatures of -38°C, -48°C, -66°C and -80°C, respectively (Sullivan and Wallace, 1972). Fully grown embryos inside the eggs enter an obligatory diapause before the onset of cold weather (Tuleschkov, 1935; Andrewartha and Birch, 1954; Danilevskii, 1965; Leonard, 1968). The metabolic rate is very low during diapause. Oxygen consumption was 60 mm^3 per g/live weight/hr at 20°C and the total fat content

consumed during overwintering (from September to May) was 34%. When temperature dropped below 0°C, only 1.9% of the fat content was utilized, and the consumption was minimum when the temperature descended to -10°C. Eggs increase in cold hardiness as the fall season progresses and this increase is associated with a change in composition of the neutral fats and the ratio of saturated to unsaturated acids. A high iodine number indicates a high ratio of unsaturated acids with a low melting point in cold hardy eggs (Pantyukhov, 1964).

The length of exposure to cold weather influences the duration of diapause. Forty days or less at 5°C has little effect on the eggs, but approximately 50% of the eggs will hatch after being exposed to 5°C for 70 days. Percentage hatching decreases if the time of exposure exceeds 200 days (Masaki, 1956).

In the field, hatching starts in the spring when average weekly temperatures climb over 10°C for a period ot two or three weeks (Maksimovic, 1958; Leonard, 1968) and females hatch first. Unusually early hot weather may cause hatching before foliation of the trees and the starving larvae are killed by a following cold period (Grozdanović-Simic, 1958).

GYPSY MOTH PARASITOIDS AND PREDATORS

This literature review outlines the information only

about the most commonly recovered parasitoids and known predators of the gypsy moth in America, native and imported from Europe and Japan, and that have some impact over gypsy moth population control.

Parasitoids of the Gypsy Moth

The gypsy moth was first reported in Quebec (Short, 1926; Cardinal, 1967) and New Brunswick in 1924 and 1936, respectively, but control procedures were successful and eradication was subsequently achieved several times prior to 1965 (McLaine, 1938; Cardinal, 1967; Leohard, 1974). During the late sixties, the moth became established in southern Quebec, south of Montreal. Since then, surveys have found egg-masses within three miles west of the Ontario border (Brown, 1968). To the east, egg-masses have been located as far as Richmond and Trois Rivieres counties (Caron, personal communication, 1976)[a] and flying males have been captured in Lotbiniere, Athabasca, Nicolet and Wolfe Counties, areas considered sensitive to infestation in the near future. Recently, surveys found egg-masses at Thetford Mines and Shawinigan (Schmidt, 1977).

Soon after the establishment of the gypsy moth in North America, a program of parasite importation was implemented by the U.S.D.A.* (Howard and Fiske, 1911). Parasites were imported from Europe and Japan, and work continued actively until 1914 (Griffiths, 1976). From 1922 to 1933 work on beneficial insects

*U.S. Department of Agriculture

[a]A. Caron. Agriculture Canada. Montreal, Quebec.

was resumed in the United States and Europe (Burgess and Crossman, 1929; Dowden, 1962).

This activity started over with renewed impetus and several agencies operate programs and laboratories where parasitoids of the gypsy moth are reared. Shipments of imported parasites from Spain came in 1963, and recently new shipments were sent from France, Yugoslavia, Austria, Germany and Morocco.

The U.S.D.A. at Moorestown, New Jersey and the Connecticut Agricultural Experimental Station at New Haven, Connecticut, together, released parasites from 1963 to 1965. Other U.S.D.A. laboratories have programs in biological control of the gypsy moth dating back to 1963. U.S.D.A. laboratory at Otis Air Force Base in Barnstable Co., Maine released parasites and contributed some stocks for the Trenton laboratory of the New Jersey Department of Agriculture. The Trenton laboratories, supported by the U.S.D.A. provided material to be released in several states, starting in 1971 and locally from 1963 in New Jersey.

Several state and U.S.D.A. laboratories are currently working on the gypsy moth biological control problem (Sabrosky and Reardon, 1976).

In Canada, because parasites released against the browntail moth also attack the gypsy moth, it can be said that the release program started even before the moth was reported for the first time in Canada (1924), with an importation of parasites

of the brown-tail moth Nygmia phaeorrhoea (Donov.) from the U.S.D.A. gypsy moth laboratory at Melrose, Massachusetts (Griffiths, 1976). This program was carried out between 1905 and 1911. Of all the species released, two were gypsy moth enemies, a tachinid larval parasitoid, Compsilura concinnata (Meigen) and a carabid predator on larvae and pupae, Calosoma sycophanta (L.). Only C. concinnata was recovered and became established (Tothill and McLaine, 1916; McGugan and Coppel, 1962).

From 1929 to 1934, during the program against the satin moth, Stilpnotia salicis, four species were released in eastern Canada, but did not include Quebec (McGugan and Coppel, 1962). Apanteles melanoscelus Ratz. was one of the species released, becoming established in all the release areas. Eupteromalus nidulans (Thom.) released during the same program fortunately did not become established (McGugan and Coppel, 1962; Forbes and Ross, 1971) because it was more active as a hyperparasite of braconids (Apanteles melanoscelus between them) than as a primary parasite (Howard and Fiske, 1911; Muesebeck and Dohanian, 1927; Burgess and Crossman, 1929).

In 1937, during the control program against the forest tent caterpillar Malacosoma disstria Hbn., small numbers of the sarcophagid Sarcophaga aldrichi Park were released near Sudbury, Ontario (McGugan and Coppel, 1962). Pimpla turionellae (L.) was released between 1935 and 1958 in Ontario against the

European pine shoot moth, Rhyacionia buoliana (Schiff) but these releases were unsuccessful (McGugan and Coppel, 1962).

Egg Parasites

One of the first species imported into the United States from Japan was the egg parasite Ooencyrtus kuwanai (How.) (Hymenoptera: Encyrtidae) in 1909 (Fiske, 1910; Howard and Fiske, 1911; Muesebeck and Dohanian, 1927; Burgess and Crossman, 1929).

It was released for the first time in Massachusetts (Howard and Fiske, 1911; Burgess and Crossman, 1929) and became established around the release area, although it had a very low natural dispersal.

O. kuwanai is an internal parasitoid of the unhatched gypsy moth caterpillar inside the egg (Howard and Fiske, 1911). The percentage of attack by O. kuwanai reported by Burgess and Crossman (1929) from 1912 to 1927 ranged between 0.06% to 4.18%.

In Connecticut in 1960, Dowden (1961) reported attacks ranging from 11 to 14% parasitism in July and August and increasing to 40% at the end of the summer. In 1962 in Massachusetts and Connecticut, Dowden (1962) found between 40% and 45% parasitism by O. kuwanai, and again in Connecticut (1972) Weseloh reported between 29% to 42% attack.

This species has never been introduced or recovered in Canada, and its range is more restricted toward the north

than that of L. dispar (Burgess and Crossman, 1929; Bess, 1961; Weseloh, 1972). Unfortunately the overwintering adult of O. kuwanai is highly sensitive to low temperatures. This diminishes the possibility of it being established in the northern range of gypsy moth (Griffiths and Sullivan, 1978); however, it does survive the winter in Maine (D. Leonard, personal communication).[a]

In warmer areas of Europe and North Africa O. kuwanai has been successfully introduced from the United States (Templado, 1957; De Lépiney, 1927,1929,1930). The role of the egg-parasites, O. kuwanai and Anastatus disparis is controversial in relation to the percentage of attack on gypsy moth eggs. O. kuwanai has been reported as a hyper-parasite of A. disparis (Bjegović, 1963) and a more efficient parasite of the primary host, but A. disparis has the ability to withstand lower winter temperatures than O. kuwanai, supercooling even to a lower degree than gypsy moth eggs (Bjegović, 1964; Sullivan et al., 1977).

A. disparis Ruschka was introduced to the United States from Europe and Japan in 1906 and released in 1908 in Massachusetts (Howard and Fiske, 1911; Burgess and Crossman, 1929). The program continued until 1932, and after 1909 all colonizations were made from material obtained in New England (Burgess and Crossman, 1929).

A. disparis is a true egg parasite, rarely attacking eggs

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in which the embryos have started development (Howard and Fiske, 1911). This small wasp has more ability to withstand cold climate than O. kuwanai (Sullivan et al., 1977) but its natural dispersal is very low, in part because females do not fly.

Its percentage of successful parasitism varies considerably. Some workers report a very high effectiveness. Kurir (1944) reported A. disparis, as a highly successful parasite in Yugoslavia, reaching 68.5% of attack. In Bulgaria, Stefanov and Keremedchiev (1961) found 80% to 95% parasitism. However, Templado (1957) reported only 15% attack and Romanyk (1966) gave 9% as maximum level of parasitism.

In the United States the percentage of parasitism reached a maximum of 27.86% and a minimum of 0.21% in Massachusetts during the years 1912 to 1927 (Burgess and Crossman, 1929). Clausen (1957) reported 30% parasitism but this percentage declined to 10% in 1927. Bess (1961) reported from 7% to 35% during the years 1937 to 1944.

This insect has never been recovered in Canada. Griffiths (1976) in his complete review, reports other egg-parasites recovered from the gypsy moth in Europe. Hadronotus howardi Mokr & Oglm; Hadronatus lymantriae Masner and Telenomus phalaenarum Ness (Thompson, 1946; Dowden, 1962), 4650 specimens of Telenomus phalaenarum were released unsuccessfully in the United States during 1927 (Dowden, 1962).

Larval Parasitoids

One of the most important parasitoids attacking early instar larvae of gypsy moth is the braconid wasp Apanteles melanoscelus Ratz. (Schaffner, 1934; Burgess and Baker, 1938). A. melanoscelus is native to Europe, especially the southern part, and the north of Africa (Burgess and Crossman, 1929). It has been introduced and successfully established in New England (Crossman, 1922; Burgess and Crossman, 1929; Dowden, 1962; Reardon et al., 1973).

This species has two generations per year, and overwinters as a mature larva inside the cocoon. Adults emerge the next spring to attack first and second instar gypsy moth larvae (Crossman, 1922; Muesebeck and Dohanian, 1927; Burgess and Crossman, 1929; Shapiro, 1956; Clausen, 1956; Dowden, 1962; McGugan and Coppel, 1962; Reardon et al., 1973; Weseloh, 1973).

Potentially, A. melanoscelus could be very effective in controlling gypsy moth populations, but the high hyperparasitism to which it is subjected diminishes its value as a control agent (Crossman, 1922; Muesebeck and Dohanian, 1927; Burgess and Crossman, 1929; Shapiro, 1956; Forbes and Ross, 1971).

A. melanoscelus was released in the United States for the first time in 1911, with yearly releases until 1959 (Burgess, 1915; Burgess and Crossman, 1929). In Quebec it was recovered for the first time in 1971 (J.S. Kelleher, personal communication)[a].

[a]J.S. Kelleher. B.R.I. Agriculture Canada. Ottawa.

Recent studies on A. melanoscelus have dealt specially with host-parasite relationship and parasite impact (Parker, 1933; Tigner et al., 1974a; Weseloh, 1972).

Phobocampe disparis Viereck (Muesebeck et al., 1951) was introduced to the United States from Italy in 1912 and released in Massachusetts during several years (Burgess and Crossman, 1929; Muesebeck and Parker, 1933; Dowden, 1962). First recoveries were reported the same year (1912), and since then, almost every year in small quantities. It has never been recovered in Canada.

P. disparis is specific to the gypsy moth. It hibernates as an adult within its cocoon. Adults emerge about the time gypsy moth eggs begin to hatch. Females oviposit internally in first and second instar larvae, the mature larva issuing from the 4th instar caterpillar drops to the ground, spins its cocoon, completes development and overwinters (Howard and Fiske, 1911; Burgess and Crossman, 1929; Muesebeck and Parker, 1933; Griffiths, 1976).

Hyperparasitism is very high and causes heavy mortality. Winter mortality is also high and P. disparis seems to be not well adapted to its host, because phagocitosis is another important mortality factor (Burgess and Crossman, 1929; Muesebeck and Parker, 1933).

Four exotic species of tachinid parasites are doing some effective control of the gypsy moth. They are Blepharipa pratensis Meigen (Herting, 1975), Compsilura concinnata Meigen (Thompson, 1946), Exorista larvarum (L.) (Stone et al., 1965), Parasetigena silvestris R.D. (Stone et al., 1965).

B. pratensis was introduced to the United States from Europe in 1907 and released during several years in New England. It was recovered by the first time in 1910, became established and the program of colonization continued until 1933 (Howard and Fiske, 1911; Burgess and Crossman, 1929; Dowden, 1962). In Canada it has not been reported. This species is a larval parasitoid but issues from its host after this pupates. The females lay small micro-type eggs on the leaves where gypsy moth larvae feed. After they are ingested, the small maggot issues, bores the intestinal wall, and enters the body cavity, and feeds until the host has reached full grown or pupal stage. Then the maggot bores a hole in the pupa, issues and drops to the ground for pupation and hibernation (Howard and Fiske, 1911; Burgess and Crossman, 1929; Clausen, 1956; Dowden, 1962).

Some authors (Bess, 1961; Weseloh, 1973) have reported B. pratensis as parasitizing small numbers of gypsy moth in New England. Other workers (Burgess and Crossman, 1929; Clausen, 1956; Odell et al., 1974) have found a high percentage of

parasitism by this insect in the same region.

Compsilura concinnata Meig., a tachinid fly, and a known parasitoid of varied hosts, was introduced to the United States from Europe in 1906, being released periodically until 1959. First recovered in Massachusetts in 1909, C. concinnata became successfully established (Howard and Fiske, 1911; Burgess, 1915; Schaffner, 1934).

Material from domestic stock was successfully released in several Canadian provinces from 1912 to 1937 (Tothill, 1916; Tothill and McLaine, 1916; McGugan and Coppel, 1962; Forbes and Ross, 1971). C. concinnata is a multibrooded species, with three or four generations per year; it is highly polyphagous and has been recovered from nearly 200 species of Lepidoptera; it overwinters as an immature larvae in an alternate host, other than the gypsy moth; in the spring the larva develops rapidly, issues from its host, and pupates in the soil. Females larviposit internally, one to four small maggots, piercing the skin of the caterpillar. These parasitoids will emerge as a mature larva from gypsy moth pupae (Howard and Fiske, 1911; Burgess and Crossman, 1929; Schaffner, 1934; Burgess and Baker, 1938; Clausen, 1956; Dowden, 1962; Sabrosky and Reardon, 1976; Griffiths, 1976).

Herting (1960) considered C. concinnata as being less

important than B. pratensis, Exorista larvarum and Parasetigena silvestris against the gypsy moth. In the United States most authors consider it the most important or one of the most important control factors of gypsy moth (Schaffner, 1934; Burgess and Baker, 1938; Clausen, 1956). Dowden (1962) reported that C. concinnata was not important in Europe during rearing work conducted in the 1920's and 1930's, but in the United States it has been very important.

Exorista larvarum (L.) is another tachinid fly imported to New England from Italy in 1906 and yearly until 1911. There were no recoveries and the program started again in 1923 to 1959. The first recovery was reported in 1940 in Connecticut, and now this species is well established throughout the range of the gypsy moth. In Canada, Griffith (1976) listed it as recovered from other hosts but not in the gypsy moth.

E. larvarum has several generations per year (three to four generations) and is highly polyphagous. Herting (1960) reported 54 species from 9 Lepidoptera families as hosts. Females lay large, white conspicuous macrotype eggs on the caterpillar skin, and the young maggots burrow immediately into the host. They issue as a mature larvae and pupate in the soil (Howard and Fiske, 1911; Burgess and Crossman, 1929; Britton, 1935; Dowden, 1962; Campbell, 1967; Griffiths, 1976; Sabrosky and Reardon, 1976).

Herting (1960) and Dowden (1962) reported that E. larvarum is considered one of the most important parasitoids of gypsy moth in Europe. In the United States, although recovered in 1940 for the first time, it has few records of recoveries. In 1941 it was recovered from gypsy moth larval collections from 11 townships in Maine, New Hampshire and Massachusetts (Sellers, 1953). It was released in New Jersey in 1968-1974, but there were no recoveries. The fate of recent releases in Pennsylvania and Maryland is still unknown (Sabrosky and Reardon, 1976).

Parasetigena silvestris R.D. was imported from Central Europe from 1906-1911 and was released at North Andover, Massachusetts in 1910. There were no recoveries. A new colonization was attempted during 1924-1933 at several localities in Massachusetts, New Hampshire, Maine and Connecticut. First recoveries were reported at Boxford, Massachusetts in 1927. It is considered well established in the gypsy moth territory (Howard and Fiske, 1911; Burgess and Crossman, 1929; Clausen, 1956; Dowden, 1962; Griffiths, 1976, Sabrosky and Reardon, 1976). This species has not been reported in Canada. P. silvestris is a univoltine species that hibernates as a mature larva inside its puparium. Females lay the eggs on the integument of the caterpillar. The eggs are large, whitish and macrotype and several of them can be seen sometimes on one caterpillar,

but usually only one parasitoid will develop per host. The mature maggot commonly issues from late instar caterpillars or rarely pupae (Howard and Fiske, 1911; Burgess and Crossman, 1929; Clausen, 1956; Herting, 1960; Dowden, 1962; Griffiths, 1976).

European authors have given importance to P. silvestris. Herting (1960) ranked it third after B. pratensis and E. larvarum.

Pupal Parasitoids

The role of Sarcophaga aldrichi Park. in relation to the gypsy moth is somewhat controversial. Howard and Fiske (1911) mentioned the confusion and the lack of research in this matter. They stated that sarcophagids are truly parasitic upon grasshoppers, but with the current knowledge it is not possible to state the same with respect to lepidopterous hosts.

Campbell (1963a,1967) reported that S. aldrichi is a scavenger, feeding on dead pupae and most of these pupae are killed by parasitic Ichneumonidae stinging them. Theronia atalantae, Itoplectis conquisitor and Pimpla pedalis sting gypsy moth pupae, feed on them, sometimes lay eggs, and open the way for Sarcophaga aldrichi.

Two native ichneumonid species (Pimpla pedalis Cress. and Theronia atalantae) attack gypsy moth pupae. Campbell

(1963a,1967) states that many more pupae are stung by this wasp than the number of actual ovipositions. In 1974 P. pedalis was recovered in Glengarry County, Ontario from larval collections of gypsy moth (Griffiths, 1976). T. atalantae has been recovered in Canada from other hosts (Griffiths, 1976).

Brachymeria compsilurae Crawf. is a native species, hyperparasitic on gypsy moth parasites. It attacks tachinid flies, and among them several of the most important gypsy moth parasitoids. B. compsilurae has been recovered from C. concinnata, B. pratensis and P. silvestris.

The hyperparasite attacks the maggots when they are inside their host and the wasp will issue from the puparium of the tachinid. It has one or more generations per year, depending on the number of generations of the host (Dowden, 1935; Griffiths, 1976).

Brachymeria intermedia Ness. has received very good reports as a parasite of gypsy moth pupae. It is an introduced species shipped from Europe in 1909. Despite several colonizations in the years after introduction, it did not become established or at least it was never recovered (Burgess and Crossman, 1929).

In 1960 Burks reported B. intermedia recovered from a leaf roller pupa, collected in Massachusetts in 1942.

Leonard (1966b) found the parasitoid attacking tortricid pupae in Connecticut and gypsy moth pupae in Connecticut and Maine (Leonard, 1967, 1971).

B. intermedia has two and a possible partial third generation per year, hibernates as an adult under the bark of fallen trees, etc. (Dowden, 1935).

Several authors reported a high population of B. intermedia parasitizing gypsy moths in Europe, but these records of abundance account for one season, with practically no recoveries afterward (Webber, 1937; Howard and Fiske, 1911; De Lépiney, 1930). In New England, Leonard (1967, 1971) obtained small numbers of this parasite (4.7 and 3.6%, respectively).

Grimble (1975), after releasing 44,000 specimens in Lordville, New York, found no significant correlation in the percentage of parasitism after the release. It has not been recovered previously in Canada (Griffiths, 1976).

Predators of the Gypsy Moth

Forbush and Fernald (1896) mentioned a few native species of insects, spiders and vertebrate predators of the gypsy moth. Howard and Fiske (1911) and Burgess and Crossman (1929) reported on exotic species introduced from Europe, together with some

native species. This importation work was part of the program of biological control of the gypsy moth launched by the U.S.D.A. and the State of Massachusetts at the turn of the century. Several species of Calosoma and Carabus were imported from Europe from 1905 on, but only Calosoma sycophanta (L.) and two species of Carabus were recovered later (Burgess and Crossman, 1929; Dowden, 1962). Calosoma sycophanta was released in Canada in several provinces including Quebec between the years 1912 and 1918, against other hosts (Tothill and McLaine, 1916), but there were no later recoveries and it is considered as not established in Canada (McGugan and Coppel, 1962).

Calosoma frigidum Kirby, a native North American species, has also been reported preying on gypsy moths in New England (Bess, 1961) and it has been recovered in Quebec (Larochelle, 1975) and Ontario (Rivard, 1964), but not attacking the gypsy moth.

Some species of Pentatomids are reported feeding on the gypsy moth. Forbush and Fernald (1896) described the life history of Podisus serieventris Uhl.. Campbell (1967) found unidentified specimens of Pentatomids feeding on eggs and larvae of the gypsy moth. There are no records of Pentatomids found feeding on the gypsy moth in Canada (Griffiths, 1976).

Forbush and Fernald (1896) mentioned two species of spiders seen feeding on eggs, larvae and adults of the gypsy

moth. Spiders are known at least as casual feeders on the gypsy moth (Burgess and Crossman, 1929; Bess, 1961). Campbell (1974), after 17 years of observation, rarely observed spiders or ants predating on the gypsy moth. Furuta (1977) found that predation by two species of spiders on caterpillars was negligibly small and inversely density-dependent.

Forbush and Fernald (1896) treated extensively the role of birds as predators of the gypsy moth. They listed thirty-eight species feeding upon the gypsy moth. McAtee (1911) gave a list of forty-six species of bird predators and discussed their role as disseminators of the pest. Campbell (1974) reported that birds can be important predators of large larvae, but their role will be effective usually only at sparse population densities. In Europe, Turček (1948,1950) reported nine species of birds eating gypsy moth larvae, but concluded that the birds probably play a role in keeping down sparse populations but are not effective during outbreaks. Furuta (1972) found birds caused mortality, second only to mortality during air-borne dispersal. Campbell and Sloan (1977) reported that sparse populations of gypsy moth maintain their stability thanks to the activity of predacious birds and small mammals.

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III. THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS IN THE DEVELOPMENT AND BEHAVIOR OF THE GYPSY MOTH (*LYMANTRIA DISPAR* L.)[1] IN QUEBEC

[1] Lepidoptera: Lymantriidae

ABSTRACT

Eggs of Quebec populations of the gypsy moth Lymantria dispar L. (Lepidoptera: Lymantriidae) hatched in the first week of May in 1977. Hatching is affected by temperature and humidity. Survival of starving newly hatched larvae was higher at 19°C and 100% R.H. than at 25°C and lower percentage R.H. Older larvae (Instar IV, V, VI) showed a different food preference from more southern populations. In decreasing order, they preferred birch, oak and maple. Pupal sex ratio varied widely among plots and among collecting sites. Flying males captured with sticky traps showed a periodical pattern of attraction to traps, influenced only slightly by minimal temperatures. Population trends were obtained for all sampling sites.

INTRODUCTION

The gypsy moth originated in Eurasia, but now has many races occupying different countries and territories. A European race was introduced to North America (Bess, 1961). Goldschmidt (1934), in his comprehensive work, found many differences between geographic populations of Lymantria dispar, but differences in behavior and development rate between populations within the same strain have not been so thoroughly studied. Leonard (1966) stated the importance of these studies on variation, as essential tools in the study of population dynamics. Quebec has been invaded by the gypsy moth via the United States since 1924, but it only became established in the last decade. Consequently, there is little information on the development and behavior of the Quebec population.

MATERIALS AND METHODS

Study Sites

Two areas, one located near the border between Quebec and New York State in Huntingdon County (lat. 45 05 N, long. 74

11 W), referred to as Havelock after the nearest town, and the other, a forested area at the McGill Gault Estate at Mont St. Hilaire, Rouville County (lat 45 30N, long 74 04 W), were chosen as intensive study sites. The Havelock site was within an area which had been sprayed with insecticide (Sevin-4) for several years until 1970, by the Plant Protection Division, Canada Department of Agriculture. Spraying was stopped because the desired results were not obtained and the pest continued spreading (Forest Insect and Disease Survey Report, 1972).

The St. Hilaire site has no record of chemical treatment. The population at Havelock was established before that at Mont St. Hilaire, and the woodlot in which it was established was untended. The ground cover was thick with mixed grasses, moss and lillies of the valley, and was dotted with rock outcrops.

The understory was composed of Bracken Fern (Pteridium aquilinum (L.) Kuhn), Ostrich Fern (Metteuccia striuthioptenis L.), Raspberry (Rubus strigoms Midrx, Rushes (Juncus spp), and the overstory of White Pine, (Pinus strobus L.), Eastern Hemlock (Tsuga canadensis)(L.) Carr, Gray Birch (Betula populifolia Marsh), Sugar Maple (Acer saccharum Marsh), American Beech (Fagus grandifolia Ehrh).

The Gault Estate at Mont St. Hilaire is owned by McGill University, and its natural state has not been altered. The collecting sites were located at Lake Mountain (900 m), one of

several peaks of Mont St. Hilaire. The forest is composed of Ulmus americana (L.), Fraxinus nigra (Marsh), Betula lutea (Michx), Fagus grandifolia (Ehrh), Acer rubrum (L.), Acer saccharum (L.), and Juglans cinerea (L.). Ground cover was mainly composed by Solidago canadensis (L.), S. rugosa (Mill.), Steironema ciliatum (L.) Raf., Muhlenbeizia mexicana (L.) Trin, Desclampsia flexuosa (L.) Trin. and Paa pratense (L.).

The criteria used in selecting these two sites over other infested places were: high population density, the lack of an insecticidal spray program and the differences in forest composition and altitude.

Sample plots in each woodlot consisted of five 0.5 acre randomly located sites. In each of these 0.5 acre plots, sub-plots of 0.04 ha. were established for egg-mass counts and defoliation measurements.

Sampling

Eggs

Direct counts of all egg-masses seen per 0.1 acre plot were made in the fall, when the deciduous leaves had fallen and before snow fell. All plots were carefully examined and a complete tally of egg-masses present was made using the technique of Connolla et al. (1966). To calculate the mean number of eggs per egg-mass, an average of 25 egg-masses per sub-plot were

collected prior to hatching in the spring, from ground level to 5 m and allowed to hatch. After hatching was completed, unhatched eggs were examined under a microscope to determine the probable cause of death.

Larvae and Pupae

The population of first instar larvae was taken to be the number of successfully hatched eggs per plot, a value obtained by calculating the average number of successfully hatched eggs from selected egg-masses collected in the spring from below and above the snow level.

Late instar larvae (IV, V and VI instar) were collected on the bole, near the base, and under burlap bands placed at breast height on three trees in each subplot. Late instar larvae feed at night and during the day they rest under barkflaps and crevices near the base of the trunk (Campbell and Sloan, 1977). This behavioral trait was also noted by Odell and Godwin (1979) who indicated that 95 per cent of large larvae used barkflaps placed at a height of 1.5 m, as resting sites.

Records of weekly collection during the whole summer period were taken in each year (1977 and 1978). Larvae were classified by instar, measuring the head (capsule). Some of the larvae remained small without molting or molted fewer times than expected (Forbush and Fernald, 1876).

Pupal numbers were estimated, by counting, after adult emergence was completed, all dead pupae and all empty pupal cases from which adult moths had emerged. The ratio of dead pupae to the total sample gave an estimate of the proportion of the total pupae that died.

Sex Ratio

The sex ratio of pupae and adults was easily determined by examining empty pupal cases as they show a sexual dimorphism (Campbell, 1963). Where possible, dead pupae were examined to establish cause of death.

Effect of Temperature and Relative Humidity Upon Embryonation and Hatching of Eggs

Embryonation

Newly laid eggs were collected and placed immediately under controlled conditions in cabinets at 80% relative humidity and 16 h photoperiod at four different temperatures (10°C, 15°C, 20°C, 25°C) to measure their influence on embryonation. Each treatment was replicated four times and one egg-mass quartered was used for each series (four egg-masses in total). Eggs were dehaired, gently, to allow microscopic observation, and placed in Petri dishes (5.8 cm diam. x 1.7 cm height).

Hatching

Egg-masses collected in the spring were subjected to

different conditions of temperature and Relative Humidity. One cluster provided eggs for all the different treatments (50 eggs per treatment, all 200 eggs from one cluster) and each series was replicated four times.

Relative Humidity was controlled using different concentrations of KOH solutions (Solomon, 1951), placed at the bottom of desiccators. Eggs were left to hatch in small bivalve boxes (Khattat and Stewart, 1975) deposited in the free air space of the desiccators. The desiccators were placed in cabinets with controlled temperatures.

Food Preference

Fourth, fifth and sixth instar larvae were collected from oak trees from the field, placed individually in food containers (12x10x8 (cm)), starved for 24 hours and then presented with a choice of leaves of oak (Quercus rubra L.), paper birch (Betula papyrifera), sugar maple (Acer saccharum Marsh) and horse chestnut (Aesculus hippocastanum L.). Photocopies of leaves used were made prior to feeding and after feeding. All areas of leaves used were measured with a compensating planimeter.

One series was fed with birch leaves covered with a horse chestnut leaf extract, prepared by macerating the leaves in a mortar and pestle, adding distilled water (10 cc water per leaf,

then filtering. Series I leaves had both surfaces covered with the extract and Series II only one side. All larvae were kept in cabinets at 23°C, 80% R.H. and 16 hours photoperiod and the food consumed in 24 hours was recorded.

Determination of Flight Period

Five disparlure (gypsy moth pheromone) traps, provided by the Division de la Protection des Vegetaux, Ministere de l'Agriculture du Canada, Quebec, were placed in four separate sites (20 traps) in the Morgan Arboretum of Macdonald College Campus, Ste. Anne de Bellevue (lat. 4525 N long. 7356 W), attached to trees at breast height. Daily records (from July 14 until August 15) of the numbers of males trapped were obtained, and related to daily maximum and minimum temperatures and wind speed and direction.

RESULTS AND DISCUSSION

Hatching of Eggs

Figure 1 shows the life cycle of the gypsy moth in Quebec. First instar larvae appeared in the first week of May with most hatching in the second week and by the end of May all hatching had been completed.

Egg hatching is affected by temperature and humidity, as has been reported by Maksimovic (1958) and Leonard (1970).

Given the more northern latitude of the Quebec population, later hatching was expected, compared with populations in New England. Burgess and Baker (1938) gave different dates of hatching for different latitudes - May 1 in southern New England, May 25 to the northernmost areas. Most authors give the first week of May as the first date of hatching (Burgess and Crossman, 1929; Britton, 1935; Bess, 1961; Leonard, 1968; Baker, 1972). However, the starting date for Quebec populations in 1977 and 1978 was also the first week of May with most hatching occurring during the second and third week of May and hatching was completed by the last week. Figure 2 shows cumulative hatching during 1977.

If only extrinsic factors such as temperature were involved in the regulation of the time of hatch, northern populations should hatch when warmer temperatures appear. Goldschmidt (1934) states that time of hatching is not only a function of temperature (a minimum of temperature is needed), but also a function of an internal process he calls "readiness to hatch", concluding that "a number of genetic factors, which might be racially different, must be involved in the case."

Egg-masses taken from the field on May 2, 1977 were placed under controlled conditions of temperature and relative humidity. Tables 1 and 2 show the results found. Hatching took place earlier at higher temperatures with 25°C being the optimum.

Maksimovic (1958) had similar results in Yugoslavia. The eggs in one egg-mass hatched over a period of 3 - 5 days (Table 1).

Relative humidity also influenced the rate of hatching with those eggs at higher Relative Humidity hatching first (Table 2).

Larval Period and Feeding Behavior

Female caterpillars have six instars, males only five; however, Leonard (1966) found that both sexes sometimes underwent one additional instar.

After hatching, larvae remain on the egg-mass without feeding for some time, then start looking for food or spin their silken thread being dispersed by ballooning.

The life span of starving, newly hatched caterpillars under different relative humidity regimens was tested (Figure 3). Survival was enhanced by high humidity, but higher temperatures reduced the survival time. Resistance of starving first instar larvae can be of great survival value in the field, in the case of early hatching with no immediate availability of food.

Figure 4 illustrates the phenology of the gypsy moth during the summer of 1977 at Havelock. The last adults were captured by pheromone traps around mid-August.

Larvae reach instar IV by mid-June, at which time extreme defoliation starts, especially when the caterpillar population

is dense.

Tables 3-5 show the amount of food consumed and feeding preferences of larvae. Instar VI ate 203 cm^2 more leaf area than instar IV larvae, and instar V ate 121 cm^2 more compared with instar IV larvae (Table 3). Larvae fed on paper birch consumed 105 cm^2 more leaf area than those fed on maple and 36 cm^2 more oak surface than maple (Table 4). Maple was classified as not being a favored food by Mosher (1915), but a few individuals reached adulthood feeding on maple leaves.

Birch leaves whose surface was spread with extract of horse chestnut leaves, were not touched until the extract dried out and even when dry, were not eaten in great amounts (Table 5). This preference is clearly reflected in the forest stands, where oak, birch and beech are severely defoliated, compared with not so favored species as maple. Moreover, some of the trees, within a given species are more defoliated than other specimens (Campbell and Sloan, 1977).

Adlung (1957) sprayed oak and hazel leaves (favored hosts) with extracts of leaves from black alder and horse chestnut (non-favored food) and found that the extracts discouraged larval feeding.

Considering that the deciduous forest of New England reaches its boundaries just north of Lake Erie, Lake Ontario and the Quebec-United States border (Hosie, 1975) gypsy moth

caterpillars will have to find new host-plants; those that are relatively more abundant on the northern forest. This change appears to be already in progress in Quebec, as the results of these tests suggest, birch was consistently preferred over the primary host, oak. Capinera and Barbosa (1977) found that larvae reared on red oak-white pine diet yielded a higher number of eggs per mass than all other categories. White pine is a characteristic tree in the Great Lakes-St. Lawrence Region, but its range also extends into the southeastern parts of the Boreal Forest Region and Acadian Forest Region (Rowe, 1972).

Pupal Development and Sex Ratio

Males start pupating first, around the last week of June. The last pupae were found the first week of August, during both field seasons (1977-1978). The sex ratio among pupae and adults, varied greatly from one plot to the other, and between sites (Table 6). Mortality factors such as disease and parasitism tend to cause differential mortality between sexes in the gypsy moth (Campbell, 1963b). At Mont St. Hilaire the pupal sex ratio including diseased, parasitized and healthy pupae was 26 males to 74 females, but diseased pupae showed a ratio of 41 to 59 and parasitized pupae 58:42 males to females. Results from Havelock showed 52:48 male to female for total pupae, 58:42 and 24:76 males to females for diseased and

parasitized individuals, during the 1978 season.

Blepharipa pratensis, a tachinid parasitoid, causes differential mortality among larvae killing more females than males (Burgess and Crossman, 1929). Because female larvae go through one more instar than male larvae, they are more susceptible to attacks by parasites or disease.

Adult Emergence, Flying Period and Mating

Gypsy moth males are strong fliers, searching for the female flying upwind, attracted by the scent released by virgin females. In some cases, males have been found in places far from their supposed original point; a male gypsy moth found in the Channel Islands, off the coast of Brittany in 1968, is believed to have come from Spain or North Africa (Rutherford, 1969).

Adults start emerging during the latter part of June until late August and early September (Burgess and Crossman, 1929; Britton, 1935). In Quebec, males were first captured during the second week of July and the last during the second week of August (Figure 5). Daily records of capture of males with Delta traps scented with disparlure showed a periodical pattern of response to the attractiveness of the trap, with the minimal temperature as the only factor showing a slight influence on this pattern ($F = 4.35$, $P = 0.05$) (Figure 6).

Females usually do not fly. There are reports of flying females in Russia (Mikkola, 1971) and United States (Sandquist et al., 1973). Zwolfer (1972) reports flying Japanese females from Hokaido.

At Mont St. Hilaire, Quebec, a female gypsy moth was found trapped in a Delta trap on July 21, 1978. The location of the trap precluded access by crawling and the moth was stuck in the center of the sticky surface (Figure 7). This female was dissected and found empty. She was able to deposit scales as in normal oviposition and was a normal female (1.5 cm length, 2 cm wing span).

Males fly upwind following the trail of scent released by "calling" virgin females. When females release sex pheromone, they do it in a typical "calling" position, protruding and retracting the last abdominal segments (Doane, 1968). Males, when nearing the source of pheromone, are assisted by sight in locating the female. Copulation takes place shortly after, lasting from three minutes to one hour. Very short copulation time, 4.5 or 6 minutes, results in egg-masses with scattered and small eggs, which are not fertile. Normal fertile eggs are laid in only one mass of eggs and abdominal hair, cemented with a secretion produced by accessory glands (Doane, op. cit.).

A few eggs remain inside the body cavity of the female after oviposition, but their proportion to total number of eggs

is not significant. . . From 120 females dissected after oviposition only 2% of them had more than 50 eggs remaining.

Embryonation takes place immediately after oviposition. Eggs placed at 10°C did not show embryogenesis, at 15°C they took between 27 and 30 days to embryonate and at 21°C they took between 13 and 21 days to complete embryogenesis (Figure 8).

Fertility and Population Trend

The number of eggs per female was related to weight of female. Figures 9 and 10 show the regressions obtained in 1978 at Havelock and Mont St. Hilaire. Regressions were similar in form for each population.

Female fecundity seems to be closely correlated with population changes. Population change, during a generation is indicated by the ratio of the number of egg-masses at the beginning of a year to the number of egg-masses at the end of the same year. The index of population trend (Morris and Miller, 1954) was calculated as the relation between number of eggs per acre at the end of the generation and number of eggs at the beginning of the generation, this relation being expressed as a percentage (Table 7). The same trend can be drawn for the number of eggs per mass. Campbell (1963b) and Capinera and Barbosa (1977) related increasing density with decreasing pupal weight, which results in females that lay smaller egg-masses. Small egg-masses,

show less eggs per egg-mass, thus affecting population levels (Figure 11).

Population density in Havelock showed a gradual decline after reaching numbers of several thousands of egg-masses per acre without causing severe defoliation. Trend value (I = 52.5% for 1979) shows this decline accentuated. Reasons for this decline are probably based on a higher winter mortality (1977 = 26.2%, 1978 = 37.8%) and a high impact of disease and parasite attack, especially in 1977 (Table 8).

At Mont St. Hilaire, a reverse trend was observed. The population increased in density, regardless of high mortality caused by disease. Winter mortality was only 14.9 in 1978, not as high as in Havelock.

A sparse population at the Morgan Arboretum was in the increasing phase. No disease was found and Apanteles melanoscelus was the only parasitoid recovered from this site.

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Table 1. Percentage hatching per day of gypsy moth eggs collected from Havelock, and kept at different controlled temperatures and 80% R.H. (mean value of four replicates) (April 1977).

Temperature (°C)	No. of Eggs	Days to Hatching 1	2	3	4	5	6	7
15	200					18.6	73.9	7.4
20	200		22.2	39.1	36.6	1.5	0.3	
25	200	15.6	72.1	9.6	2.2			
30	200	10.5	66.8	20.6	1.9			

Table 2. Percentage hatching per day of gypsy moth eggs collected from Havelock (April, 1977) and kept at different Relative Humidity values (%) and two constant temperatures (mean value of four replicates).

Temperature (°C)	Days No.	Relative Humidity (%) 14	40	80	100
23	1	30.3*	67.2	88.4	94.3
	2	64.6	29.8	10.5	5.6
	3	5.0	2.4	1.5	0
	4	0	0.3	0	0
31	1	24.4	23.9	67.1	67.5
	2	61.2	69.0	32.8	32.5
	3	13.2	7.0	0	0
	4	1.0	0	0	0

*No. eggs 100 per series.

Table 3. Leaf area consumed by instar V and VI larvae, related to area consumed by instar IV, without and with area wasted during feeding, included.

Instar	Consumed	Mean	Consumed + Wasted	Mean
IV	0	92.6	0	141.9
V	121.3±10	174.3	126.9 ± 12.1	214.2
VI	203.9±10	295.4	199.9 ± 12.2	340.8

$P < 0.01$

Table 4. Leaf area consumed by instar IV larvae on Beech and Oak related to area consumed on maple, with and without area wasted during feeding included.

Tree Species	Consumed	Mean	Consumed + Wasted	Mean
Maple	0	141.6	0	192.5
Oak	36.7±10.1	177.5	26.8 ± 12.2	218.8
Beech	105.9±10	245.3	97.2 ± 12.1	287.6

$P < 0.01$

Table 5. Birch leaf area completely covered, partially covered and not covered by horse chestnut extract consumed in cm^2 by IV instar larvae*.

	n	Mean ± S.D.
Completely covered	25	50.08 ± 18.3[a]
Partially covered	25	77.7 ± 20.4[b]
Not covered	25	99.2 ± 36.2[c]

*Any two means associated with the same letter are not significantly different as determined by Duncan's New Multiple-Range Test at the 0.01 level.

Table 6. Sex ratio of field collected pupae total, parasitized and diseased and of pupae under burlap traps.

Plot	Mont St.Hilaire 1978	Havelock 1977	Havelock 1978
N =	850	605	720
	Male:Female	Male:Female	Male:Female
1	22.3:77.6	52.6:47.3	38.4:61.5
2	21.2:78.8	47.7:52.2	51.7:48.2
3	25.0:75.0	62.6:37.3	37.8:62.1
4	41.0:58.9	41.7:58.2	80.0:20.0
5	21.6:78.3	34.2:65.7	37.7:62.2
			60.0:40.0*
			60.6:39.4*
Average total pupae	26.2:73.7	47.7:52.2	52.3:47.6
Average Parasitized pupae	57.9:42.1	51.0:48.9	24.1:75.8
Average diseased pupa	41.1:58.8	59.9:40.0	58.2:41.7
Sex ratio under burlap	52.4:47.5	38.2:61.7	59.1:40.8

*Collections outside plots.

Table 7. Index of population trend and mean numbers of egg-masses, eggs and larvae I in 0.04 ha. plots (Havelock and Mont St. Hilaire, Quebec).

	No. Egg-masses	Eggs	Larva I	I=100 $\frac{N+1}{N}$ [a]	Year
	264	124,456	91,802.2	96.5	1977
Havelock	286	120,120	74,714.2	52.5	1978
	139	63,099	-	-	1979
	259	94,940	80,794.2	133	1978
Mont St. Hilaire	395	126,400	-	-	1979

[a] $N+1$ = eggs at the end of the generation.
N = eggs at the beginning of the generation.

Table 8. Summary of oviposition and hatching of gypsy moth eggs. Quebec.

	Havelock			Mont St. Hilaire		Morgan Arboretum	
	1976	1977	1978	1977	1978	1977	1978
Estimated no. egg-masses per acre	2648	2860	1396	2594	3950	27	40
Mean number eggs per egg-mass	470	420	452	366	320	940	872
Estimated[1] hatching per acre (%)	73.8	62.2	-	85.1	-	78.8	-

[1] Percentage survival after winter.

Figure 1. Life cycle of the gypsy moth in Quebec (1977-1978)

ADULT
PUPAE
LARVAE
EGG
J
J
A
S
O
N
D
J
F
M
A
M

Figure 2. Cumulative hatching period of gypsy moth eggs at Macdonald College (Quebec, 1977).

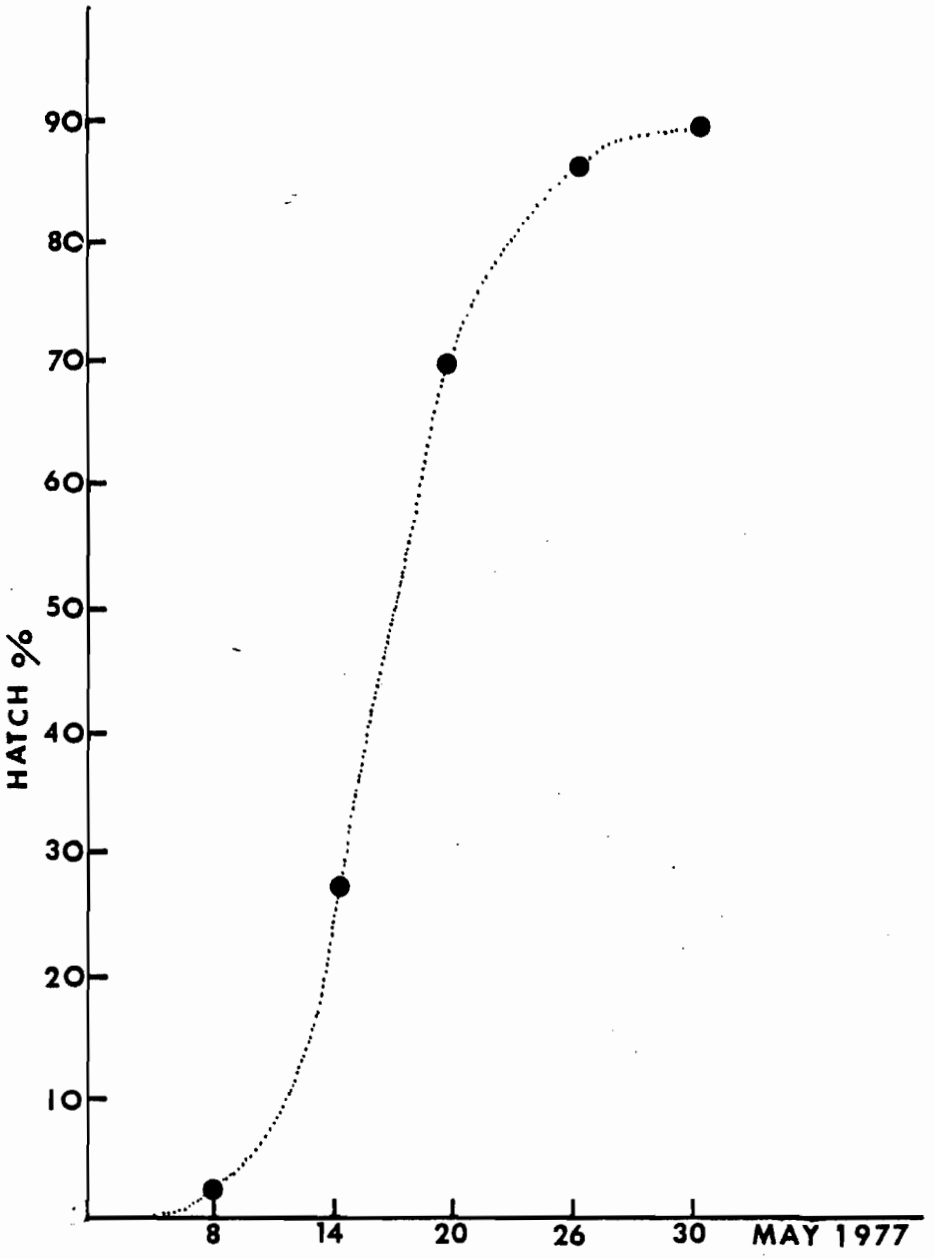

HATCH %
90
80
70
60
50
40
30
20
10
8
14
20
26
30
MAY 1977

Figure 3. Life span of newly hatched larvae of gypsy moth under different R.H. and temperature treatments, in starving conditions.

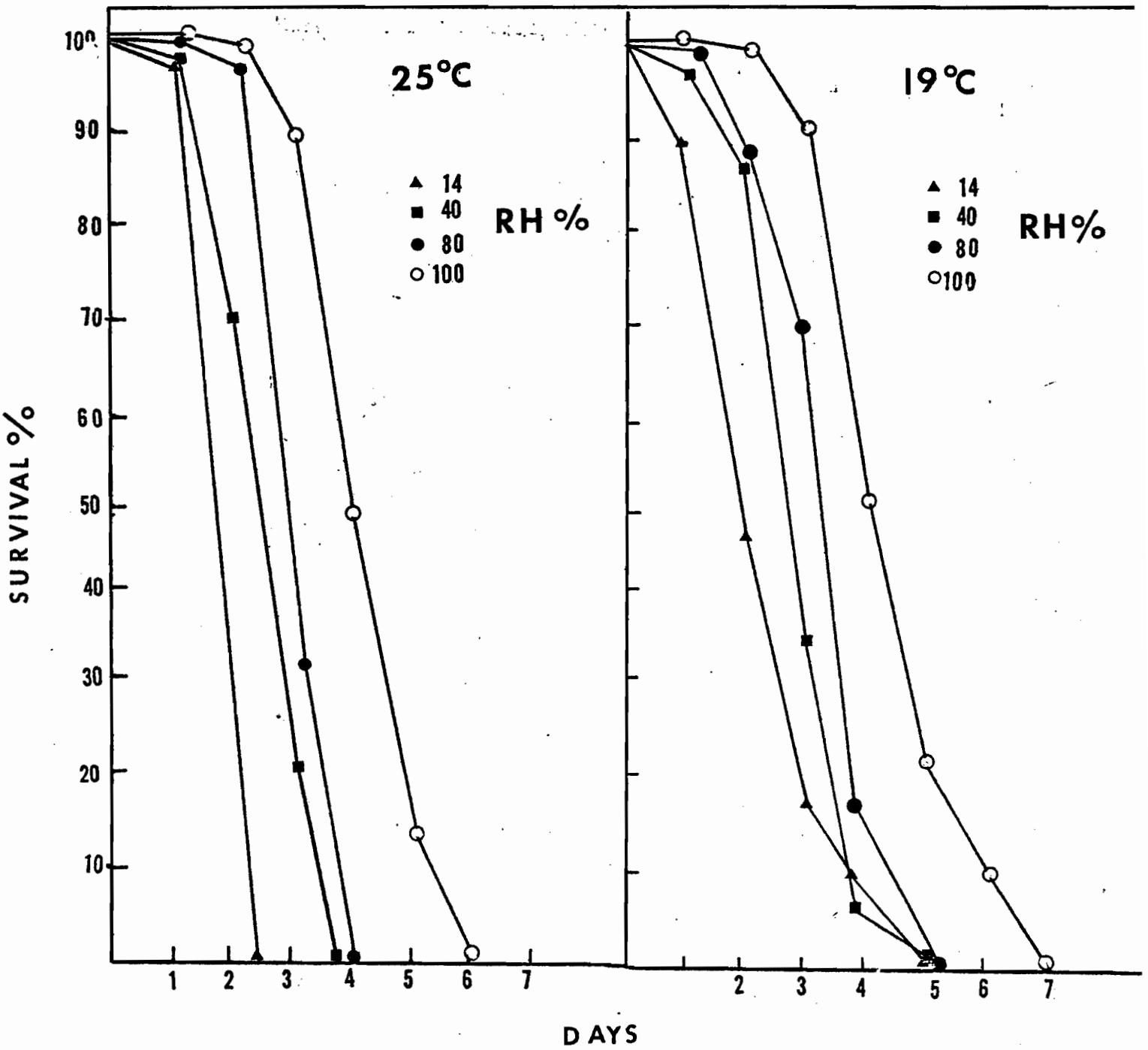

25°C
19°C
14
40
80
100
RH %
RH%
SURVIVAL %
DAYS
100
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7

Figure 4. Percentage of larva (instar I to VI), pupae and adults of gypsy moth collected weekly during the season from Havelock (Quebec).

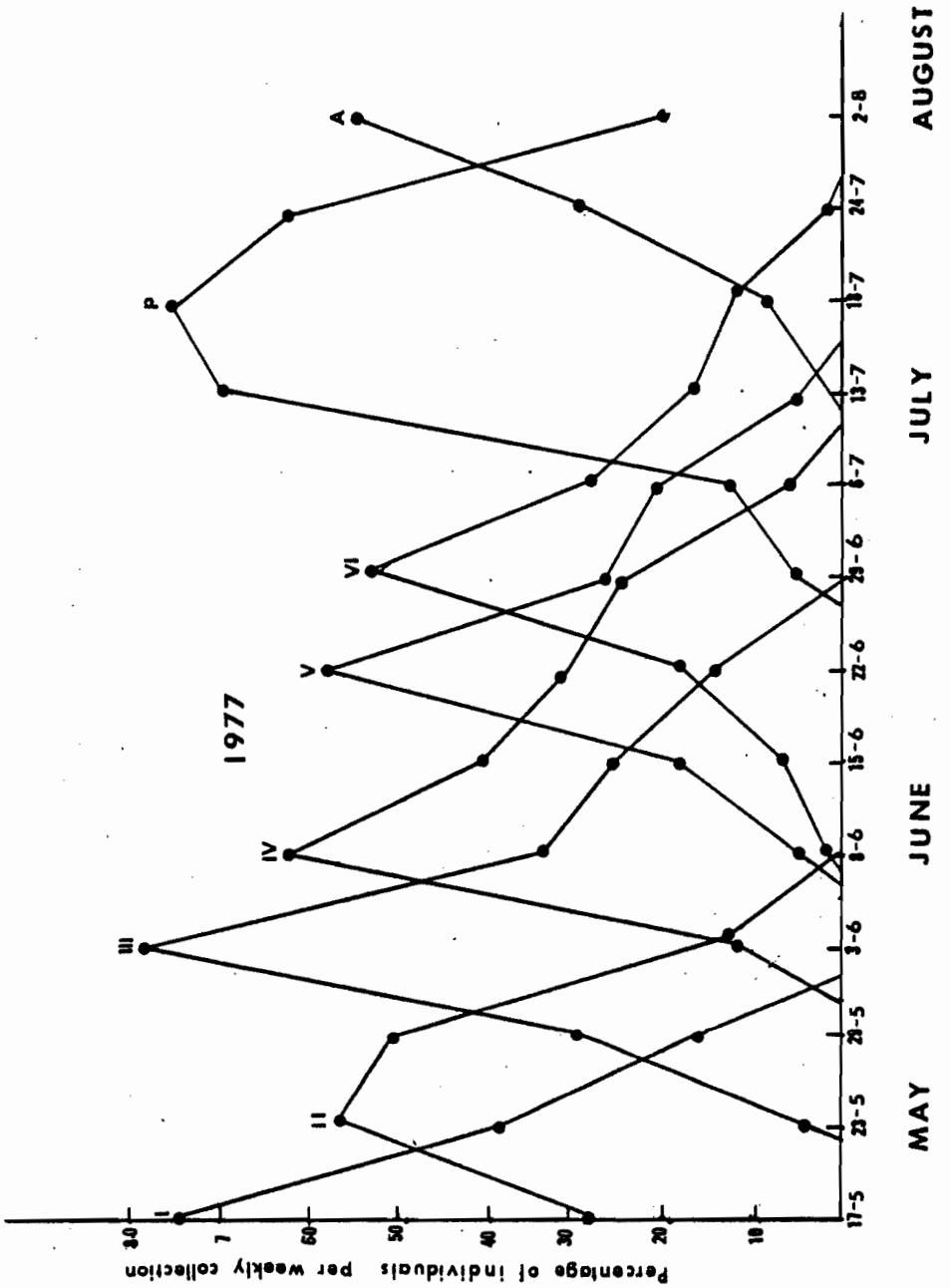

Percentage of individuals per weekly collection
80
70
60
50
40
30
20
10
1977
I
II
III
IV
V
VI
P
A
17-5
23-5
29-5
3-6
8-6
15-6
22-6
29-6
6-7
13-7
18-7
24-7
2-8
MAY
JUNE
JULY
AUGUST

Figure 5. Cumulative catch of male gypsy moth with pheromone scented Delta traps, during the whole flying period, Macdonald College, Quebec (1977-1978).

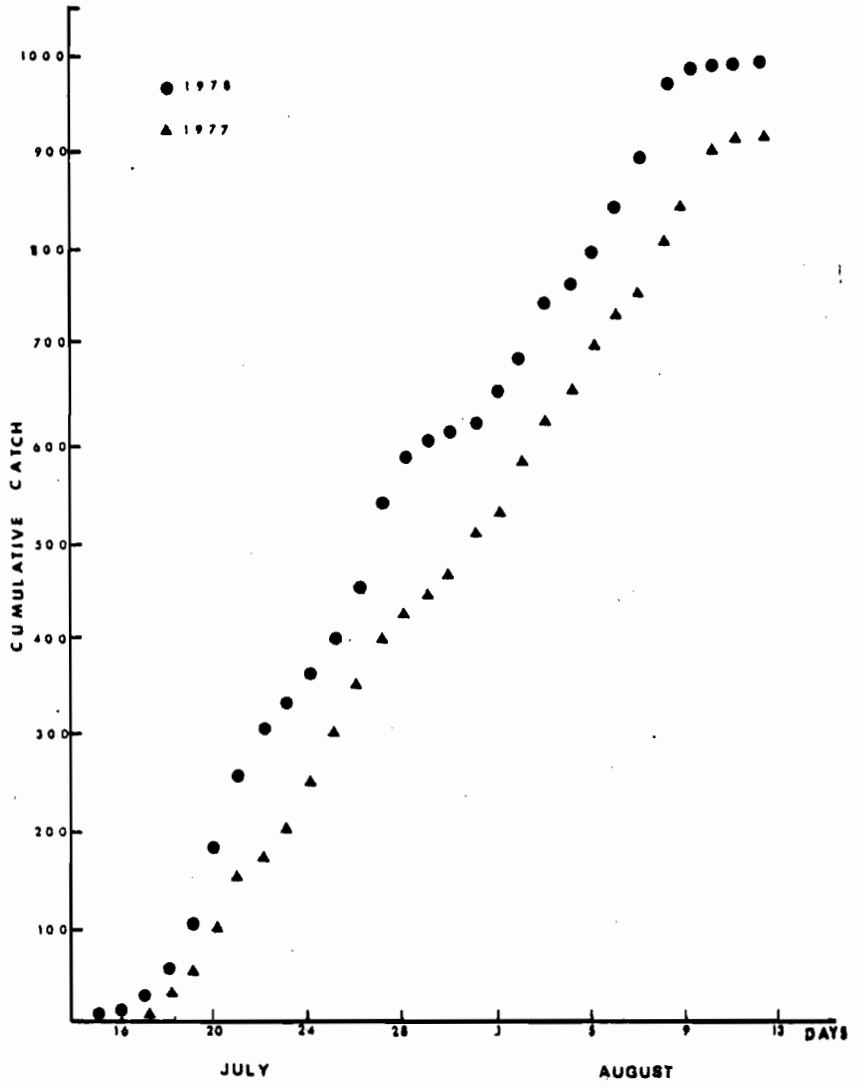

1978
1977
CUMULATIVE CATCH
1000
900
800
700
600
500
400
300
200
100
16
20
24
28
3
8
9
13
DAYS
JULY
AUGUST

Figure 6. Wind speed, daily minimum and maximum temperature, and daily catch of male gypsy moth in 20 traps at Macdonald College (1978).

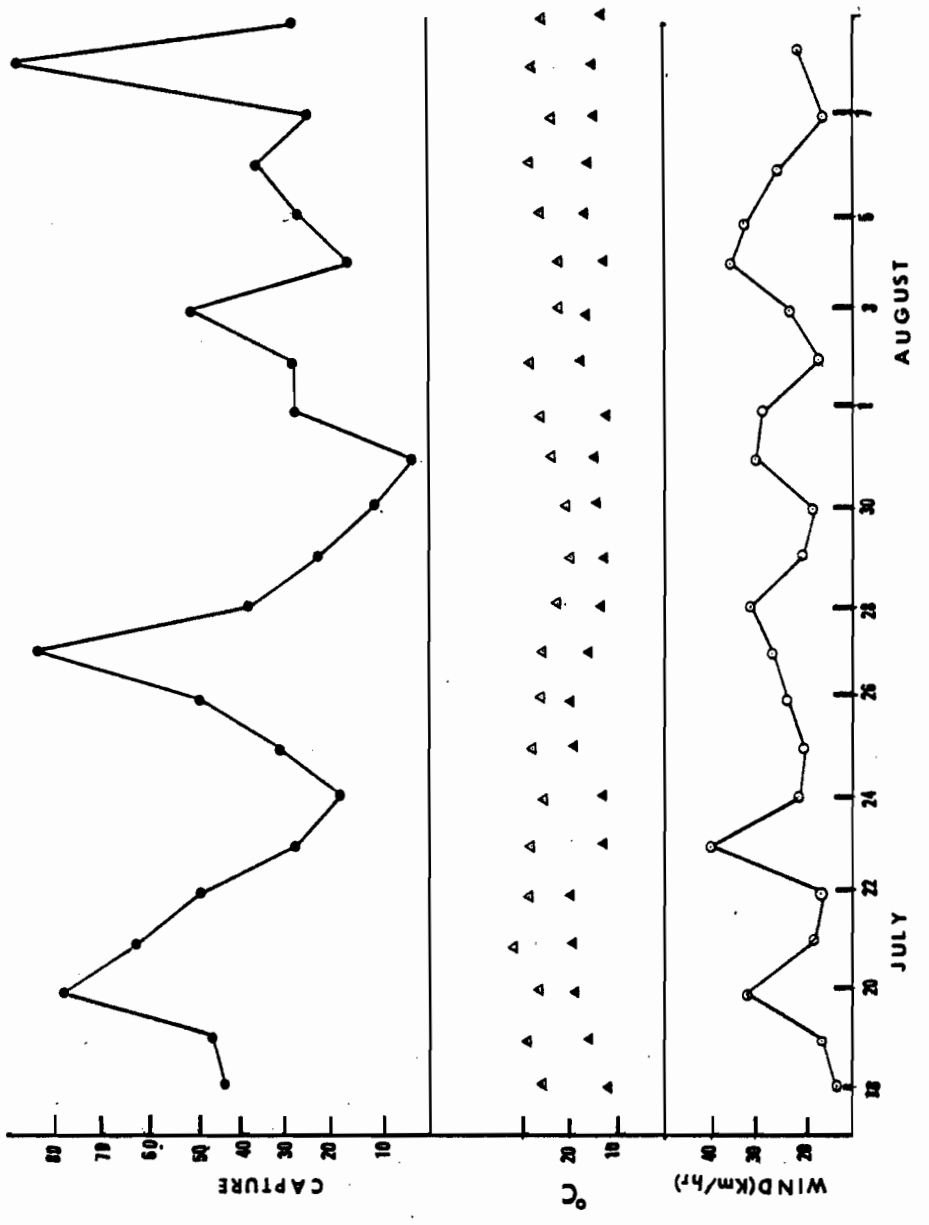

CAPTURE
80
70
60
50
40
30
20
10
°C
20
10
WIND(Km/hr)
40
30
20
JULY
AUGUST
28
20
22
24
26
28
30
1
3
5
7

Figure 7. Female adult caught in Delta sticky trap. Mont St. Hilaire, Quebec (1978).

Figure 8. Eggs of gypsy moth at different times after oviposition.

A. newly laid

B. eight days after oviposition

C. sixteen days after oviposition, embryogenesis completed

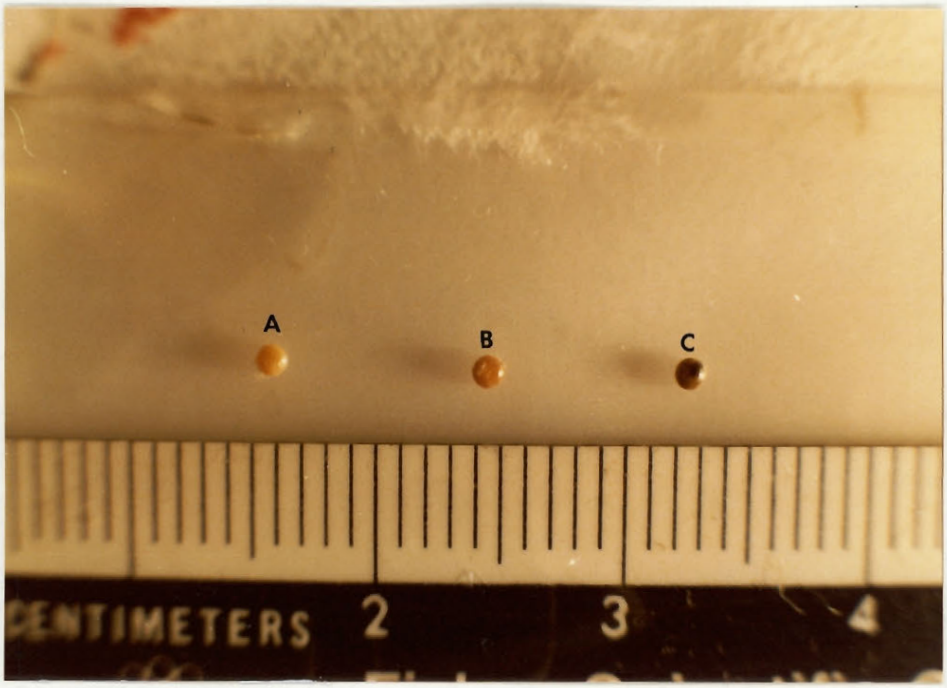

A
B
C
CENTIMETERS 2 3 4

Figure 9. Regression of fecundity (y) against fresh weight (x) of female gypsy moth for the 1978 season (Havelock, Quebec).

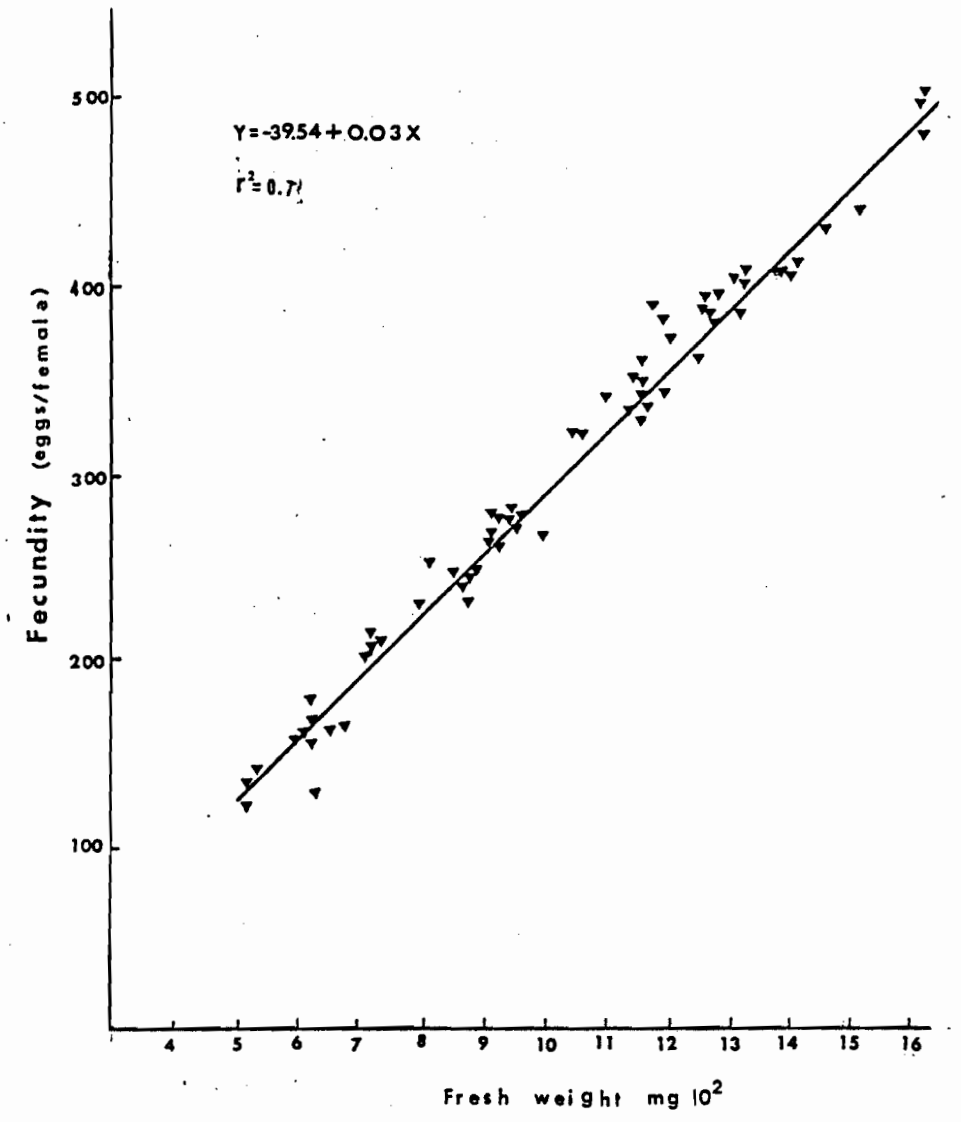

Y=-39.54+0.03X
r²=0.71
Fecundity (eggs/female)
100
200
300
400
500
4
5
6
7
8
9
10
11
12
13
14
15
16
Fresh weight mg 10²

Figure 10. Regression of fecundity (y) against fresh weight (x) of female gypsy moth for the 1978 season (Mont St. Hilaire, Quebec).

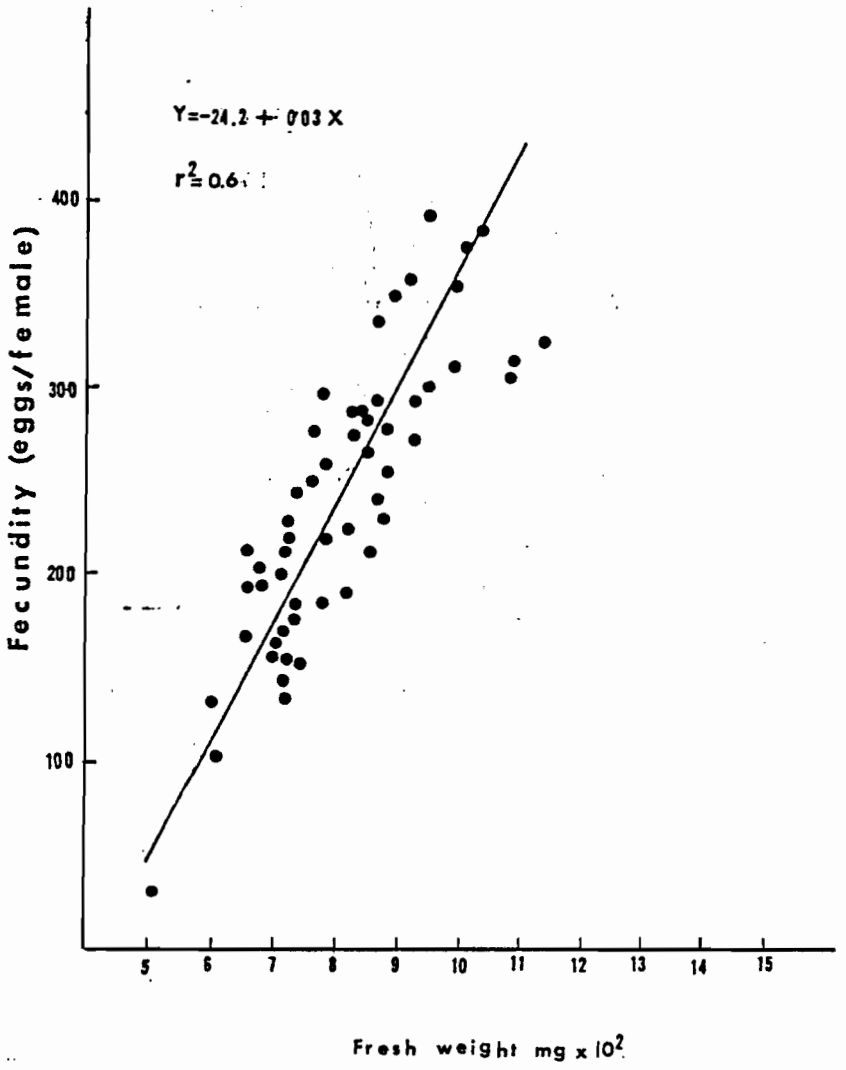
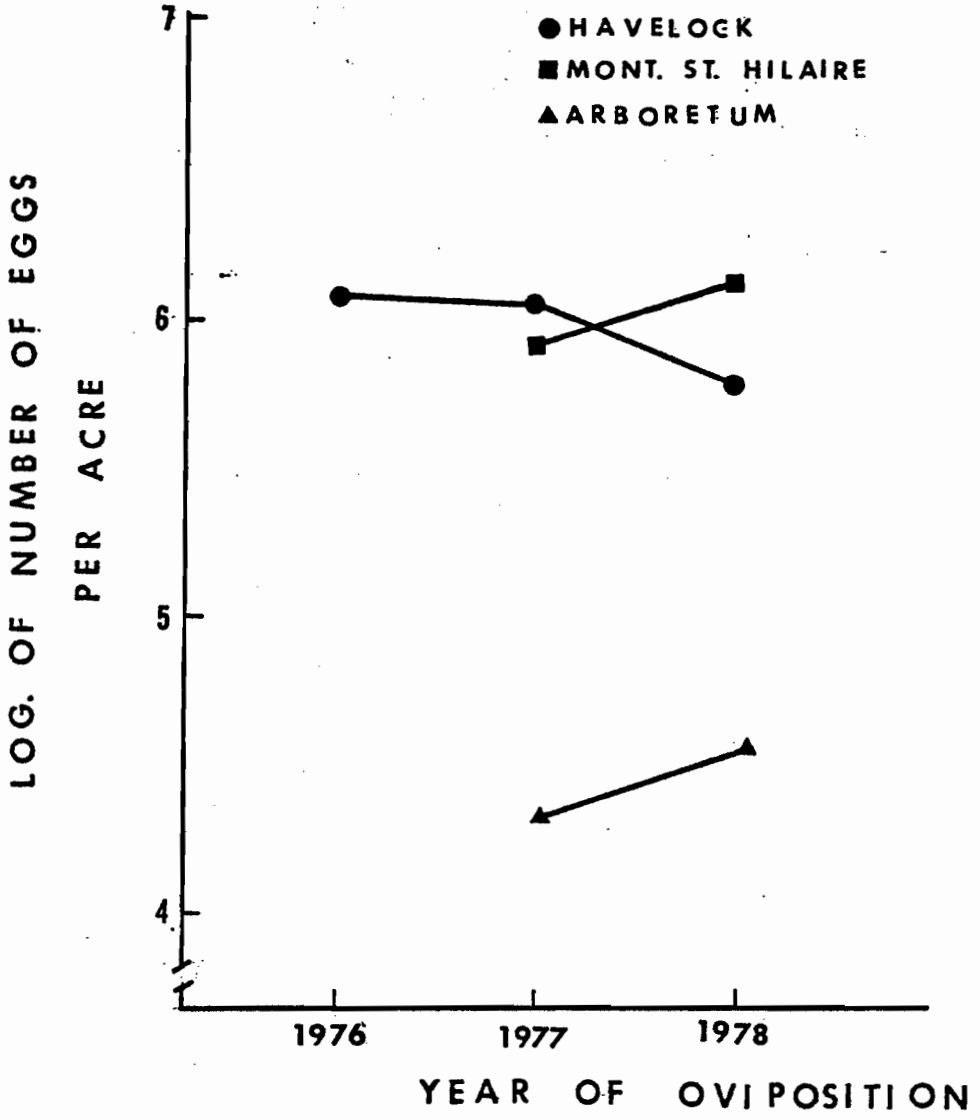

Y=-24.2 + 0.03 X
r² = 0.6
Fecundity (eggs/female)
400
300
200
100
5
6
7
8
9
10
11
12
13
14
15
Fresh weight mg x 10²

Figure 11. Gypsy moth population fluctuations during two years in three sampling sites in Quebec.


HAVELOCK
MONT. ST. HILAIRE
ARBORETUM
LOG. OF NUMBER OF EGGS PER ACRE
7
6
5
4
1976
1977
1978
YEAR OF OVIPOSITION

IV. COLD HARDINESS AND WINTER MORTALITY OF FULLY FORMED EMBRYOS OF THE GYPSY MOTH *LYMANTRIA DISPAR* (LEPIDOPTERA, LYMANTRIIDAE) AND ITS ECOLOGICAL SIGNIFICANCE[1]

[1]Submitted to publisher

ABSTRACT

Measurements of the supercooling points of eggs of the gypsy moth, Lymantria dispar L. (Lepidoptera, Lymantriidae), collected in two sites in Quebec, at various levels above the ground, indicate that the species is well able to withstand the Quebec winter. A high percentage of egg-masses were laid above snow cover level; however, winter mortality was never higher than 39.7% (even above the snow cover), suggesting the development of a more cold-hardy population.

Winter mortality was positively correlated with the length of exposure to low winter temperatures and to the degree of cold experienced, and these two factors were affected by a protective snow cover.

INTRODUCTION

The gypsy moth, after invading New England, has spread towards the north and east, reaching areas bounded by the -30°C mean extreme winter isotherm and beyond (Sullivan and Wallace, 1972). In Europe and Asia, the insect can be found as far north as 58°N (Figure 12). Comparison of climatic and geographic regions where the gypsy moth is established both in

Eurasia and North America indicates that as long as suitable host plants exist, the insect is not likely to limit its range to the present distribution area in Canada. Low winter temperatures were not considered to be a deterrent factor in the dispersal of the pest (Sullivan and Wallace, 1972).

Supercooling points and subsequent mortality from freezing of the overwintering embryos were determined to assess the ability of the local population near Montreal to survive subzero temperatures and its capability of spreading northward.

MATERIALS AND METHODS

Supercooling Points Determination
(of single eggs)

Supercooling points were measured using a YSI tissue implantation thermister (No. T2725, Canlab) attached with glycerine to the surface of a single egg. The thermister, with an egg attached was enclosed in a glass cylinder whose open end inside a thermos-container was sealed with a small gelatin capsule. The thermos-container, with liquid air as the cooling source, was fitted with a hollow aluminum rod, perforated to facilitate a good gradient of temperature. The metal rod had a second glass tube as an inner lining. The thermocouple,

enclosed in the first glass cylinder never touched the walls of the rod. The opening of the thermos container was plugged with glass wool (Figure 13).

The cooling curve was recorded on a YSI model 43 telethermometer and a Mark VIII YSI recorder with a chart drive of two inches per hour. Rebounds in the cooling curve, caused by the released heat of fusion of the sample, when this suddenly froze, were easily located on the curve . A cooling rate of 2°C per minute was adopted as standard.

Effect of Snow Cover

Three selected gypsy moth egg-clusters collected from Havelock (lat. 4505N long. 7411W) in August 1977 were separated into six pieces approximately the same size. One piece of each egg-mass (3 replicates) was placed in a bivalve plastic cage, 4.5 x 4.5 x 4.5 cm, as described by Khattat and Stewart (1975). Cages were placed at six different levels: ground level, 50 cm, 1 m, 1.5 m, 2 m and 3 m respectively at an exposed outdoor site on the shore of Lac St. Louis at Macdonald College (lat. 4525N long. 4356W) (Figure 14). Each level set up was connected with a thelethermometer (YSI 2465, Canlab) by means of an air thermocouple YSI (YSI T2620, Canlab). Survival was determined by examining eggs for successful hatching in spring.

Egg-masses were also collected before hatching in Spring

from Havelock and Mont St. Hilaire (lat. 54 33 N, long. 73 05 W), and percentage hatching was recorded in the laboratory. Ten groups of twenty-five or more egg-masses were collected, at 50 cm intervals from ground level to 4.5 m above ground.

Effect of Different Exposure Times to Cold Temperatures on Survival of Overwintering Eggs of Gypsy Moth

Eggs overwintering in a small open insectarium from August 1977 until January 1978 were placed in a cardboard box lined with styrofoam (Figure 15), and placed inside a freezer. The temperature inside the box was recorded using a recorder (Mark VII) connected to a thelethermometer (YSI T2465, Canlab), with an attached air probe located inside the box. The eggs were subjected to different low temperatures (-14°C, -20°C, -24°C, -30°C) for different times (7 days, 15 days, 30 days) in January 1978, and data on hatching analyzed using Duncan's New Multiple Range Test. Other egg-masses were exposed for 6, 12 24,48,72 hrs. at -27° and -30° C.

RESULTS AND DISCUSSION

The gypsy moth inhabits many regions where winter air temperatures reach well below the freezing point of eggs. Factors, other than air temperature which influences survival, are oviposition site, extent of snow cover and cold hardiness

of eggs expressed as an ability to supercool. Supercooling depends, partly, at least, on glycerol concentration and lowering of freezing point due to a glycoprotein antifreeze.

Supercooling Points

Supercooling points of eggs acclimatized in the field until late November and held later for one week at different temperatures are given in Table 9 . Also, supercooling points of eggs collected from the field and assayed immediately when newly laid (late July), in mid-winter (mid-January) and at hatching time (early May) are given (Table 10). The eggs acclimated at -12°C and -20°C did not show a significant difference between their mean supercooling points (series 1). The mean freezing point of newly laid eggs was a very low -24.9°C and mean supercooling points of eggs ready to hatch was -25.7°C, showing that the eggs are protected against freezing temperatures during the whole stage; however, there was mortality, as expected, during the winter months.

Effect of Snow Cover

Table 11 shows survival of eggs laid on trees in the three experimental sites. More than 90% of the eggs survived below snow cover. Eggs laid above snow cover still survived well although at a reduced level and height above the snow was not a significant factor. Eggs overwintering in an exposed

lakeside site at Macdonald College also showed the value of snow cover. (Figure 16).

Summers (1922), working in New England, found 100% mortality of egg-masses when the air temperature reached -31.7°C (-25°F) and they were not protected, and most (70%) of the egg-masses recovered by him were found at heights above 5 feet.

In Yugoslavia, Maksimovic (1958) reported 88.8% survival of eggs above the snow but he did not indicate any preference for oviposition height. Leonard (1972) found 66% survival below the snow line in Maine. He also found only 19.1% of the egg-masses to be laid above 5 feet contrasting with Summers' (1922) findings of 70% of egg-masses laid above 5 feet, and with our own findings in all three sampling sites (Table 12).

Our results (Tables 11,12) suggest that regardless of the low winter temperatures, most eggs above snow cover will hatch. There is a direct relationship between mortality rate, degree of cold and the time of exposure to cold. Figure 17 represents graphically the quality and quantity factor of lethal low temperatures. The multiple correlation coefficient between length of exposure to cold, time of exposure and mortality is $r = 0.8012$. Mortality increased with exposure to lower temperatures. Table 13 shows that eggs which had been acclimatized above snow cover in the field were more cold=hardy than those acclimatized below snow cover.

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Leonard, D.E. 1972. Survival in a gypsy moth population exposed to low winter temperature. Environ. Entomol., 1: 549-554.

Maksimovic, M. 1958. Experimental research on the influence of temperature upon the development and the population dynamics of the gypsy moth (Liparis dispar L.) (In Serbo-Croatian) Posebna Tzd. Biol. Inst. N.R. Srbije, 3: 1-115 (Transl. 1963, OTS 61-11203, 95 p.).

Summers, J.N. 1922. Effect of low temperature on the hatching of gypsy moth eggs. U.S. Dep. Agric. Bull., 1080: 1-54.

Sullivan, C.R. and D.R. Wallace. 1972. The potential northern dispersal of the gypsy moth, Porthetria dispar (Lepidoptera: Lymantriidae). Can. Entomol., 104: 1349-1355.

Table 9 . Supercooling points of gypsy moth eggs acclimated at various temperatures in the laboratory.

Series 1	Acclimation Temperature (°C)			
	0	-7	-12	-20
n	15	15	15	15
x(°C)±S.D.	-28.1±0.29	-29.5±0.35	-30.1±0.14	-30±0.13
Range (°C)	-26.5 to -32	-27 to -32	-27.5 to -32	-27.5 to -32
Acclimation time (weeks)	1	1	1	1

Table 10. Supercooling points of gypsy moth eggs collected at different times from the field and assayed immediately.

Series 2,3,4	$\bar{x} \pm$ S.D. (°C)
Eggs before embryogenesis (late July)	-24.9 ± 0.24
Eggs collected in winter (January)	-30.5 ± 0.08
Eggs from hatching clusters (early May)	-25.7 ± 0.09

Table 11. Percentage survival of overwintering eggs of gypsy moth in egg-masses of various heights above ground level in three sites (Quebec, 1977).

Height Above Ground (m)	Survival (%) Macdonald College 1977	Havelock 1977	Havelock 1978	Mont St.Hilaire 1978
0-0.5	92.5[a]	91.2[a]	94.2[a]	89.1[a]
0.5-1.0	69.8[b]	72.3[b]	74.4[b]	87.7[a]
1.0-1.5	68.2[b]	71.6[b]	67.1[b]	85.7[a]
1.5-2.0	66.9[b]	71.0[b]	60.2[b]	81.9[a]
2.0-2.5	66.6[b]	69.8[b]	65.1[b]	80.0[a]
2.5-3.0	61.3[b]	69.4[b]	63.5[b]	80.2[a]
3.0-3.5	-	62.3[b]	61.6[b]	81.1[a]
3.5-5.0	-	61.9[b]	65.0[b]	82.0[a]
Extreme minimum temperature (°C)	-27.2	-29.4	-27.4	-28.4
Monthly Mean				
December	-6.2	- 5.2	-7.0	- 7.7
January	-16.7	-16.8	-12.7	-11.8
February	-12.5	-16.9	-14.1	-12.0

Any two means associated with the same letter are not significantly different as determined by Duncan's New Multiple Range Test at the .05% level.

Table 12. Percentage oviposition and hatching of gypsy moth egg-masses overwintering in the field at two levels (Quebec, 1977,1978).

	Oviposition Height	Macdonald College		Havelock			Mont St. Hilaire	
		1977	1978	1976	1977	1978	1977	1978
Oviposition %	Below 1.5 m	39.7	42.3	30.7	45.2	33.9	25.3	27.4
	Above 1.5 m	60.3	57.7	69.3	54.7	66.1	74.6	72.6
Hatching %	Below 1.5 m	86.4	-	87.0	91.2	-	87.2	-
	Above 1.5 m	88.7	-	60.3	70.8	-	83.0	-

Table 13. Percentage mortality[a] of field acclimatized gypsy moth eggs exposed in the laboratory to different low temperatures for different periods of time.

Acclimation Temperature (°C)	Oviposition Site Related to Snow Cover	Exposure Time (hours) 6	12	24	48	72	Control
-27	Below	14.4(120)[b]	16.6(145)	46.6(141)	82.2(123)	100(154)	4.0(50)
	Above	4.0(168)	26.0(151)	35.0(134)	61.0(131)	87.0(131)	3.2(80)
-30	Below	78.0(175)	97.0(189)	100(178)	100(181)	100(196)	7.2(120)
	Above	39.0(154)	54.0(171)	73.0(163)	98.0(151)	100(171)	5.2(48)

a = each value is the average of four replicates.

b = values in brackets represent number of eggs.

Figure 12. World distribution map of the gypsy moth, Lymantria dispar, modified and updated from "Distribution Maps of Insect Pests." Commonwealth Institute of Entomology (1953).

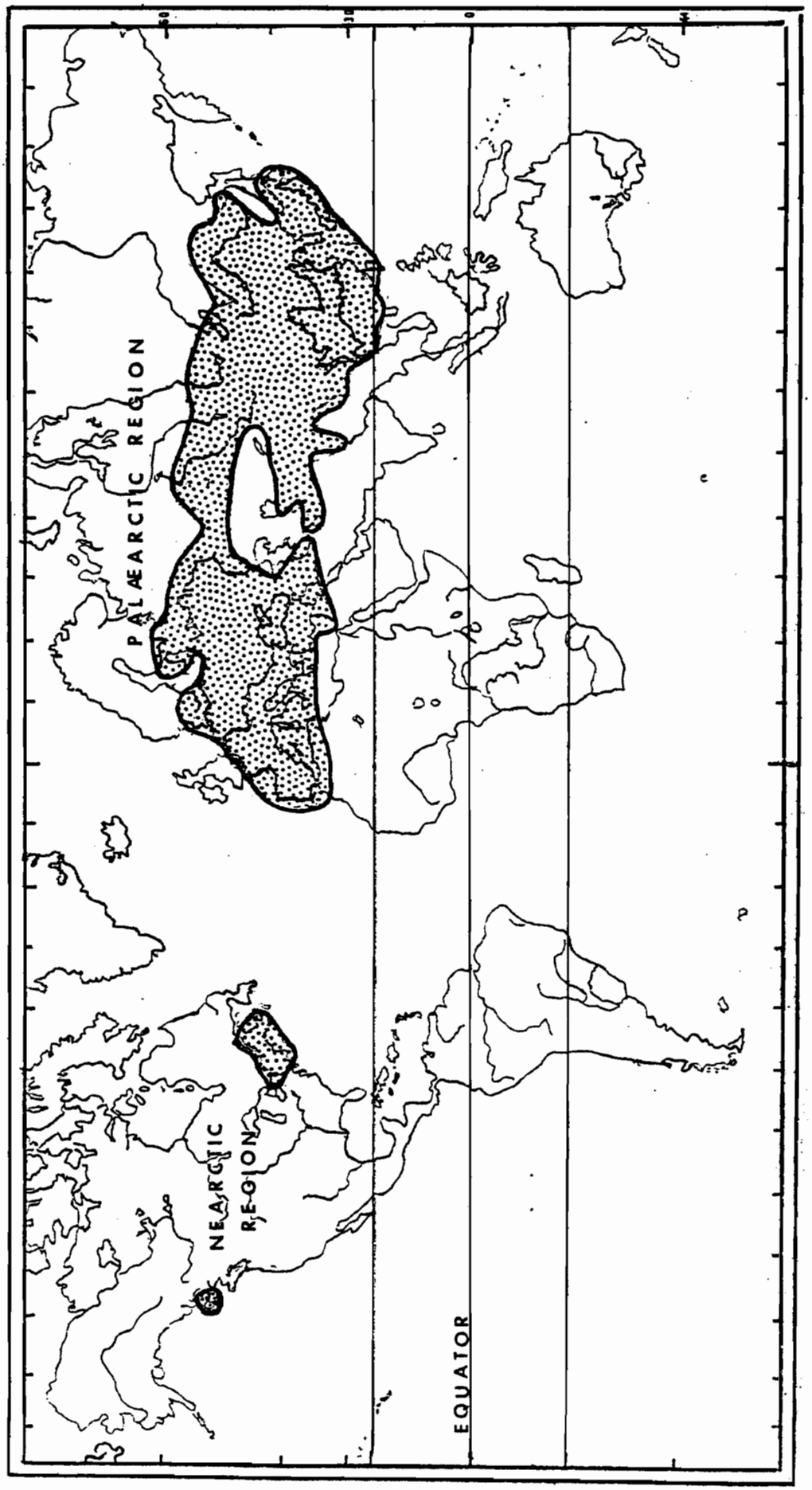

PALÆARCTIC REGION
NEARCTIC REGION
EQUATOR

Figure 13. Apparatus to determine the supercooling point of gypsy moth eggs.

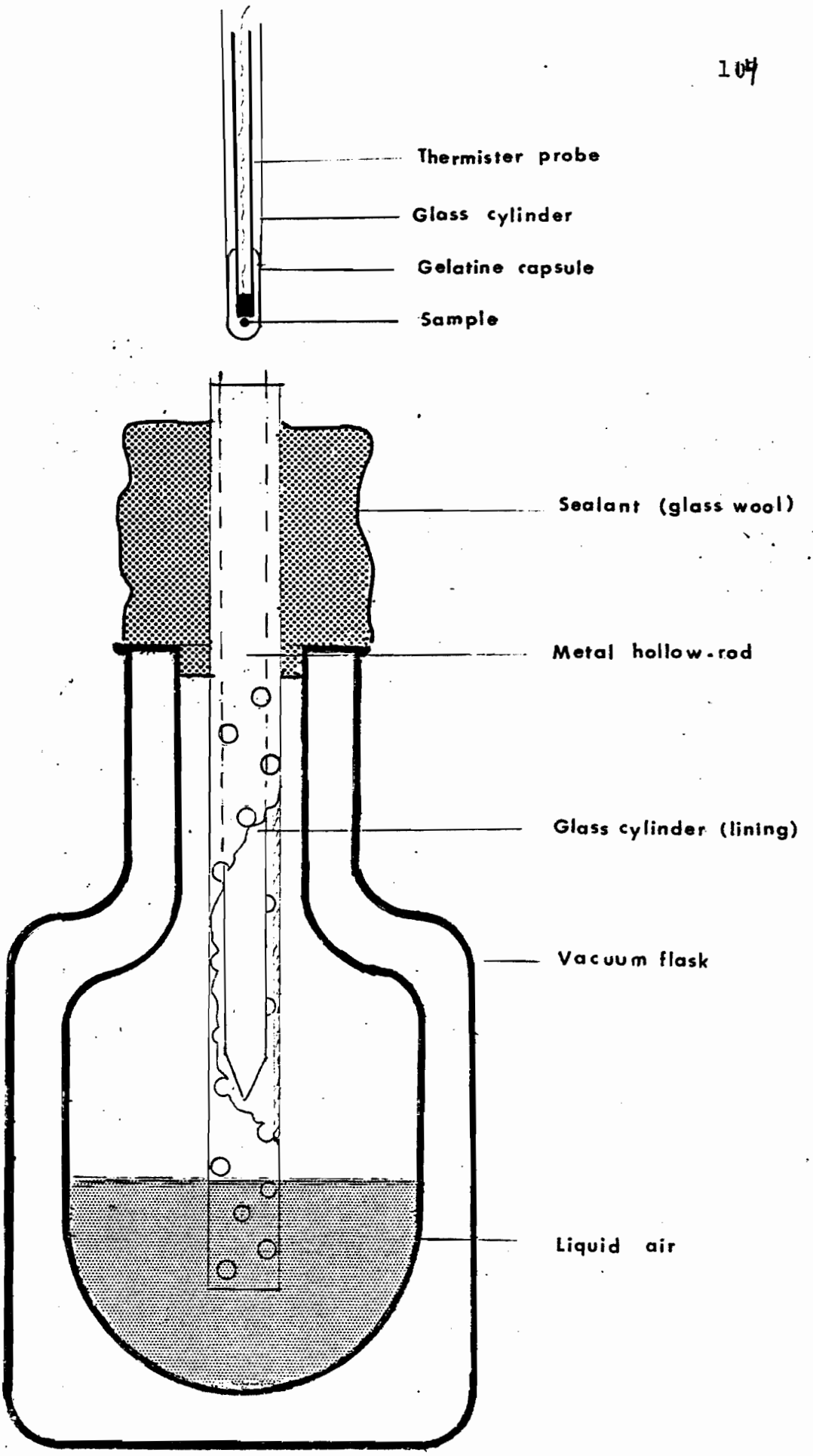

Thermister probe
Glass cylinder
Gelatine capsule
Sample
Sealant (glass wool)
Metal hollow-rod
Glass cylinder (lining)
Vacuum flask
Liquid air

Figure 14. Eggs of gypsy moth overwintering in the field at different levels at Lac St. Louis, Macdonald College, Quebec, 1977.

Figure 15. Insulated box.

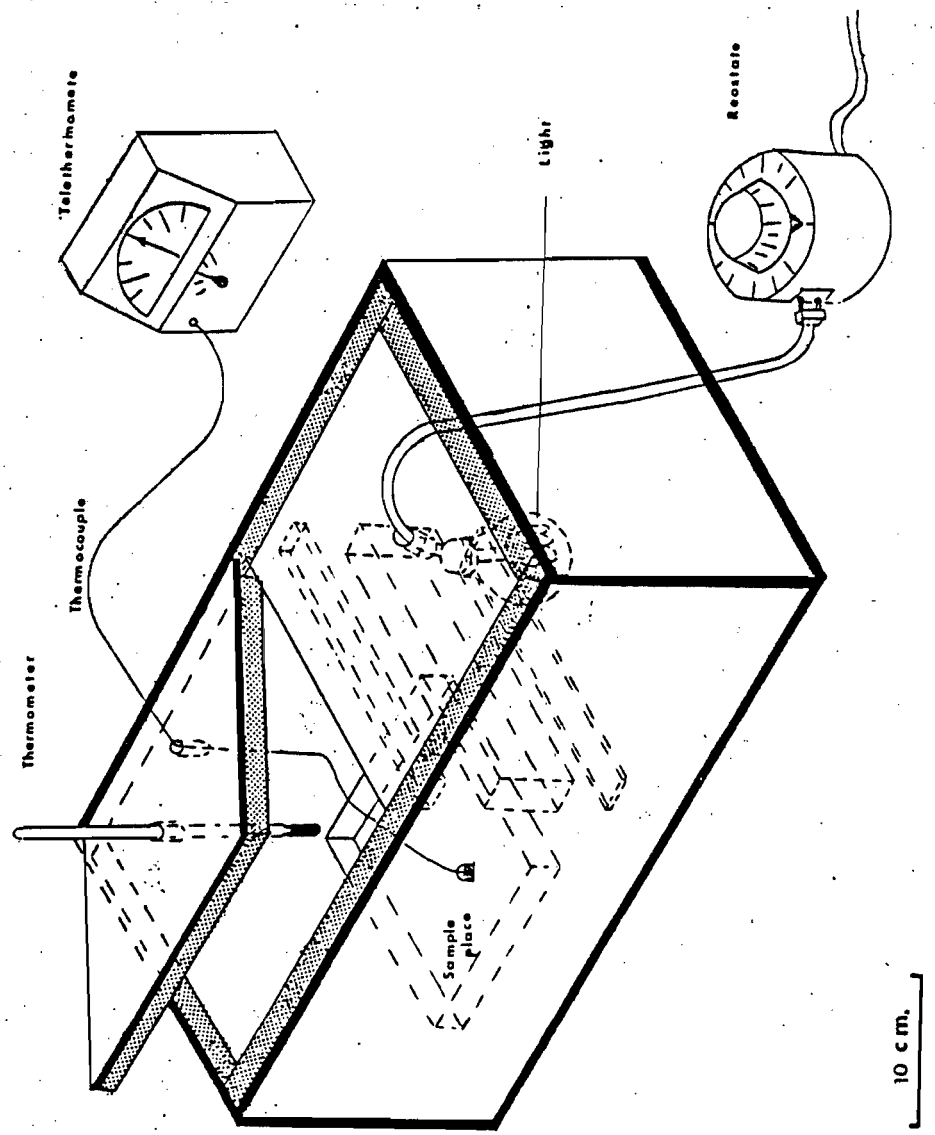

Telethermometer
Light
Reostate
Thermocouple
Thermometer
Sample place
10 cm.

Figure 16. Percentage survival of gypsy moth eggs at different heights above ground level (at Macdonald College, Quebec, 1977).

$$\hat{y} = 117.49 + 1.857X_1 + (-3.196X_2)$$

$$r = 0.7064$$

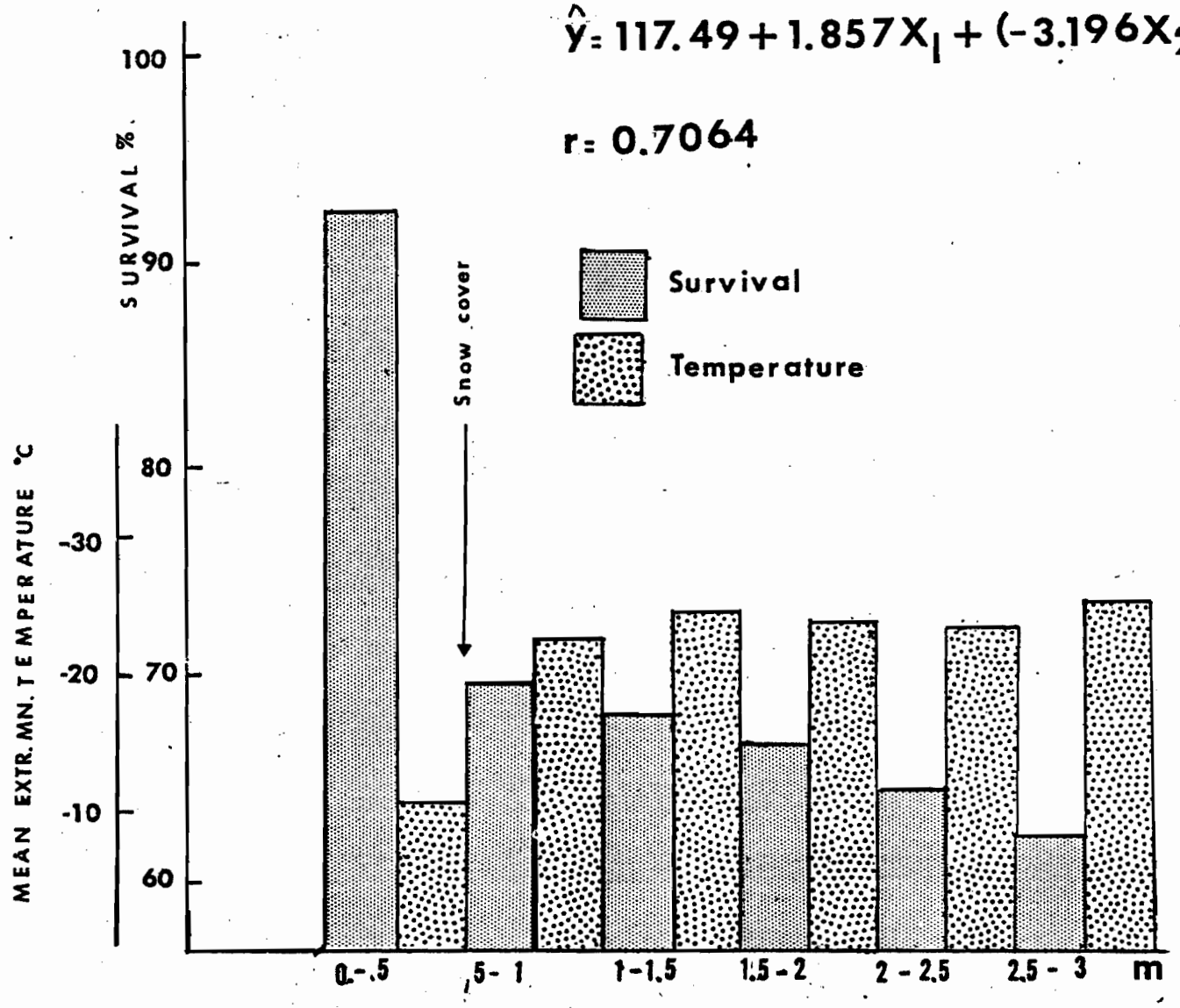
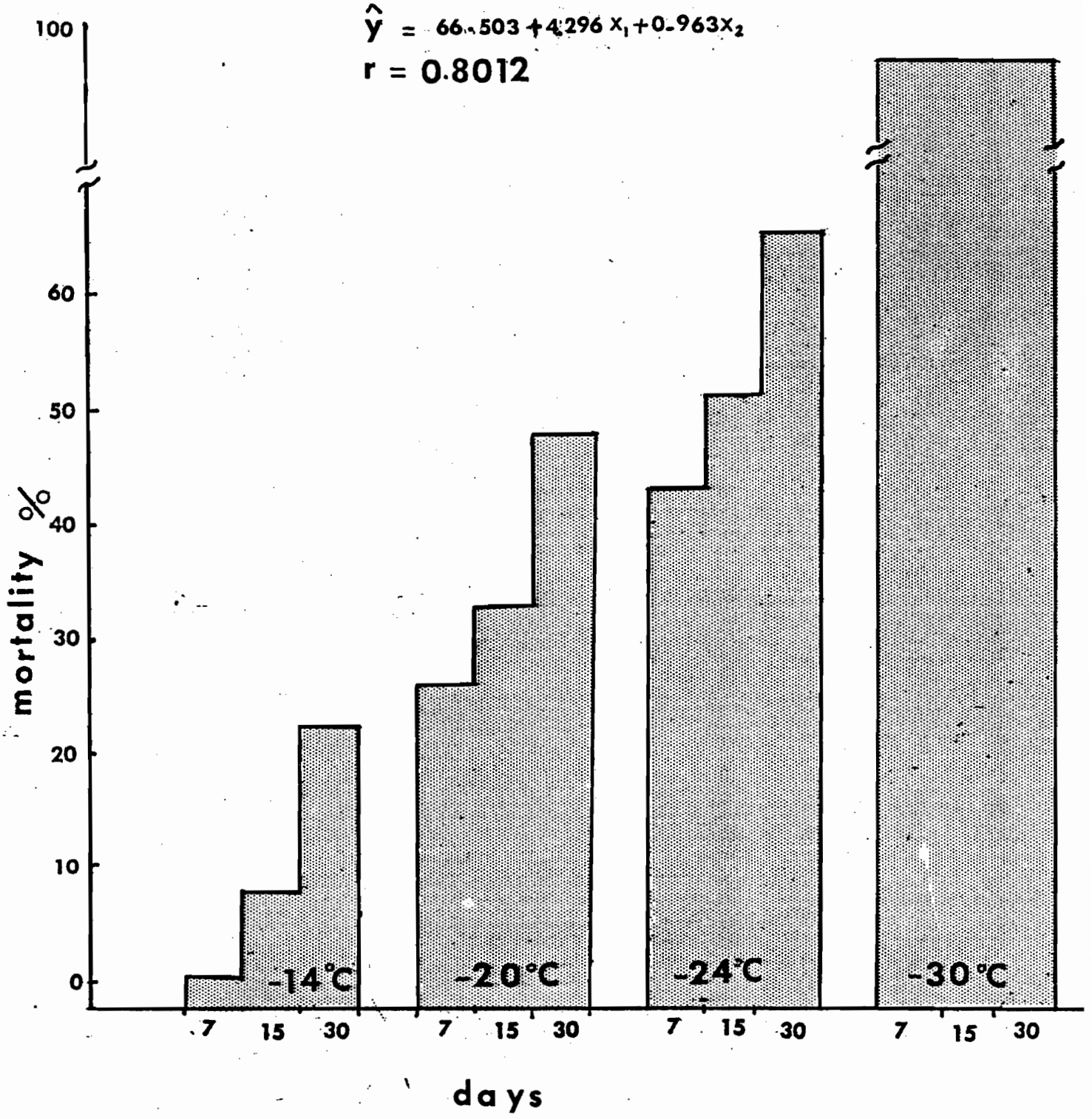


Figure 17. Percentage mortality of overwintering gypgy moth eggs exposed for various times to different low temperatures.


$\hat{y}$ = 66.503 + 4.296 x_1 + 0.963 x_2
r = 0.8012
100
60
50
40
30
20
10
0
mortality %
-14°C
-20°C
-24°C
-30°C
7
15
30
days

V. INFLUENCE OF LOW TEMPERATURE ON SURVIVAL OF FULLY FORMED EMBRYOS OF THE GYPSY MOTH, LYMANTRIA DISPAR (LEPIDOPTERA, LYMANTRIIDAE) AND THE ADAPTIVE SIGNIFICANCE FOR THEIR WINTER SURVIVAL IN CANADA[1]

[1]Submitted to publisher

ABSTRACT

The gypsy moth, Lymantria dispar (L.), overwinters as a fully mature embryo inside the egg. Winter survival in Quebec with or without protection afforded by snow cover is high. The eggs contain glycerol and a glycoprotein, which are cryoprotective.

The total content of free glycerol and seasonal variations in glycerol content were found to be closely correlated with the changing whole sample supercooling points.

Glycerol synthesis begins with the onset of the cold temperatures in late fall, and the beginning of warm spring weather is responsible for its depletion.

A glycoproteic substance was found in the eggs especially in the external yolk which surrounds the embryo until some time prior to hatching. This glycoprotein was not present after embryogenesis in early August, and at the time of hatching in early May.

INTRODUCTION

The overwintering stage of many polar and temperate zone insects have adapted themselves and are able to withstand sub-zero environmental temperatures.

Survival mechanisms such as cold-hardiness and diapause

are then very important for the overwintering embryo of the gypsy moth, as it extends its northern distribution. Most insects which have developed cold-hardiness show this to be related with a cryoprotective substance, in most cases glycerol or other polyhydric alcohol (Somme, 1964; Baust and Miller, 1970).

Recently, new substances, such as glycoproteins, have been found to be related in several organisms to the capability of withstanding low temperatures (Duman, 1977).

The overwintering stage, fully mature embryos of gypsy moth were tested for the presence and role of these substances.

MATERIALS AND METHODS

Gypsy moth female pupae were collected from the study areas (Havelock, lat. 4505N long. 7411W and Mont St. Hilaire, lat. 4533N long. 7305W) in August of each year (1977,1978) and kept separately in one-pint waxed cardboard food containers in the laboratory (22°C, 80% R.H., 16 hrs photoperiod). After emergence some females were dissected and the unfertilized eggs collected. These eggs, provided preembryogenesis groups. The remaining females were allowed to mate and lay eggs in the laboratory. The egg-masses laid by these females were stored outdoors in an open insectary.

Samples were prepared from these eggs as follows:

(1) twenty-four hours after oviposition; (2) 10 days after oviposition (during embryogenesis); (3) 45 days after oviposition (embryogenesis complete); (4) three months after oviposition (during diapause); (5) in late April (immediately before hatching). In addition to these laboratory collected eggs, egg samples were taken at monthly intervals in the field from early fall to early spring, to measure seasonal changes in glycerol content.

Glycerol content of the eggs was determined by a method of enzymatic analysis (Eggstein and Kullmann, 1974) and the determination of protein content was made by the Lowry method (Lowry et al., 1951).

Using gel electrophoresis, molecular weights of proteins were determined following the procedure of Shapiro et al. (1967).

Preparation of Eggs Homogenate

Twenty eggs (total fresh weight, 0.01508±0.0012985g[a]) were ground in 0.20 ml of a buffer phosphate solution (pH 7.4) and the solution made up to 0.40 ml using distilled water. The homogenate was centrifuged and the supernatant removed, some to be used in the immediate analysis, the remainder was stored at -24°C. Five replicates of twenty eggs each from different clusters were prepared for each test, in each separate analysis.

a: mean ± S.D.

Determination of Glycerol Content

The egg homogenate sample (0.10 ml) was mixed with 1.0 ml of solution 1 (glycylglycine buffer pH 7.4 and 7 mg reduced nicotinamide-adenine dinucleotide (NADH) and 22 mg adenosine-5'-triphosphate (ATP) and 11 mg of phosphoenolpyruvate (PEP) and magnesium sulfate and stabilizers all diluted in 11 ml of redistilled water) and 1.9 ml of redistilled water and 0.01 suspension 2 (pyruvate kinase suspension ca 240 U and lactate dehydrogenase-ca 220 U), optical densities were read after 5-7 minutes using a spectrophotometer (Beckman 220). 0.01 ml of suspension 3 (glycerokinase-ca 34 U) were added to start the reaction. After 5-10 minutes, optical densities were read at two-minute intervals until the reaction stopped.

The concentration of glycerol was calculated using the following equation:

$$c = \frac{V \times MW}{\varepsilon \times d \times v \times 1000} \times \Delta E \ (g/l)$$

where ΔE = optical density difference

V = final volume (ml)

v = sample volume (ml)

MW = molecular weight of substance assayed

d = light path (cm)

ε = extinction coefficient of NADH

for glycerol

$$c = \frac{3.02 \times 92.1}{6.3 \times 1 \times 0.1 \times 1000} \times \Delta E = 0.4414 \ \Delta E \ (\text{g-glycerol/l. sample solution})$$

This reaction is based on the phosphorylation of glycerol by adenosine-5'-triphosphate (ATP) to glycerol-3-phosphate, with glycerokinase (GK) catalysing the reaction.

(1) Glycerol + ATP $\xrightarrow{GK}$ glycerol-3-phosphate + ADP

(2) ADP + PEP $\xrightarrow{PK}$ ATP + pyruvate

(3) Pyruvate + NADH + H^+ $\xrightarrow{LDH}$ lactate + NAD^+

The amount of NADH consumed in the above reaction is stoichiometric (equivalent) with the amount of glycerol. NADH is determined by means of its absorption at 340 nm.

For a more detailed explanation of the method, see Eggstein and Kuhlmann (1974).

Determination of Total Protein Content of the Embryos

The procedure followed is known as the Lowry method (Lowry, 1951) and consists of measurement of protein with Folin phenol reagent after alkaline copper treatment.

The egg sample was prepared as for glycerol determination. The method requires a standard curve, and crystalline bovine serum albumine (BSA) was used as a standard.

B.S.A.: Stock Solution of BSA at a concentration of 1 mg/ml

Two ml of this solution were mixed with 8 ml of distilled water to give a final volume of 10 ml. Each ml of this solution therefore contains 200 µg of protein and this solution was used to construct the standard curve.

Reagent 1:

- 1 ml of 1% Cu SO_4

1 ml of 2% Na-K Tartvate

1 ml of this mixture is added to 50 ml of 2% Na_2CO_2 containing o.1 N-NaOH (51 ml volumen total)

Reagent 2: (Folin Reagent)

Phosphomolybdic acid, .05 ml for each measurement.

After reading optical densities (OD) at 660 nm, the following equation was used to obtain the concentration of the sample.

$$\text{Concentration sample} = \frac{\text{OD sample}}{\text{OD standard}} \times \text{Concentration standard}$$

Determination of Protein Molecular Weights

Molecular weights of proteins were determined by comparing electrophoretic mobility for samples with mobilities of marked polypeptide chains with known molecular weights (Weber and Osborne, 1969). Electrophoretic mobility was calculated as:

$$\text{Mobility} = \frac{\text{distance of protein migration}}{\text{length after destaining}} \times \frac{\text{length before staining}}{\text{distance of dye migration}}$$

The method of Shapiro et al. (1967) was used. This established that the separation of proteins by polyacrylamide gel disc electrophoresis in the presence of the anionic detergent sodium dodecyl sulfate is dependent on the molecular weights of their polypeptide chains. Each protein migrates at a characteristic

rate and stack up as a series of discs.

As standards, 3 proteins were compared:

(1) B.S.A. (Bovine Serum Albumin) = 68,000 daltons

(2) Ovoalbumin 43,000 daltons

(3) Chymotrypsinogen 25,700 daltons

Preparation of Gels

15 cm long glass tubes with an inside diameter of 6 mm were used for mounting the gel mixture. Acrylamide 10% (running gel, separation gel or small pore gel) was placed in the tube, then covered with a layer of buffer (pH 8.8). Polymerization was completed in 30 minutes.

The covering buffer was replaced by acrylamide 3 per cent (large pore gel or stacking gel) to a depth of 1 cm. The separation gel was approximately 10 cm thick. The sample material to be analyzed was added on top of this.

Separation gels were prepared in 30 ml of buffer solution pH 8.8 (0.375 M Tris-hydroxymethylaminomethane-HCl (Tris-HCl) and 0.1% sodium dodecyl sulphate (SDS), containing 3 g of acrylamide and 0.08 g of N,N'-bis-methylene acrylamide.

Stacking gels were prepared in 10 ml of buffer solution pH 6.8 (.125 M Tris-HCl and 0.1% SDS) containing 0.3 g acrylamide and 0.008 g of N,N'-bis-methylene acrylamide.

Both gels were polymerized chemically by the addition of

0.03 ml of tetramethylethylendiamine (TEMED) and 0.015 g of ammonium persulphate as a catalyst.

The electrode buffer (pH 8.3) contained 0.025 M Tris and 0.192 M glycine and 0.1% SDS.

The sample buffer final concentration was 0.0625 M Tris-HCl (pH 6.8), 1% SDS, 20% glycerol, 1% 2-mercaptoethanol. A mixture of 0.10 ml of sample buffer, one drop of bromophenol blue at 0.001 per cent and ¼ of the egg homogenate was immersed for 1-5 minutes in boiling water and this dissociated completely the proteins (Maizel, 1969).

The gel tubes were arranged vertically in an electrophoresis set-up apparatus containing electrode buffer. Electrodes were connected to the two buffer solutions and electrophoresis was carried out for 6 hours with a current of 3 mA per tube (10 tubes), using a power supply type 3290 LKB. The gels were then removed from the tubes, stained and excess stain removed.

Two kinds of stains were used - (1) Protein staining in general: Coomassie Brilliant Blue R250:0.50 g Coomassie blue Brilliant in 18 ml acetic acid, 89 ml methanol and 93 ml distilled water; (2) stains for protein-bound carbohydrates - (a) PAS (Clarke's method) and (b) Alcian blue staining of glycoproteins in acrylamide disc electrophoresis (Wardi and Michos, 1972).

Embryo Separation

The egg corion was punctured and then opened. The embryos were carefully extracted, washed in buffer solution and then used to prepare sample solution by the method described above. The external yolk from all eggs was also prepared as sample solution.

Supercooling Points Determination

The method was described in Section IV.

RESULTS AND DISCUSSION

Glycerol Content and Supercooling Points

Glycerol content and supercooling points of the overwintering embryo of the gypsy moth were determined in eggs collected at monthly intervals throughout the winter to establish and evaluate a possible correlation between these two factors, and the degree of cold-hardiness reached.

Supercooling points decreased steadily as fall progressed and field temperatures decreased. At the same time the free glycerol content increased (Table 14). Eggs analyzed before embryogenesis started showed only traces of glycerol, but glycerol content started to increase immediately after embryogenesis was completed. Table 14 shows that the glycerol level climbed steadily during late fall reaching a peak in December

and keeping this level during the winter.

Baust and Miller (1970) reported fluctuating values during the winter months, December to March, following fluctuations in temperature. Figure 18 shows that glycerol level reached a plateau during the coldest months of January and February. The level reached during December was 7.8 mg/g fresh weight but this fell suddenly at the end of April to 0.2 mg/g fresh weight. Somme (1964) and Mansingh and Smallman (1972) showed the same trend in their data for other insects.

During late February and March supercooling points increased and glycerol content decreased to a trace, just before hatching in May. Although there was a very high correlation ($r=0.9$, Fig. 19) between glycerol content and supercooling ability during most of the winter, this relation did not persist into early spring. Supercooling points did not increase quickly as glycerol levels decreased and immediately prior to hatching eggs could still supercool to $-25.7 \pm 0.1^{o}C$. Newly emerged larvae, prior to feeding, froze to $-14.5 \pm 0.6^{o}C$. This ability probably affords protection against spring frosts (Table 14).

The plot of mean supercooling points was almost a mirror image of the glycerol content curve (Figure 18), and this finding is similar to the data of Somme (1964), Baust and Miller (1970) and Mansingh and Smallman (1972).

The relation between glycerol content, diapause and cold hardiness is still controversial. Somme (1964) found glycerol in several diapausing insects, but after diapause was broken, glycerol was lost in all species. The same phenomenon has been reported by Dubach et al. (1959) and Salt (1959). Mansingh (1971) considered cold hardiness to be directly related to diapause. He stated that a lower metabolic rate attained during diapause affords greater cold hardiness. Salt (1961) however, considered diapause and cold hardiness as two independent phenomena, only casually concurrent in time.

Eggs were collected from the field in February and kept for up to two weeks at 22°C, 80% R.H. and 16 hours photoperiod. The eggs were checked at three-day intervals for glycerol levels until hatching (Table 15). When eggs were removed from cold, the glycerol content decreased as they approached hatching. At the same time their supercooling points started to rise.

Glycoprotein Content

Besides reports on the relationship between cold hardiness and levels of glycerol (Chino, 1957; Salt, 1959; Somme, 1964), there are studies on the possible role of sorbitol and amino acids (Somme, 1967; Mansingh, 1967), carbohydrates (Tano, 1964; Somme, 1967) and unsaturated fatty acids (Pantyukhov, 1964). Although the relation between insect low temperature

tolerance and low molecular weight polyols has been well studied, there is little or no research on the possible role of large molecular weight molecules on cold hardiness in insects. Duman (1977) however, reported the presence of glycoproteins in the larvae of the darkling beetle, Meracantha contracta (Coleoptera, Tenebrionidae) and related these to the low temperature tolerance of this insect. It is now evident that cold hardiness depends on more than one solute. Chino (1957), Somme (1964,1969), Mansingh and Smallman (1972) have suggested dual systems of cryoprotection.

Overwintering embryo of gypsy moth were assayed for glycoprotein content and level as well as supercooling points of single eggs from the same cluster.

Table 16 shows protein molecular weights of proteins from embryo, and their mobility in the electrophoretic gel acrylamide. From approximately fourteen visible discs of protein, three bands (those numbered II, III and XIII) were obtained by specific glycoprotein stains (Figure 20). Dialized samples of egg containing these glycoproteins showed a change when tested monthly. Glycoprotein content rose steadily from September until midwinter, when it started decreasing, to disappear in May (Table 17).

Molecular weights of the glycoproteins were determined by plotting protein electrophoretic mobility against the

logarithm of the known polypeptide chain molecular weights (Figure 21). The reliability of this method was tested by Shapiro et al. (1967) and Weber and Osborne (1969), who reported good agreement between their results and known values, but they stated the possibility of different results if the glycoproteins studied contain large amounts of carbohydrates or lipid material. Using this method, the molecular weights of the three glycoproteins were found to be respectively, II = 118.000 daltons, III = 109.000 daltons and XIII = 42.000 daltons.

The total protein content of gypsy moth larvae does not change appreciably during the year. Pantyukhov (1964) found a very low variation in the total nitrogen content of eggs throughout the year and he suggested that nitrogen is probably not used as an energy substrate. Although the total protein content of eggs does not change, the type of protein in the eggs does change (Figure 22).

Analysis of eggs during the process of embryogenesis showed a glycoprotein fraction (P XIII), which remains during the whole year with small changes in concentration. In September, when the fully formed embryo enters diapause (Leonard, 1968), another glycoprotein (P III) is found, concurrent with the lowering of the sample solution freezing points. The amount of this glycoprotein increased during January and February, when they reached a peak. With the beginning of the warmer temperatures,

their concentration starts declining to reach zero in May, at which time the eggs are hatching (Figure 22, C-D).

Analysis of the embryo and the external yolk separated (yolk inside the gut of the embryo is called internal yolk, Capinera et al., 1977) gave a higher percentage of glycoprotein for the external yolk than for the larva, whereas glycerol is almost totally restricted to the larva (Table 18). Considering that the overwintering larvae are surrounded by this external yolk, ice propagation through larval tissues would occur easily if no antifreeze substance were present in it. A similar situation can be found in the Antarctic limpet, Patinigera polaris. This mollusc surrounds itself with an envelope of mucus when it is caught in the near-shore ice. Ice propagation across the mucus is retarded down to -10°C, this being attributed to the presence of an unknown thermal hysteresis producing factor (Hargens and Shabica, 1973), thermal hysteresis being the difference between the freezing and melting points.

The same kind of macromolecular antifreeze is found in the hemolymph of Antarctic fish (De Vries and Wohlschlag, 1969) and in the intertidal mussel, Mytilus edulis (Theede et al., 1976).

Figure 23 shows the seasonal changes in glycoprotein and glycerol as related to low temperatures.

CONCLUSIONS

As winter approached the supercooling points of eggs decreased and this phenomen was associated with an increase in glycerol concentration; at the same time increasing levels of glycoproteins were found.

The glycerol is almost totally confined to the larva inside the egg, whereas the glycoproteins were found in the external yolk remains.

A dual cryoprotective system could have developed because the larvae inside the egg is surrounded by the external yolk, which could freeze and inoculate ice into the tissues of the larva. A substance that depresses the freezing point of the yolk would be of survival value.

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Table 14. Seasonal glycerol content and supercooling points of overwintering embryos of the gypsy moth taken from the field at Havelock, Quebec.

Collection Date	Glycerol Concentration (mg/g fresh wt.)	Supercooling Points (°C)
17 Aug.	3.6	-26.2 ± 0.4
15 Sept.	4.3	-26.4 ± 0.3
19 Oct.	6.2	-27.8 ± 0.1
15 Nov.	7.2	-28.3 ± 0.4
15 Dec.	7.8	-28.7 ± 0.3
16 Jan.	7.7	-29.4 ± 0.2
15 Feb.	7.8	-29.6 ± 0.1
14 Mar.	6.4	-28.3 ± 0.3
15 Apr.	6.7	-27.5 ± 0.4
10 May	0.2	-25.7 ± 0.1
12 May	0.09	-14.5 ± 0.6

Table 15. Glycerol content and supercooling points of post-diapause eggs of gypsy moth, developing at 22°C, 80% R.H. and 16 hours photoperiod.

Time at Incubation Temperature (days)	No.of Eggs	Glycerol Content (mg/g fresh wt)[a]	Supercooling Points (°C)
0	20	7.8 ± .06[a]	-29 ± 1.2[a]
3	20	7.0 ± .04	-28 ± 0.4
6	20	6.4 ± .01	-28 ± 1.7
9	20	6.1 ± .06	-26 ± 0.3
15	20	0.16± .04	-25.6 ± 0.2

[a] $\bar{x}$ ± S.D.

Table 16. Molecular weights and mobility in acrylamide gel electrophoresis of proteins extracted from eggs of the gypsy moth.

Proteins	Molecular Weights (daltons)	Electrophoretic Mobility (mm)
I	119000	11
II	118000	12
III	109000	22
IV	107000	25
V	103500	31
VI	103000	33
VII	94000	39
VIII	86000	42
IX	72000	50
X	63000	55
XI	56000	60
XII	46000	68
XIII	42000	72
XIV	25500	92

Table 17. Monthly content of glycoproteins in eggs of the gypsy moth and their supercooling points.

Collection Time	No.of Eggs	Total Protein Content mg/g fresh wt	G.P. II mg/g fresh wt	G.P. III mg/g fresh wt	Supercooling Points (°C)
Aug.	20	45.3	0	0	-25.3
Sept.	20	47.0	0	3.3	-26.8
Oct.	20	46.2	0.6	4.2	-27.9
Nov.	20	50.2	2.0	6.2	-28.6
Dec.	20	47.8	5.9	9.6	-30.1
Jan.	20	43.1	5.2	8.4	-30.2
Feb.	20	43.8	5.0	8.6	-30.0
Mar.	20	49.0	4.2	3.7	-29.3
Apr.	20	51.3	2.5	3.5	-27.8
May	20	46.5	0.09	0	-25.3

Table 18. Concentration of glycoprotein and glycerol in the overwintering embryos of the gypsy moth and in the external yolk surrounding them.

	Concentration[a] in Whole Egg mg/g Fresh Wt	Embryo (%)	External Yolk (%)
Glycerol	7.9	85	15
Glycoproteins	47.8	18.8	81.1

[a]Mean value of ten replicates.

Figure 18. Seasonal variations of supercooling points and glycerol content of gypsy moth eggs.

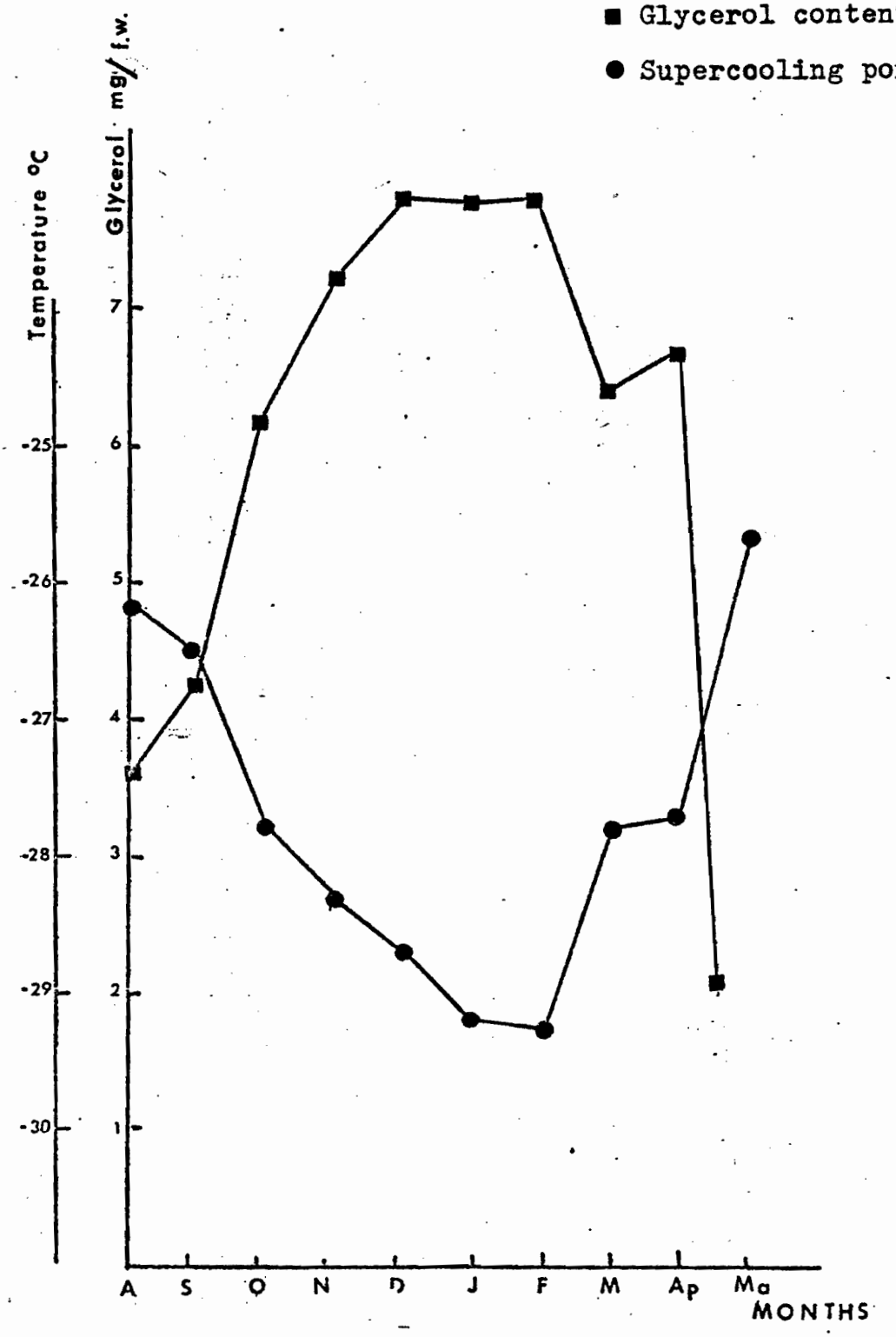

■ Glycerol content
● Supercooling points
Temperature °C
Glycerol mg/f.w.
-25
-26
-27
-28
-29
-30
7
6
5
4
3
2
1
A
S
O
N
D
J
F
M
Ap
Ma
MONTHS

Figure 19. Linear regression line of glycerol content vs. supercooling points.

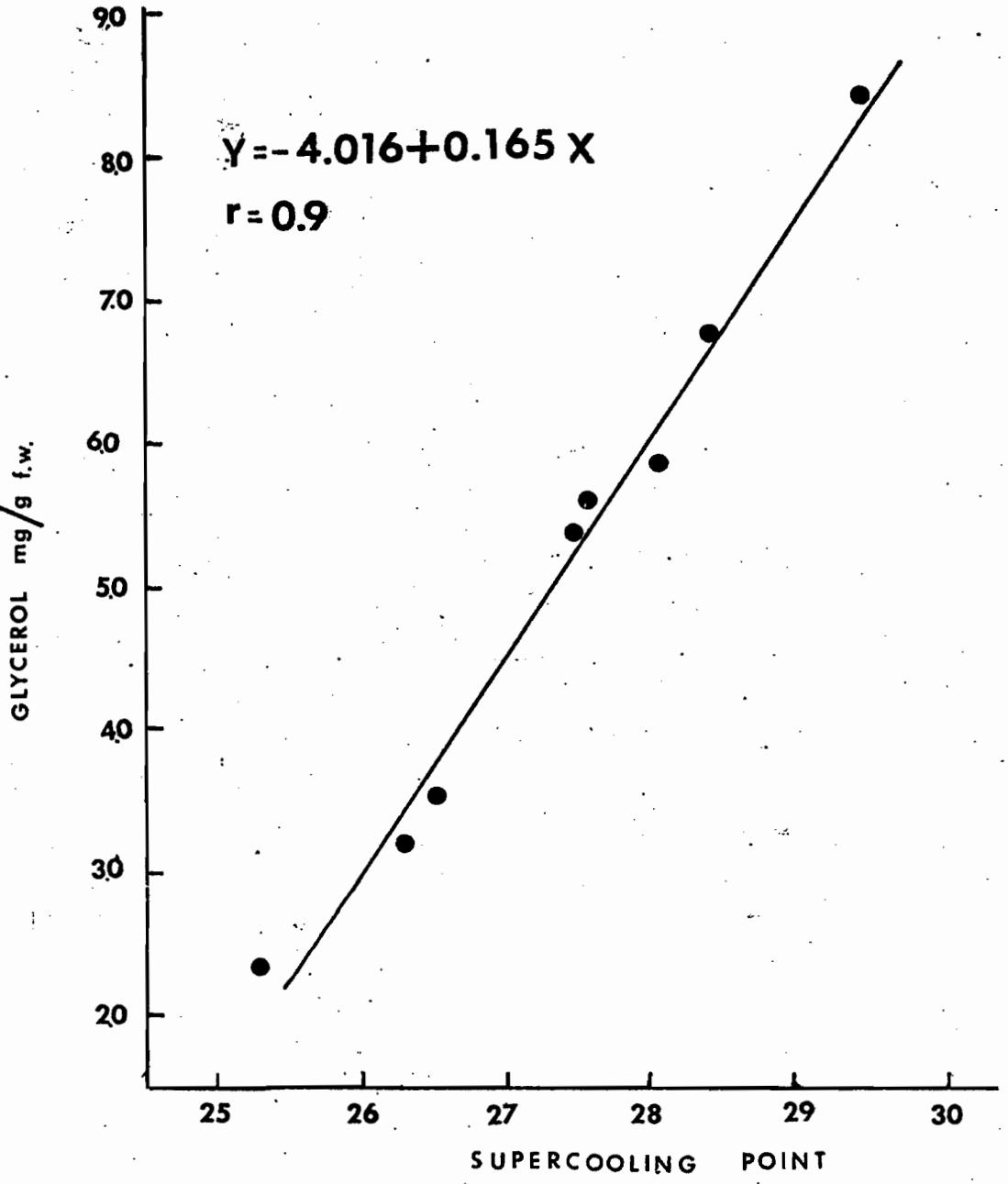
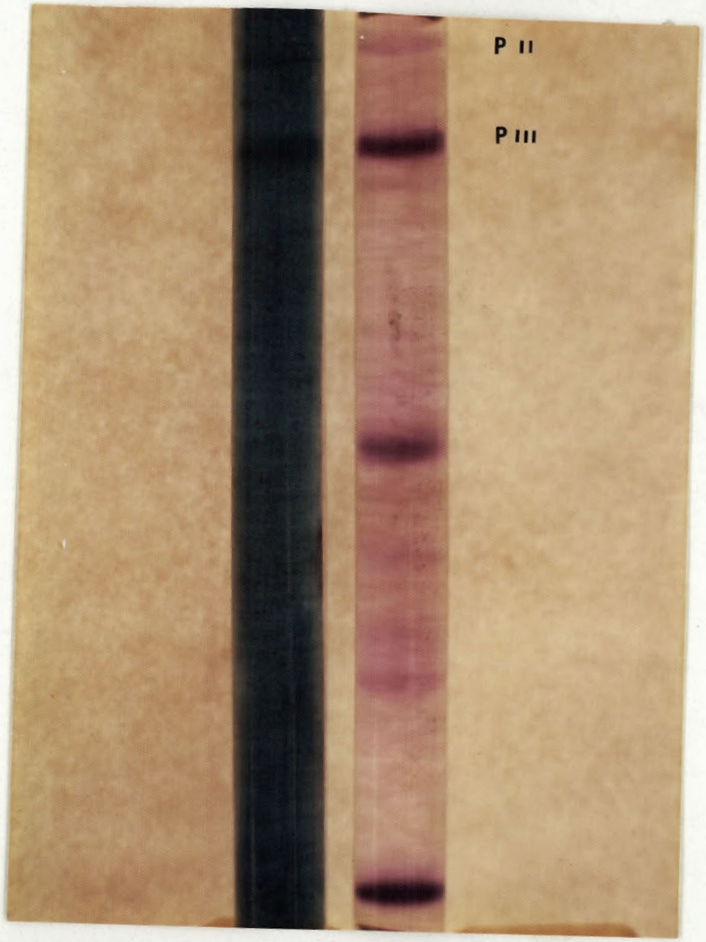

Y=-4.016+0.165 X
r=0.9
GLYCEROL mg/g f.w.
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
25
26
27
28
29
30
SUPERCOOLING POINT

Figure 20. A. Acrylamide gels at 10% stained and distained, showing bands of glycoprotein (stain: Alcian blue).

B. Acrylamide gels showing bands of protein prior to hatching in April (left) and January (right).

A



B

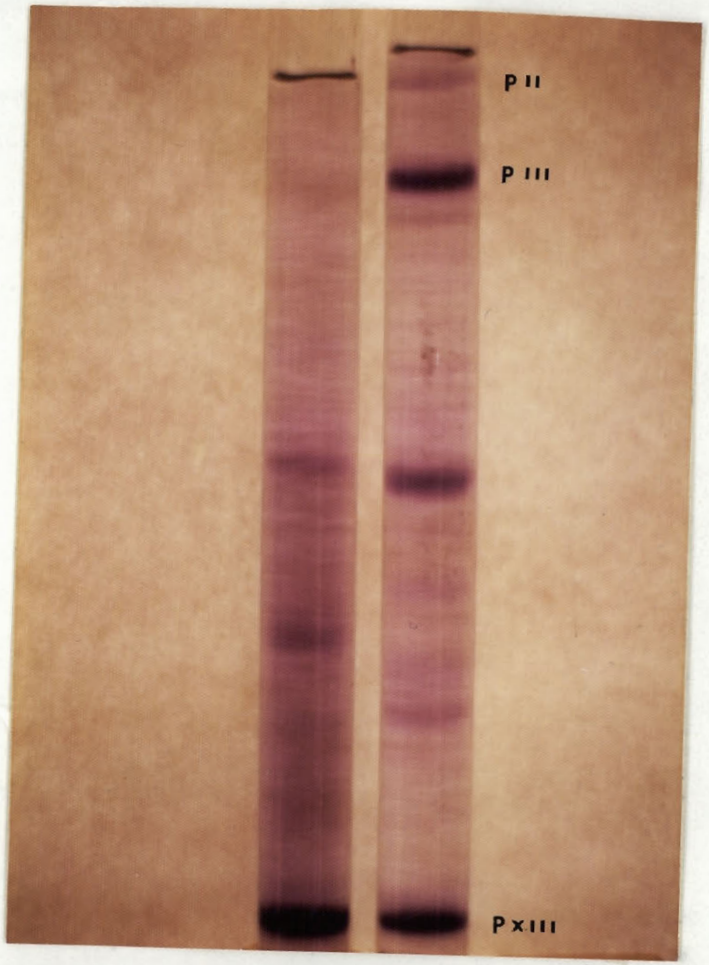


Figure 21. Molecular weights of proteins from gypsy moth eggs tested in January and determined by comparing their electrophoretic mobilities against three standards.

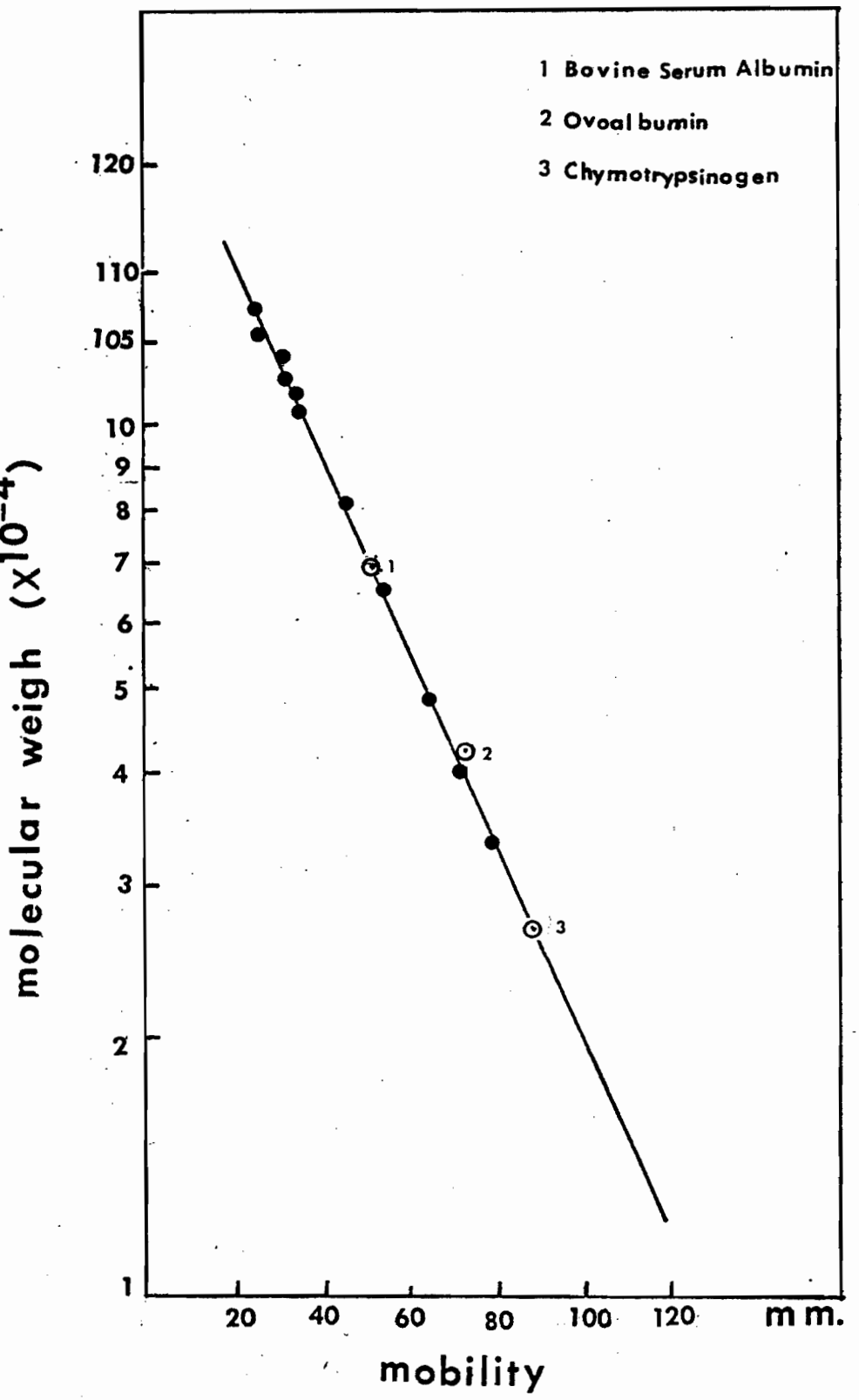

1 Bovine Serum Albumin
2 Ovoal bumin
3 Chymotrypsinogen
molecular weigh ($\chi 10^{-4}$)
120
110
105
10
9
8
7
6
5
4
3
2
1
1
2
3
20
40
60
80
100
120
m m.
mobility

Figure 22. Seasonal variation of glycoprotein band spectrophotometer readings of overwintering embryo of the gypsy moth.

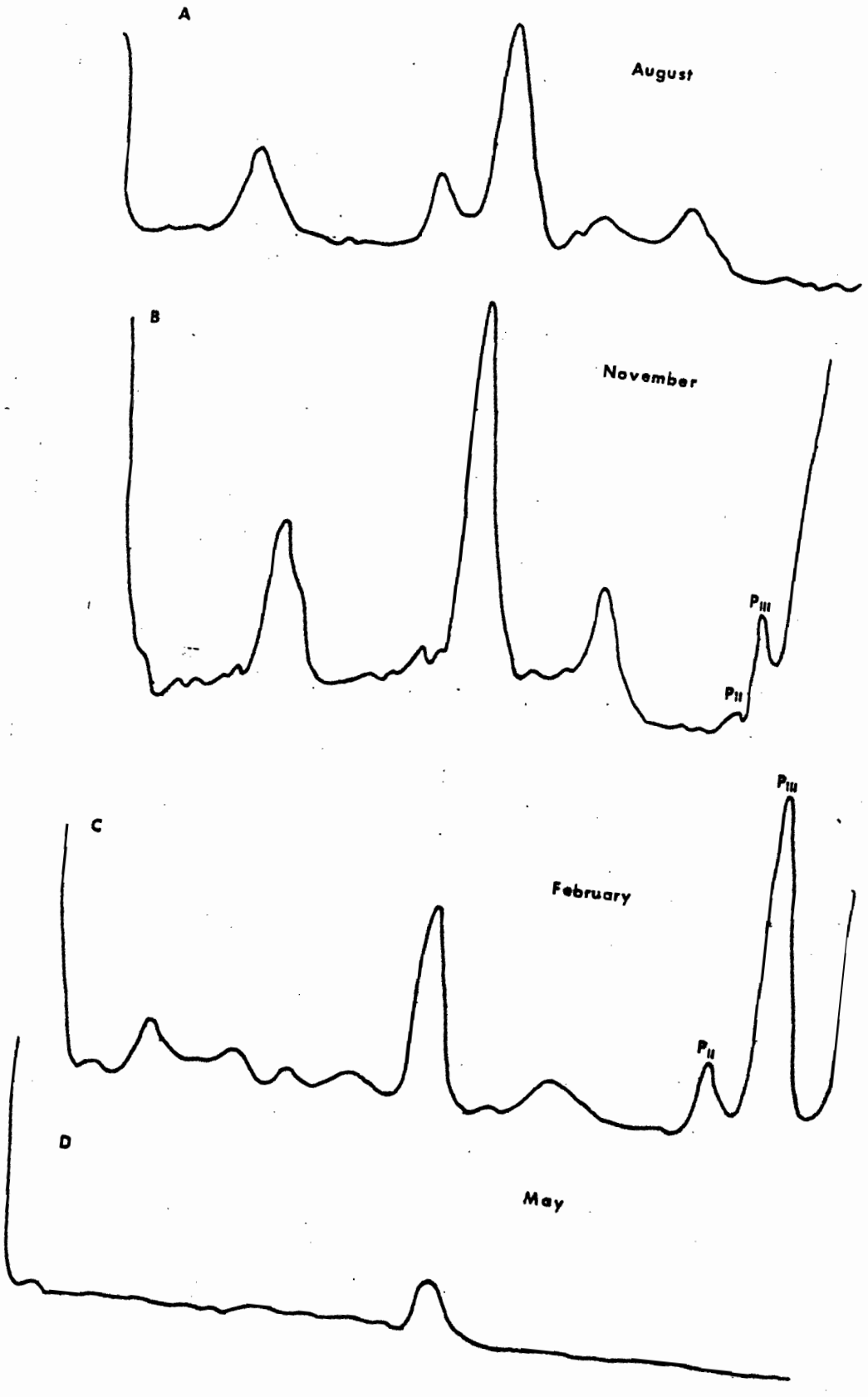
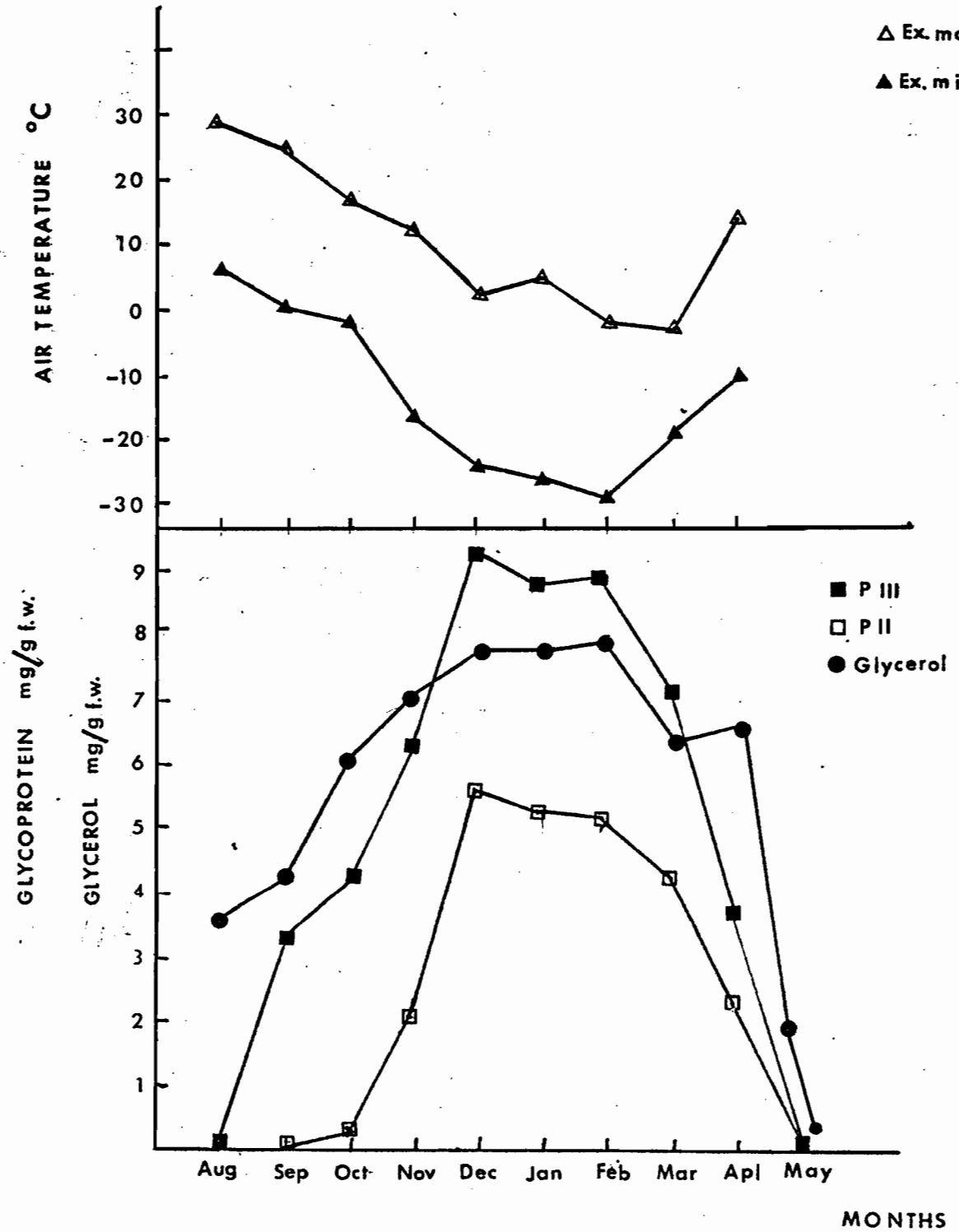

A
August
B
November
P_{III}
P_{II}
C
February
P_{III}
P_{II}
D
May

Figure 23. Seasonal variation in glycoprotein and glycerol content of gypsy moth eggs, as related to monthly maximum and minimum air temperatures.


△ Ex. max. tem
▲ Ex. min. tem
AIR TEMPERATURE °C
30
20
10
0
-10
-20
-30
■ P III
□ P II
● Glycerol
GLYCOPROTEIN mg/g f.w.
GLYCEROL mg/g f.w.
9
8
7
6
5
4
3
2
1
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apl
May
MONTHS

VI. PARASITOIDS, PREDATORS AND HYPERPARASITOIDS OF THE GYPSY MOTH LYMANTRIA DISPAR (L.) (LEPIDOPTERA: LYMANTRIDAE) IN QUEBEC[1]

[1]Submitted to publisher

ABSTRACT

Lymantria dispar (L.) larvae and pupae collected in 1977 and 1978 at Havelock, Mont Saint Hilaire and Deux Montagnes, Quebec, Canada, yielded 11 parasites and 9 hyperparasites. Blepharipa pratensis (Meig.), Compsilura concinnata (Meig.), Exorista larvarum (L.), Parasetigena silvestris (R.D.), Apanteles melanoscelus (Ratz.), Brachymeria intermedia (Nees) and Phobocampe disparis (Vier.) are exotic parasitic species, introduced to the United States or Canada for control of the gypsy moth. Sarcophaga aldrichi (Park.), Campoplex sp., Pimpla pedalis (Cress.), and Theronia atalantae fulvescens (Cress.) are native parasites. Calosoma frigidum Kirby, Podisus maculiventris Say and Lygaeus kalmii Stal. (three native species) were seen preying upon caterpillars. Fifteen species of birds were also identified as predators. Eurytoma sp., Dibrachys cavus (Walk.), Dibrachys confusus (Gir.), Habrocytus phycidis (Ash.), Bathythrix triangularis (Cress.), Exochus sp., Gelis obscurus (Say.) were recovered as hyperparasites of A. melanoscelus cocoons. Brachymeria compsilurae (Crawf.) was hyperparasitic on Compsilura concinnata.

Gypsy moth egg-masses were collected in the same areas and years, but no egg parasites were obtained from them.

INTRODUCTION

The gypsy moth is now well established as a permanent species in Quebec, and local severe infestations are being controlled by chemicals (Brown, 1976). Griffiths (1976) pointed out the paucity of gypsy moth enemies in Canada and suggested that there is great potential for biological control material to be imported. The importance of parasites and predators in the control of gypsy moth has been reflected in the large number of gypsy moth parasitoids introduced to North America by the U.S. Department of Agriculture and the State of Massachusetts, since the program against the pest was implemented in 1905 (Howard and Fiske, 1911; Burgess and Crossman, 1929; Clausen, 1956; Dowden, 1962).

In Canada, introduction of gypsy moth parasitoids started even before the gypsy moth was first reported here in 1924 (Cardinal, 1967; Brown, 1969). Between 1912 and 1918, parasites of three different pests, the brown-tail moth, Nygmia phaeorrhoea (Donov.), the satin moth, Stilpnotia salicis (L.), and the forest tent caterpillar, Malacosoma disstria (Hbn.), were introduced to Ontario, Quebec, Nova Scotia and New Brunswick (McGugan and Coppel, 1962). These parasites, which also attack the gypsy moth, are established in the United States and some of them have been recovered in Ontario (Griffiths, 1976).

As far as I know, there has been no systematic evaluation of the status of parasites in the Province of Quebec. This two-year study of heavy infestations of gypsy moth at Havelock (lat. 45 05 N, long. 74 11 W), Mont St. Hilaire (lat. 45 33 N, long. 73 05 W) and Deux Montagnes (lat. 45 30 N, long. 74 04 W) in Quebec, was designed to overcome this lack of information. Figure 24 shows the different sites and the parasites collected in each of them.

METHODS

Insect populations were sampled at two sites 120 km apart, in southwestern Quebec, in the area surrounding Montreal. The first site is a mixed forest with Grey birch (Betula populifolia Marsh) as the dominant species mixed with White pine (Pinus strobus L.), Hemlock (Tsuga canadensis (L.) Carr) and Beech (Fagus grandifolia Ehrh.) located at Havelock, Huntingdon County, near the border with the United States. The second area is primarily Beech mixed with Red oak (Quercus rubra L.), Sugar maple (Acer saccharum Marsh.) and White birch (Betula papyrifera Marsh.), located at the Gault Estate, Mont St. Hilaire, Rouville County, east of Montreal. Systematic sampling at this site was carried out in 1978 only. Limited collections were also made at Deux Montagnes and the Morgan Arboretum of Macdonald College, Ste. Anne de Bellevue.

Five plots of 1/2 acre each were sampled both at Havelock and Mont St. Hilaire. Within these plots, subplots consisting of five trees each, were established, each tree wrapped at breast height with a burlap strip folded to provide shelter for insects. Grey and white birch, beech, red oak and sugar maple were banded to determine if there were interspecific differences. Each 30 cm of burlap was taken as a unit to compensate for differences in trunk diameter (Griffiths, 1977). Collections of larvae and pupae were made from the burlap strips, weekly, during the two seasons 1977 and 1978.

Direct counts were also made, starting from a randomly selected point in each plot and collecting until 100 larvae and pupae were obtained or 1/2 hours had elapsed, whatever came first. They were then reared in separate containers in the laboratory to obtain possible parasitoids. Larvae were fed primarily oak leaves. Egg-masses were collected in the fall by searching in each plot until 100 were obtained or 1/2 hour had elapsed. They were then placed separately in petri dishes on moist paper filters. Half of the total number of egg-masses were kept at 5°C for one month, and then at 0°C until spring. The other half were kept in a small insectarium, at outdoor temperatures until hatching.

All species were identified at the Biosystematics Research Institute, Ottawa. The puparia of the four tachinid

species recovered were preliminarily identified using the key of Sabrosky and Reardon (1976) and taken later for confirmation to the B.R.I. at Ottawa.

PARASITOIDS COLLECTED

ORDER DIPTERA

Sarcophagidae

Sarcophaga aldrichi Park.

Distribution: North Africa and Europe (Thompson, 1946)

Northeastern United States and in Canada, from British Columbia to Southeastern Canada (Thompson, 1946).

Hosts: Gypsy moth prepupae and pupae, forest tent caterpillar Malacosoma disstria (Hubner.), prepupae and pupae

Baker (1972) reported this insect as a scavenger (feeding on dead pupae) of M. disstria. Campbell (1963a) did not consider it a true parasite as it only scavenged on L. dispar prepupae and pupae which had been previously stung by Ichneumonidae. In the laboratory, however, I found larvae of S. aldrichi to be capable of penetrating healthy intact pupae, especially when these were surrounded by a film of water. This species was present in all the collecting areas and Tables 20-21 show the percentage parasitism reached at the Havelock and Mont St. Hilaire sites in 1977 and 1978.

Tachinidae

Blepharipa pratensis (Meig.); Tachina pratensis Meigen 1824

Synonyms: Nemoraea scutellata Robineau-Desvoidy
Blepharipa, Blepharipoda, Crossocosmia, Sturmia scutellata (Sabrosky and Reardon, 1976)

Distribution: Widespread in the palearctic region from Europe to Japan, it was introduced to the Northeastern United States from Europe in 1907 (Stone et al., 1965).

Hosts: B. pratensis is primarily a parasite of L. dispar, but has been recovered occasionally from other hosts. Bess (1936) recovered it from Malacosoma disstria and M. americanum. Schaffner and Griswold (1934) and Schaffner (1934) also reported it from five native North American Lepidopteran hosts that are very rare and probably accidentally attacked by B. pratensis. It is a larval parasitoid; females lay small microtype eggs on the leaves where gypsy moth larvae feed. If the egg is ingested, it remains in the host as a first instar larva until the host pupates. The parasite larvae then completes its development and emerges to pupate in the soil (Griffiths, 1976).

It is now common in the Northeastern United States but levels of parasitism are very variable. Some authors (Bess, 1961; Weseloh, 1973) reported B. pratensis parasitizing small numbers of gypsy moth in New England, but other workers (Burgess and Crossman, 1929; Clausen, 1956; Odell et al., 1974) found higher percentages of parasitism by this insect in the same

region. I found levels of parasitism to be low at both major collecting sites (Tables 19 and 20).

Compsilura concinnata Meigen; Tachina concinnata Meigen

Synonym: Machaeraea (or Machaira) serriventris Rondani

Distribution: Palearctic Region, N. Africa to Japan. Introduced to the United States from 1906 to 1959 (Dowden, 1962).

Hosts: This insect is one of the most polyphagous tachinidae. It has been recovered from nearly 200 species of Lepidoptera (20 families) and 3 families of Tenthredinoidea (Clausen, 1956). Thirty-three thousand specimens of this insect were released in New Brunswick, Nova Scotia, Ontario and Quebec from 1912 to 1937 (McGugan and Coppel, 1962) and it has been recovered since from many species in Canada (Griffiths, 1976). Females larviposit one to four small larvae into the body cavity of the host (Sabrosky and Reardon, 1976). These maggots emerge when the host has developed into a late instar larva or a pupa. There are two to four generations per year, parasitizing, and hibernating in, alternate hosts.

Its effectiveness is lowered in some extent by the activity of Brachymeria intermedia and Eurytoma sp. as hyperparasites. Several authors have recorded C. concinnata as one of the most important factors in the control of the gypsy moth in the United States (Schaffner, 1934; Clausen, 1956). The percentage of parasitism recorded in different places in New

England range from 4% to 25% in Massachusetts (Burgess and Crossman, 1929) to an occasional 80% reported by Bess (1961) in New England. I found only a low degree of parasitism but it was present in all the collecting sites (Tables 19 and 20).

Exorista larvarum Linnaeus, Musca larvarum Linnaeus

Synonyms: Tachina moreti Robineau-Desvoidy, Tachina noctuarum Rondani, Tachina utilis Townsend. Other combinations: Eutachina, Tachina, or Larvaevora (or Larvivora) larvarum (Sabrosky and Reardon, 1976).

Distribution: Europe to Japan, N. Africa. It was introduced to the United States in 1906 from Italy, with releases every year until 1911 (Burgess and Crossman, 1929) and again from 1923 to 1959 with the first recoveries reported in 1940 in Connecticut. Despite few records of recoveries, it is considered to be established in New England. One specimen was obtained from an unknown host in Ontario in 1965 (Griffiths, 1976).

Hosts: This parasitoid is polyphagous and Herting (1960) cited 54 lepidopterous hosts. Females lay large, white, conspicuous eggs on the integument of the host caterpillar, usually near the anterior end. Young, newly hatched maggots bore into the host and leave it as a mature maggot, ready to pupate. Up to ten larvae can emerge from one host (Sabrosky and Reardon, 1976). Despite being considered an important parasitoid of gypsy moth by some authors (Dowden, 1962 in U.S.A.; Sisojevic, 1955 in Europe), reports on the percentage of attack are inconclusive.

Campbell (1967) found E. larvarum parasitizing late instar larvae in Northeastern New York State, but the percentage of successful attacks was very low. Possible factors influencing this finding are hyperparasitism and disease. Eurytoma sp. is a hyperparasite of E. larvarum. Tables 19 and 20 show the low level of parasitism recorded annually at all collecting sites.

Parasetigena silvestris Robineau-Desvoidy, Duponchelia silvestris R.-D.

Synonyms: Phorocera or Parasetigena agilis, Parasetigena segregata

Other combination: Phorocera silvestris

Emendation: sylvestris. (Sabrosky and Reardon, 1976).

Distribution: Palearctic Region, Europe to Japan (Stone et al., 1965). It was introduced to the United States from Central Europe between 1906-1911 and released for the first time in 1910 at North Andover, Massachusetts, but there were no recoveries. The program was started again in 1924, this time with the first recoveries reported at Boxford, Massachusetts (Burgess and Crossman, 1929). It is considered well established in most of New England (Sabrosky and Reardon, 1976), but it has not been previously reported in Canada as far as I can tell).

Hosts: This species parasitized L. dispar and the nun moth Lymantria monacha (L.). It is univoltine. Females lay microtype eggs on the larval cuticle, especially on third or fourth instar larvae. The young maggots burrow into the host and

emerge when this is a fully mature larva or pupa (Griffiths, 1976). P. silvestris parasitized 4% to 33% of gypsy moths on Cape Cod in 1970-1971 (Reardon, 1973) and in Europe it is considered an important parasite of the gypsy moth (Herting, 1960). In the Soviet Union, Shapiro (1956) found 49% attack in a dense stand but the percentage lowered to 14% in an open stand. In Quebec, one adult specimen was collected at Rigaud by Dr. D.M. Wood[a] (pers. commun.) and only puparia of P. silvestris were obtained at Mont St. Hilaire in 1978, giving a per cent parasitism of 2.8 (Tables 19 and 20).

ORDEN HYMENOPTERA

Braconidae

Apanteles melanoscelus Ratz.

Synonyms: A. solitarius (Ratz.) (De Lepiney, 1930; Nixon, 1974)

Distribution: Europe, especially the southern part, N. Africa and U.S.S.R. Introduced and released for the first time to New England in 1911, this program continued annually until 1959 (Dowden, 1962). In Canada, it was released in several provinces from 1929 to 1934 during the program against the satin moth (McGugan and Copell, 1962). In Quebec, it has never been released, but it was recovered in 1971 from gypsy moth larvae collected in Ormstown, Quebec (J.M. Kelleher, B.R.I., personal commun.). Now A. melanoscelus is established in the gypsy moth

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range in Canada (Griffiths, 1976).

Hosts: L. dispar, Hemerocampa leucostigma (J.E. Smith). Stilpnotia salicis (L.)

It has two generations per year, first generation adult females attacking early instar larvae (I-II instar) and second generation females parasitizing III-IV instar larvae and exceptionally V-VI instar larvae. The parasite overwinters as a mature larva inside a tough cocoon attached usually to a tree trunk (Burgess and Crossman, 1929). The degree of parasitism by this species is very variable. Crossman (1922) estimated 75% parasitism in Sicily in 1911. In the U.S.S.R. gypsy moth pupae collected in three outbreaks were parasitized at different levels ranging from 2% to 90% (Shapiro, 1956). In Massachusetts, Bess (1961) reported 25% parasitism on second and third instar larvae. More recently, in Connecticut, Weseloh (1973) found a negative correlation between percentage parasitism and gypsy moth density for first generation A. melanoscelus and no correlation was found for the second generation.

Grimble (1976) working on several gypsy moth parasitoids found A. melanoscelus established in Lordville, New York, but it did not have a major influence on the gypsy moth population density. A supplementary release of the parasitoid in 1976 produced no increase in levels of parasitism. Tigner et al. (1974) found no correlation between gypsy moth and A. melanoscelus

numbers. In Quebec, 1750 II and III instar larvae collected in Havelock during the summer of 1977 showed 10.8 and 4.5% parasitism respectively, by first generation A. melanoscelus (Table 19). Second generation parasitoids showed a lower percentage of parasitism, in both sites, the two years, although the short period of development makes them less susceptible to attack by hyperparasites than the first generation.

Ichneumonidae

Pimpla pedalis Cress.

Synonym: Coccygomimus pedalis (Cress.)

Distribution: Canada Transcontinental and Transition zones (Muesebeck, Krombein and Townes, 1951). Japan (Thompson, 1946).

Hosts: Lymantria dispar (L.) larvae, pupae. This species has been recovered from several hosts in Ontario and from gypsy larval collections in Glengarry County, Ontario (Griffiths, 1976). Campbell (1963a) described an interaction between this and other Ichneumonids, with sarcophagids that attack the gypsy moth, and it is assumed that this wasp attacks pupae mainly for feeding purposes rather than for oviposition. Sarcophagids tend to attack pupae stung by Ichneumonidae and the percentage of pupae attacked by the sarcophagids could be useful as an index of Ichneumonid attack (Campbell, 1963, 1975). Two specimens, only, were obtained during one of the weekly pupal collections (720

pupae) at Mont St. Hilaire in 1978 (Table 20).

Theronia atalantae fulvescens (Poda.)

This is a native North American species, which attacks gypsy moth pupae. Campbell (1963a, 1967) states that many more pupae are stung by these wasps than there are actual oviposi-tions. T. atalantae has been recovered in Canada from other hosts (Griffiths, 1976). I collected only one specimen from a gypsy moth pupa taken from Havelock in 1978.

Phobocampe disparis Viereck (Muesebeck et al., 1951).

Hyposother disparis Vier., Limnerium disparis Vier.

Distribution: Japan, Europe and U.S.S.R. Introduced to New England from Europe in 1912, it was recovered during the same season from several sites. It is established in New England, but there are few records of recoveries (Dowden, 1962). It has never been released in Canada and it is an unimportant para-site (Griffiths, 1976). Only on rare occasions has this para-site shown a high percentage of attack, and its potential effec-tiveness is diminished by high levels of hyperparasitism and an incomplete adaptation to its host. This latter situation is suggested by many findings of eggs and young larvae dead and surrounded by phagocytes of the host (Muesebeck and Parker, 1933). However, Ticehurst et al. (1978) found 30.4% parasitism in Pennsylvania and reported it as an important species. I recovered two cocoons only, from 519 gypsy moth larvae collected

from Mont St. Hilaire in 1978 (Table 19).

Chalcididae

Brachymeria intermedia Nees.

Chalcis flavipes (Panzer-Peck, 1963)

Distribution: Palearctic Region, Japan. Introduced to the Eastern United States from Europe in 1905. Despite several more introductions in the years after initial introduction, it was not recovered for some considerable time (Dowden, 1962). Now, it is established in New England (Leonard, 1967b. 1971).

Hosts: Besides parasitizing pupae of L. dispar, this chalcid wasp has been recovered from two tachinid species: Compsilura concinnata and Exorista larvarum (Figure 25). This insect is very polyphagous, parasitizing pupae of many Lepidoptera, several tachinids and one hymenopteran (Dowden, 1935). It has two and sometimes three generations per year in alternate hosts and overwinters as an adult. They become active in early spring and go through a generation before attacking available gypsy moth pupae (Dowden, 1935). Females lay eggs inside their host, which can be the gypsy moth prepupa or pupa or a tachinid larva inside the gypsy moth pupae. Only one parasite develops per host.

B. intermedia has been obtained in very large numbers in Sicily, Morocco and Algeria, and it is considered an important parasite in those places. In Spain parasitism ranged from 14%

to 65% over five years (Romanyk, 1965, 1966). In Connecticut, parasitism of up to 51% was recorded in 1970 (Doane, 1971). Leonard (1967b) in the same area found between 0.2% and 4.7% parasitism. Grimble (1976) reported 24% parasitism in New York. I found only a very low level of parasitism at Mont St. Hilaire in 1978 (Table 20).

Predators Collected

Three native species of insect predators were found at both collecting sites. Calosoma frigidum Kirby (Coleoptera: Carabidae) adults were observed preying on large larvae in the field. In the laboratory, they attacked larvae as well as pupae. C. frigidum was reported in Quebec by Larochelle (1975). Two species of stink bugs were recovered. Podisus maculiventris Say and a Euschistus nymph (Hemiptera:Pentatomidae) (Blatchley, 1926) were found under burlap traps at Havelock. Lygaeus kalmii Stal (Hemiptera: Lygaeidae) was seen feeding on disease killed larvae at Havelock. It is believed that these two species have not been previously reported feeding on the gypsy moth.

Four species of Arachnids were seen eating adult gypsy moth males that were trapped in their web. Two agelenids, Agelenopsis sp., Coras sp., a Philodromid, Philodromus praelustris Keyserling and an Amaurobid, Callobius bennetti (Blackwall), were recovered from Mont St. Hilaire. C. bennetti was common

under burlap traps. The predatory activity of birds and small mammals has a very important role in keeping sparse populations of the gypsy moth from increasing their numbers (Furuta, 1976; Campbell and Sloan, 1977). Furuta reported a drastic decrease in gypsy moth larval numbers caused by predaceous birds (Furuta, 1976).

Fifteen species of birds were found at Mont St. Hilaire and Havelock. All of them reported as predators of the gypsy moth (McAtee, 1911).

Order	Family	Common Name	Species
Piciformes	Picidae	Downy woodpecker	Dendrocopos pubescens (L.)
Passeriformes			
	Tyrannidae	Kingbird	Tyrannus tyrannus (L.)
	Tyrannidae	Wood pewee	Contopus virens (L.)
	Corvidae	Blue jay	Cyanocitta cristata (L.)
	Corvidae	Crow	Corvus brachyrhynchos Brehn
	Icteridae	Red-winged blackbird	Agelaius phoeniceus (L.)
	Icteridae	Baltimore oriole	Icterus galbula (L.)
	Fringillidae	Song sparrow	Melospiza melodia (W.)
	Fringillidae	Rose-breasted grosbeak	Pheucticus ludovicianus (L.)
	Thraupidae	Indigo bunting	Passerina cyanea (L.)
	Thraupidae	Scarlet tanager	Piranga olivacea (Gmelin)
	Vireonidae	Red-eyed vireo	Vireo olivaceus (L.)
	Troglodytidae	House wren	Troglodytes aldon (Vieillot)
	Paridae	Black-capped chickadee	Parus atricapillus L.
	Turdidae	American robin	Turdus migratorius (L.)

Hyperparasitoids Collected

Eight hyperparasite species were found parasitizing Apanteles melanoscelus Ratz in collections made at Havelock in 1977 (Table 21).

Pteromalidae

Dibrachys cavus (Walk.), Dibrachys boucheanus Ratz. (Peck, 1963)

Pteromalus cavus Walker, Pteromalus boucheanus Ratz. (Muesebeck et al., 1951)

Distribution: Eastern United States and Canada (Muesebeck, 1951; Krombein et al., 1951).

Hosts: Apanteles melanoscelus (Figure 26), other species of Apanteles, several species of Meteorus, Rogas, Hyposoter and Campoplex, sometimes tachinid puparia.

D. cavus is a cosmopolitan species with five generations per year. It has been recovered also as a primary parasite from Diprion pini L., Neodiprion sertifer (Geoff.) and Carpocapsa pomonella L. It has been recovered in Ontario from N. sertifer (Griffiths, 1976). This species parasitized A. melanoscelus heavily (63.06%) at Havelock in 1977 (Table 21).

Dibrachys confusus (Girault), Coelopisthia confusa Girault

Distribution: District of Columbia (Muesebeck et al., 1951).

Host: A. melanoscelus (Ratz.)

One specimen only was obtained from an A. melanoscelus cocoon collected from Havelock in August 1977.

Habrocytus phycidis Ashmead; Habrocytus dux Girault

Distribution: Ontario, Quebec, New England

Hosts: A. melanoscelus (Ratz.); Meterous versicolor (Wesm.); Choristoneura fumiferana (Clem.) (Muesebeck et al., 1951).

This North American species has been recovered from 14 hosts in Ontario (Griffiths, 1976). We found 4.0% of A. melanoscelus cocoons hyperparasitized by H. phycidis at Havelock in 1977.

Ichneumonidae

Bathythrix triangularis (Cresson), Mesoleptus triangularis Cresson

Synonyms: Mesostenus pallipes Provancher

Distribution: Atlantic, westward to Illinois

Hosts: A. melanoscelus, Meteorus veriscolor (Wesm.), Phobocampe geometrae (Ashm.) (Muesebeck et al., 1951).

Only one specimen was recovered from an A. melanoscelus cocoon at Havelock in 1977.

Gelis obscurus (Cresson)

Synonyms: Pezomachus obscurus Cresson, Pezolochus bucculatricis Ashmead

Distribution: North America

Hosts: Bucculatrix canadensisela Chamb., Apanteles lacteicolor Vier., A. melanoscelus (Ratz.) (Muesebeck et al., 1951).

Only one specimen was recovered from A. melanoscelus at Havelock in 1977.

Gelis tenellus (Say), Hemitelus tenellus (Say) (Muesebeck and Dohanian, 1927)

Distribution: North America

Hosts: Primary parasite on Bucculatrix sp., Quercus malivorella Riley, Coeophora pruniella Clem., C. salmani Heinr., as a hyper-parasite on A. lacteicolor Vier., A. melanoscelus (Ratz.), Meteorus acronyctae Mues. (Muesebeck et al., 1951).

Four specimens were recovered from A. melanoscelus at Havelock in 1977. Exochus sp. (Ichneumonidae) and Eurytoma sp. (Eurytomidae).

These hyperparasites were undetermined. However, the A. melanoscelus were lightly parasitized by both species.

Dibrachy cavus was, by far, the most common species recovered from A. melanoscelus; Habrocytus phycidis and Eurytoma sp. were less common with ca 4% parasitism each.

The combined percentage of parasitism by the four Ichneumonid species, Bathythrix triangularis, Exochus sp., Gelis obscurus and Gelis tenellus, was 4.9% (Table 31). Gelis tenellus has been recovered in Ontario from the gypsy moth and fourteen other hosts (Griffiths, 1976). The other three species were believed to be recovered for the first time from gypsy moth in Canada.

DISCUSSION

The population density of gypsy moth eggs and larvae at

Havelock increased slightly in 1977 and then decreased in 1978, whereas at Mont St. Hilaire population density was higher in 1978 than in 1977.

Given the short study period, I can make no meaningful interpretation of the impact of parasites on the host density. There is, however, no indication of increased parasitism at the higher host densities. No egg parasite was found in the egg-masses collected at all sites during fall and early spring each year. Apparently important mortality factors affecting gypsy moth eggs in Quebec are other than parasitism.

Dispersal of the two species, A. disparis, O. kuwanai, parasitic upon gypsy moth eggs in the United States, has been slow, specially because the females do not fly (Burgess and Crossman, 1929). Although both species are present in Maine, they have apparently not reached Quebec.

Apanteles melanoscelus was the only parasitoid showing some impact on early instar larvae, at both sites, during both years (Table 19). Mont St. Hilaire data show a smaller rate of parasitism for the year 1978, than that for Havelock, whereas the estimate of host population is very high, and probably increasing (Table 22).

Counts of second generation A. melanoscelus cocoons under burlap traps show greater numbers on preferred host trees such as birch and beech; oak, however, its primary host, did not show

as high numbers of A. melanoscelus cocoons (Table 23).

There was no significant correlation between the numbers of A. melanoscelus cocoons under burlap and the number of gypsy moth larvae found in weekly counts (Table 24). However, the weekly numbers of gypsy moth larvae and A. melanoscelus cocoons remained significantly constant ($P < .1$ gypsy moth larvae, $P < .05$ A. melanoscelus cocoons). These results are probably related to the behavior of older larvae, which usually do not disperse (Leonard, 1967a). The highest numbers of A. melanoscelus under burlap traps were collected in late June and early July (Figure 27), after gypsy moth larvae started aggregating under burlap traps.

A. melanoscelus is limited in its effectiveness by severe mortality, due mainly to heavy hyperparasitism and to a lesser extent to winter kill. To assess hyperparasites, cocoons of A. melanoscelus were collected in the fall, and kept at 5°C during the winter. In early spring they were put to 21°C and 16-hour photoperiod, and the insects which emerged were recorded and identified[a] (Table 25). Hyperparasites have previously accounted for over 95% mortality of the A. melanoscelus overwintering generation (Burgess and Crossman). We found 76.1% hyperparasitism

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[a]Specialists at B.R.I., Ottawa.

in the laboratory and 58% in cocoons that overwintered and emerged in the field. From the total number of cocoons, both in the laboratory and in the field, 14.8% and 37% respectively failed to emerge, thus totaling 90.9% and 95% of total cocoons that failed to yield a mature A. melanoscelus. Table 26 shows the level of hyperparasitism by all species at Havelock and Mont St. Hilaire during 1978.

Phobocampe disparis is not abundant in all collecting sites. Only two cocoons were obtained from IV instar larvae collected at Mont St. Hilaire on June 15, 1978.

Among the tachinid parasitoids, B. pratensis yielded the highest level of parasitism both in Havelock and Mont St. Hilaire in 1978. The higher percentage of the fly in Havelock in 1978 probably relates to the smaller host population and not to a real increase in numbers of the parasite.

C. concinnata parasitized a small percentage of larvae with major changes in any site in any year. It appears to attack about the same numbers without changes related to the host population density (Tables 19 and 20). In Havelock parasitism increased a mere 1%, however, host population decreased from an estimated 2860 egg-masses per acre in 1977 to 1396 egg-masses per acre in 1978.

Exorista larvarum was recovered both at Havelock and Mont St. Hilaire. Parasetigena silvestris was obtained from Havelock

pupal collections. Larval collections from both sites were examined, and larvae which showed white tachinid eggs were reared individually (Table 27). From 53 gypsy moth larvae parasitized, eight E. larvarum larvae emerged from which two reached adulthood. Puparia not fully identified (P. silvestris or E. larvarum) were obtained from Mont St. Hilaire pupal collections in 1978.

Sarcophaga aldrichi was recovered from large larvae, in small numbers at Mont St. Hilaire in 1978, but the mature larvae issued mostly from prepupae and pupae, reaching almost 8% parasitism at Havelock during the same year. The role of this fly is still unclear; Campbell (1963a) presented evidence indicating that the larva enters gypsy moth pupae through holes previously made by ichneumonids. I observed sarcophagid larvae entering healthy gypsy moth pupae surrounded by a film of water in the laboratory, but it is uncertain if this behavior is repeated in the field. S. aldrichi is known to be truly parasitic upon Malacosoma disstria (Hodson, 1939).

Pimpla pedalis, Theronia atalantae and Brachymeria intermedia were recovered in very small numbers. Three specimens of P. pedalis were recovered from pupae collected at Mont St. Hilaire in 1978. Only one female T.atalantae was recovered the same year from Havelock. These ichneumonids, although obtained in low numbers from the gypsy moth, probably kill many more pupae

than the number of recoveries would indicate (Campbell, 1963a).

Brachymeria intermedia was recovered from gypsy moth pupae (3 specimens) and from puparia of Compsilura concinnata, whose maggot emerged from a gypsy moth pupae. The same behavior was observed in one specimen of B. compsilurae recovered from the same host at Havelock in 1978.

Predators were assessed qualitatively during 1977-1978.

CONCLUSIONS

From this study I have concluded that most of the exotic species released in the United States and Canada against the gypsy moth have become established in Quebec on the same host (Table 28). A. melanoscelus, B. pratensis, C. concinnata and E. larvarum were recovered in significant numbers.

B. pratensis is the most important tachinid parasitoid attacking the gypsy moth in Quebec.

A. melanoscelus, although a very valuable parasitoid, is handicapped because of the heavy hyperparasitism to which it is subjected, especially by Dibrachys cavus, Gelis tenellus and Habrocytus phycidis.

B. intermedia seems to act as much as a hyperparasite upon tachinids as a parasite on gypsy moth pupae. More research on host preference of B. intermedia is needed.

No egg parasites were recovered and I suggest their

importation. Two possible candidates for introduction are Anastatus disparis Ruschka (Sullivan et al., 1977), and Ooencyrtus kuwanai (How.).

Presence of predators make interesting a future assessment of their impact.

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Table 19. Percentage parasitism by Diptera and Hymenoptera species of young gypsy moth larvae at Havelock and Mont St. Hilaire (1977, 1978), Quebec.

		Havelock 1977				Havelock 1978				Mont St. Hilaire 1978			
Parasite Species	Gypsy moth Instar	I	II	III	IV	I	II	III	IV	I	II	III	IV
Diptera													
Compsilura concinnata		-	-	0.2[1]	-	-	-	1.2	1.7	-	-	0.5	-
Exorista larvarum		-	0.5[2]	2.2[2]	3.2	-	0.3[2]	9.8[2]	4.3[2]	-	-	3.5[2]	7.5[2]
Sarcophaga aldrichi		-	-	-	-	-	-	-	0.3	-	-	0.1	-
Hymenoptera													
Apanteles melanoscelus		1.3	10.8	4.3	1.0	-	8.3	5.5	1.3	-	12.6	2.3	3.0
Phobocampe disparis		-	-	-	-	-	-	-	-	-	-	-	0.7
No. of larvae examined		225	745	1005	553	329	539	326	643	215	301	502	519
Total percent parasitism		1.3	11.3	6.7	4.2	-	8.6	16.5	7.6	-	12.6	6.4	10.8

[1]: All partial percentages = average of 5 plots.

[2]: Percentage parasitism not separated from that of P. silvestris.

Table 20. Percentage parasitism by Diptera and Hymenoptera of large larvae, prepupae and pupae of gypsy moth at Havelock and Mont St. Hilaire (1977, 1978), Quebec.

		Havelock								Mont St. Hilaire			
		1977				1978				1978			
Parasite Species	Gypsy moth Instar	V	VI	PP	P	V	VI	PP	P	V	VI	PP	P
Diptera													
Blepharipa pratensis					4.5	0.1	-	0.9	11.9	1.6	3.5	-	9.4
Compsilura concinnata		0.9	0.2	3.0	0.3	0.01	0.3	2.9	2.1	1.1	1.7	-	1.2
Exorista larvarum		2.7[1]	1.7	-	0.3	2.3	4.6	1.9	3.2	0.8	2.6	3.1	1.6[2]
Parasetigena silvestris													2.7
Sarcophaga aldrichi		-	-	12.1	2.0	-	0.6	-	7.6	1.9	1.1	4.7	7.7
Hymenoptera													
Brachymeria intermedia													0.4
Pimpla pedalis													0.2
No. of larvae examined		431	465	33	524	422	321	101	368	359	336	63	720
Total percent parasitism		3.6	1.9	15.1	4.1	2.4	5.5	5.7	24.8	5.4	8.9	7.8	22.6

[1]: Percentage parasitism Ex. larvarum includes that of P. silvestris except[2].

Table 21. Hyperparasitic species recovered from A. melanoscelus parasitizing gypsy moth (Havelock, Quebec, 1977).

Hyperparasites Recovered	Number of Hyperparasites	Percentage Hyperparasitism
Pteromalidae		
Dibrachys cavus (Walk.)	140	63.06
Dibrachys confusus (Gir.)	1	0.4
Habrocytus phycidis (Ash.)	9	4.0
Ichneumonidae		
Bathythrix triangularis (Cress.)	1	0.4
Gelis obscurus (Cress.)	1	0.4
Gelis tenellus (Say)	4	1.8
Exochus sp.	5	2.2
Eurytomidae		
Eurytoma sp.	8	3.6
No. A. melanoscelus cocoons	222	

Table 22. Estimated gypsy moth larval density and parasitism by A. melanoscelus (Havelock, Mont St. Hilaire, Quebec, 1977, 1978).

Field	Season	Number of gypsy moth larvae hatched per acre	Percentage of larvae parasitized by A. melanoscelus per acre	Number of larve parasitized/acre
Havelock	1977	915710	16.8	154052
	1978	747146	14.3	107171
Mont St. Hilaire	1978	808877	9.9	80325

Table 23. Numbers of second generation A. melanoscelus cocoons under burlap traps on different tree species at Havelock and Mont St. Hilaire, Quebec, 1977, 1978.

	Plots	1	2	3	4	5
		Havelock				
Maple (Acer saccharum Marsh)	1977	16(1)[1]	0(-)	13(1)	10(1)	12(1)
	1978	5(1)	0(-)	0(1)	8(1)	9(1)
Birch (Betula papyrifera Marsh) Var.	1977	41(2)	154(3)	124(2)	79(2)	83(2)
	1978	37(2)	58(3)	76(3)	48(2)	22(2)
Total	1977	57(3)	154(3)	137(3)	89(3)	95(3)
	1978	42(3)	58(3)	76(3)	56(3)	31(3)
		Mont St. Hilaire				
Maple (Acer saccharum Marsh)	1978	4(1)	0(-)	9(1)	0(-)	0(-)
Oak (Quercus rubra L.)	1978	0(-)	31(1)	60(1)	0(-)	93(1)
Beech (Fagus grandifolia Ehrh.)	1978	136(2)	60(2)	43(1)	211(2)	72(1)
Birch (Betula papyrifera Marsh) Var.	1978	0(-)	0(-)	0(-)	105(1)	95(1)
Total	1978	140(3)	91(3)	113(3)	316(3)	250(3)

[1]: Numbers in brackets are the numbers of trees sampled.

Table 24. Distribution of gypsy moth larvae and A. melanoscelus cocoons under burlap traps on trees (Havelock, Quebec, 1978).

Plot(n)	Number of gypsy moth larvae per trap[1]				Number of A. melanoscelus cocoons			
	Date				Date			
	15-6	22-6	29-6	6-7	15-6	22-6	29-6	6-7
1(3)	67	125	132	28	7	8	13	7
	4[a]	5	4	5	2[a]	4.5	4	4
2(3)	57	181	129	69	9	11	16	10
	5	4	5	2	1	25	3	2
3(3)	74	209	192	85	4	23	32	12
	3	3	3	1	4	1	1	1
4(3)	92	247	248	59	6	11	24	8
	2	2	1	3	3	4.5	2	3
5(3)	109	271	235	57	3	8	11	5
	1	1	2	4	5	4.5	5	5

[1]: Multiple rank correlations test (Friedman, 1937).

[a]: Ranks are shown beneath the numbers.

(n): Number of burlap banded trees.

Table 25. Second generation A. melanoscelus cocoons, hyperparasitism and mortality (Havelock, Quebec, 1977).

	Laboratory		Field	
	No. of cocoons	%	No. of cocoons	%
A. melanoscelus emerged	20	9	15	4.9
Hyperparasite emerged	169	76	177	58
Larvae dead inside cocoon	33	14.8	113	37
A. melanoscelus mortality [a]	202	90.9	290	95
Total (cocoons)	222		305	

[a]: Total percentage, considered all factors.

Table 26. Levels of hyperparasitism of A. melanoscelus overwintering generation, at different dates in 1978, at Havelock and Mont St. Hilaire, Quebec.

	Plots	1	2	3	4	5	Collection date
Mont St. Hilaire	% parasitism	14	21.8	41	15.6	36	30 Aug.
		69.7	87.2	78.3	72.3	91.1	28 Oct.
	Total cocoons	140	91	112	316	250	-
Havelock	% parasitism	27	-	7.6	10.5	16.6	6 Aug.
		81.3	64.8	59.3	75.4	88.6	17 Oct.
	Total cocoons	42	58	76	56	31	-

Table 27. Record of Tachinid eggs on larvae collected at Havelock (1978), Quebec.

Date	Total larvae	No. larvae with eggs	% larvae with eggs	No. eggs/larvae 1	2	3	4	5	Total eggs
8-6-78	324	17	5.2	12	3	0	0	2	28
15-6-78	529	33	6.0	30	2	0	1	0	38
22-6-78	296	20	5.7	17	1	2	0	0	25
29-6-78	222	11	4.9	9	0	0	1	0	13
6-7-78	46	4	8.6	4	0	0	0	0	4

Table 28. Parasitoids reared from the gypsy moth, Lymantria dispar (L.) in Quebec (1976-1978).

Parasitoid	Status	Stage attacked
O. Diptera		
F. Sarcophagidae		
Sarcophaga aldrichi (Park.)	P/S	Prepupae, pupae
F. Tachinidae		
Blepharipa pratensis (Meig.)[1]	P	Larvae
Compsilura concinnata (Meig.)	P	larvae
Exorista larvarum (L.)[1]	P	Larvae
Parasetigena silvestris (R.-D.)[1]	P	Larvae
O. Hymenoptera		
F. Braconidae		
Apanteles melanoscelus (Ratz.)[2]	P	Larvae
F. Chalcididae		
Brachymeria intermedia (Nees.)[1]	P/H	Pupae
F. Ichneumonidae		
Campoplex sp.[1,3]	P	Larvae
Phobocampe disparis (Vier.)[1]	P	Larvae
Pimpla pedalis (Cress.)[2]	P	Pupae
Theronia atalantae fulvescens (Cress)[1]	P	Pupae

P: Primary Parasite H: Hyperparasite S: Scavenger

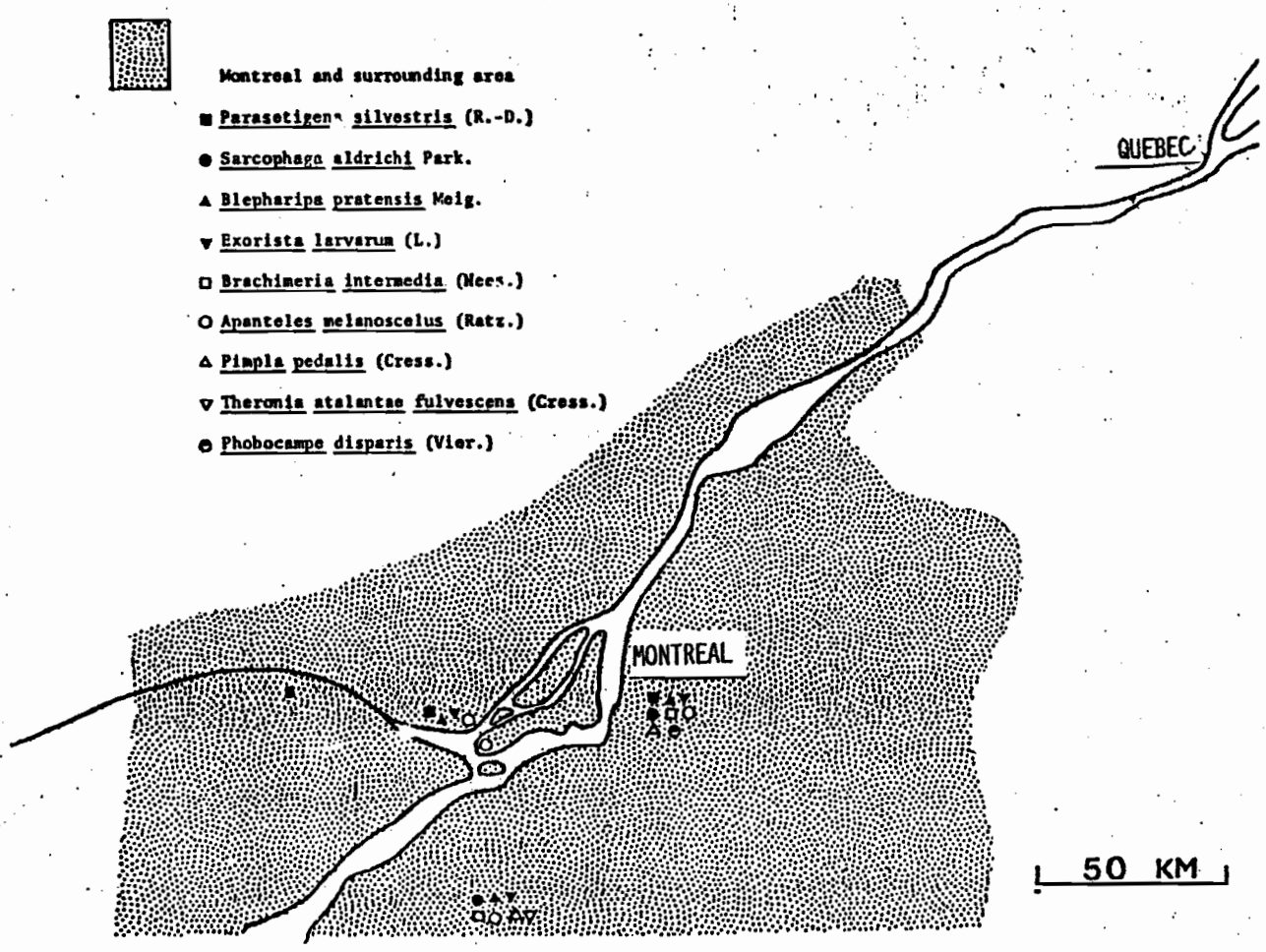
[1]: Indicates species not recovered previously in Canada.

[2]: Indicates species not recovered previously in Quebec.

[3]: Genus needs revision.

Figure 24. Distribution map of the gypsy moth in Quebec (1977).

Figure 1. Distribution map of the gypsy moth in Quebec (1977).



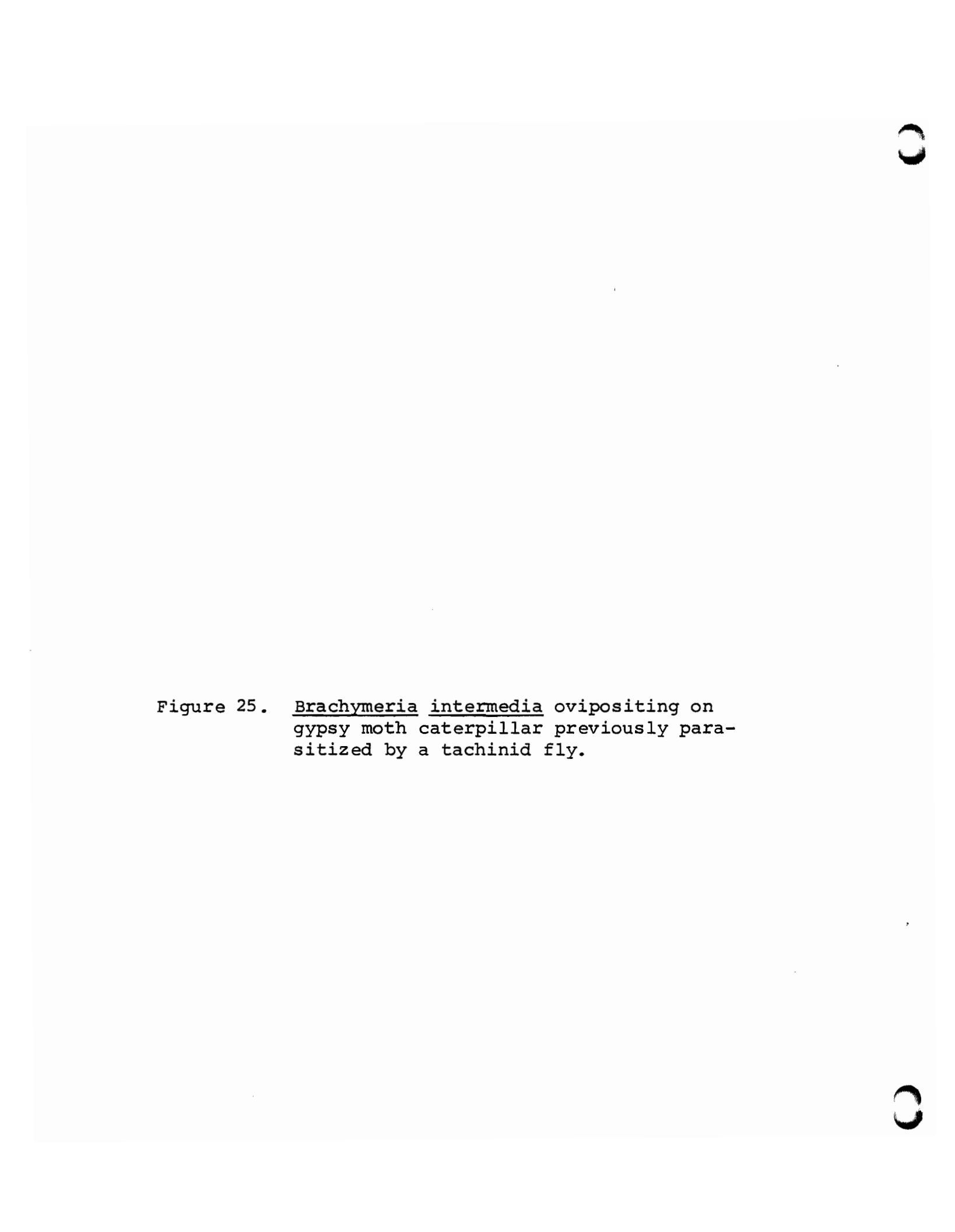


Figure 25. Brachymeria intermedia ovipositing on gypsy moth caterpillar previously parasitized by a tachinid fly.

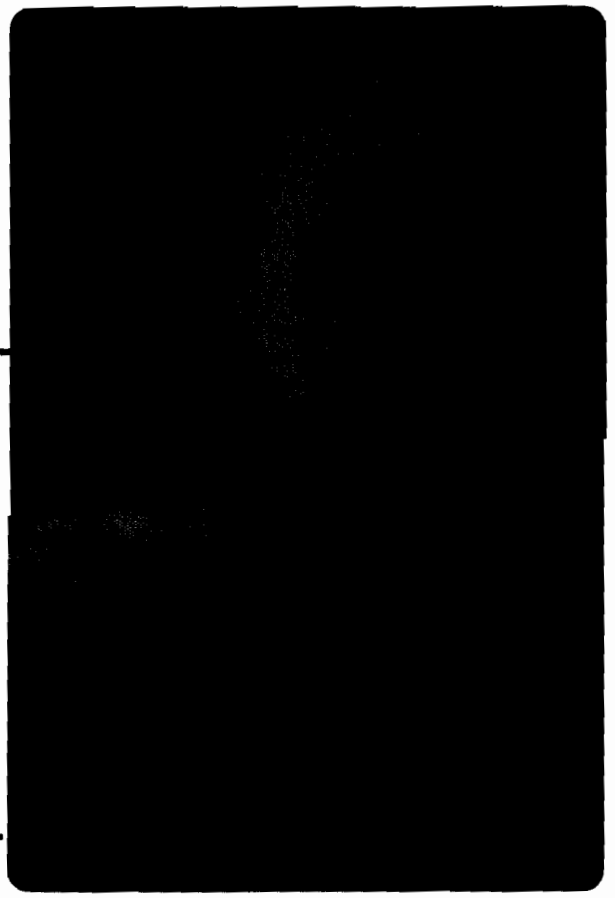
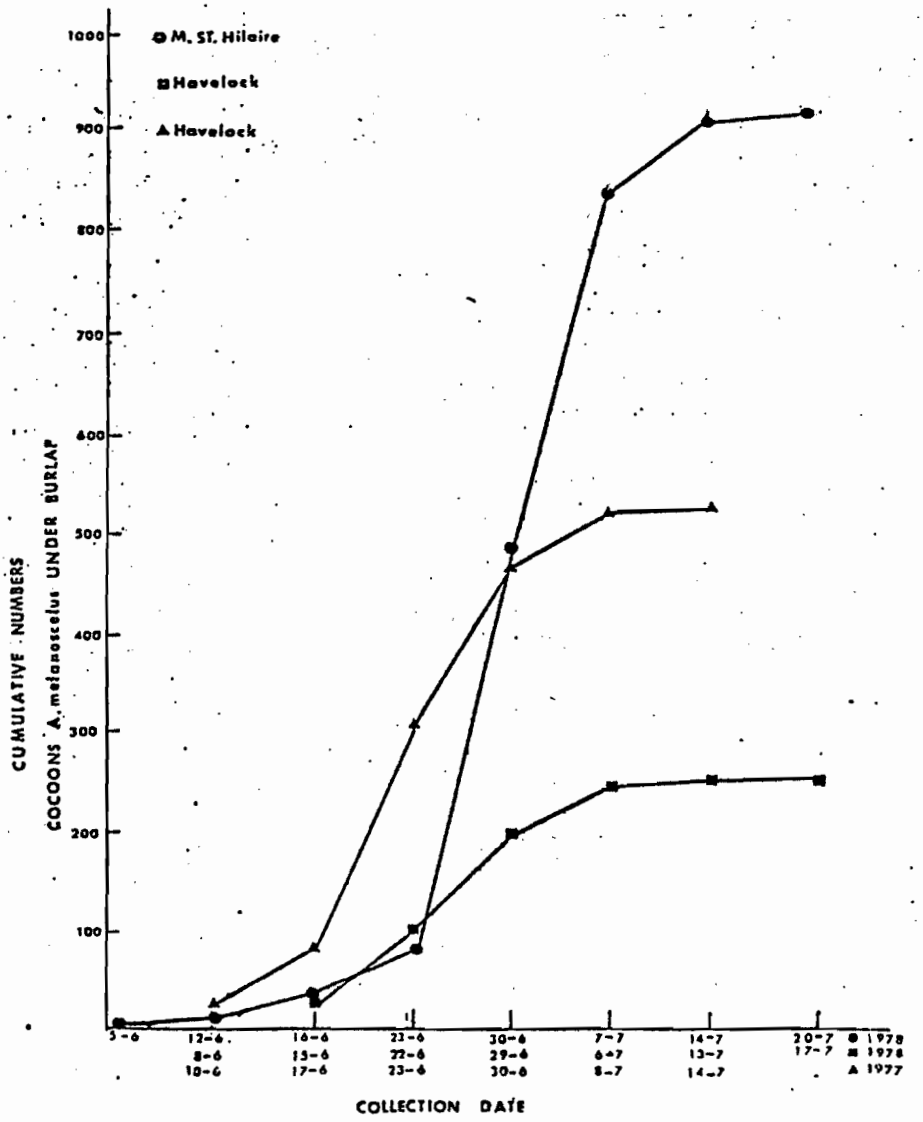


Figure 26. Dibrachys cavus ovipositing on second generation A. melanoscelus cocoon.

Figure 27. Cumulative numbers of second generation Apanteles melanoscelus cocoons collected weekly under burlap traps (Mont St. Hilaire, 1978, Havelock, 1977, 1978).


M. ST. Hilaire
Havelock
Havelock
CUMULATIVE NUMBERS
COCOONS A. melanoscelus UNDER BURLAP
1000
900
800
700
600
500
400
300
200
100
5-6
12-6
8-6
18-6
16-6
13-6
17-6
23-6
22-6
23-6
30-6
29-6
30-6
7-7
6-7
8-7
14-7
13-7
14-7
20-7
17-7
1978
1978
1977
COLLECTION DATE

VII. IMPACT OF DIMILIN [R] SPRAY ON GYPSY MOTH PARASITOIDS[1]

[1]Submitted to publisher

ABSTRACT

Dimilin [R] (1(4-chlorophenyl)-3-(2,6 difluorobenzoyl)-urea, an insect growth regulator for control of the gypsy moth, was applied once at .06 lb AI in 0.5 gal (4.76 liters/ha) of water per acre, using a Grumman Ag Cat aircraft. Gypsy moth larval mortality was high, ca 50% after one week and 100% after ten days. Apanteles melanoscelus mortality was ca 80% after two weeks. Tachinids showed 100% mortality.

INTRODUCTION

Dimilin [R], an insect growth regulator, was applied in a camping area of southern Quebec (St. Antoine Abbe, Huntingdon County, lat 45 05 N, long. 74 11 W), as a field trial to test its impact upon the gypsy moth and its parasitoids during the spring of 1977

Work was carried out by the Department of Agriculture with the collaboration of the Laurentian Forest Research Centre (L.F.R.C.), who measured the effect of the Dimilin on the gypsy moth. The objective of this study was to assess the impact upon the parasitoids of the gypsy moth during this field test.

The parasites involved in this research were Apanteles melanoscelus (Hymenoptera: Braconidae) and the tachinid parasites (Exorista larvarum and Parasetigena silvestris).

[R] Thompson-Hayward Chemical Company T.M.

Dimilin interferes with the formation of insect cuticle inhibiting the deposition of chitin (Post and Vincent, 1973). Granett and Dunbar (1975) found Dimilin highly effective against the gypsy moth and field tests also showed A. melanoscelus to be susceptible to the chemical.

MATERIAL AND METHODS

The site selected, a 440 acre (178 ha) area, was sprayed with Diflubenzuron (Dimilin (1-(4-chlorophenyl)-3-(2,6 difluorobenzoyl)-urea),using a Grumman Ag Cat aircraft equipped with a standard boom and droplet breakup. Dimilin 25% WP was applied once at the rate of .06/lb/AI in 0.5 gal (4.76 liters/ha) of water per acre.

Three plots (1 ha each) were selected and subplots of 300 m^2 were chosen in each plot. A control plot (100 m^2) was established 1 mile away from the sprayed area (Figure 28). The most common tree species were Betula populifolia Marsh, Acer saccharum (Marsh.) and Fagus grandifolia (Ehrh.).

At the time of application (May 30, 1977) most gypsy moth larvae were in third instar. First generation Apanteles melanoscelus were in the larval stage inside the caterpillars. Adult tachinids (Exorista larvarum L., Parasetigena silvestris) were attacking the caterpillars.

Larvae were collected, 48 hours before and one week after

spraying, from foliage at heights up to 3 m, the tree trunks and the litter within 0.5 m of the trunks, taken to the laboratory and reared in food containers in groups of ten until parasite emergence was completed. Oak leaves were used as food. All containers were kept in an outdoor insectarium.

Burlap bands were placed around one tree in each subplot, and a single collection of A. melanoscelus cocoons was obtained from these, one week after spraying, kept in gauze-covered boxes at the insectarium and observed for emergence.

Mortality of A. melanoscelus inside cocoons was determined by observing lack of emergence and the criterion for tachinids was to dissect dead gypsy moth larvae showing eggs on their integument.

RESULTS AND DISCUSSION

Table 29 summarizes results obtained one week after spraying with Dimilin. Mortality of gypsy moth larvae was high (42.8%) and the remaining 57% died in the laboratory within five days of collection. The rate of parasitism by A. melanoscelus was low but almost half of the specimens collected were dead and from 13 individuals that spun cocoons only 5 emerged. This suggests that even parasitoid larvae completing successfully their larval stage, can be affected and will fail to

emerge. Collections of A. melanoscelus cocoons under burlaps (Table 30) show that a significant proportion of them failed to emerge. Granett and Weseloh (1975), in laboratory experiments, found that older A. melanoscelus larvae were less sensitive to Dimilin and suggested the possibility of timing sprays to minimize A. melanoscelus mortality. Granett et al. (1976) sprayed on three dates, May 23, May 29 and June 4 in Connecticut, U.S.A. They obtained a decreased per cent emergence of A. melanoscelus after the first spray, while the second and third sprays did not affect the emergence rate compared with the control.

Tachinid larvae collected after spraying were all dead inside dead caterpillars.

Regardless of the high effectivity of Dimilin, as a gypsy moth killer, more research is needed to evaluate its impact on non-target insects and on the environment as a whole.

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Table 29. Numbers of gypsy moth larvae, A. melanoscelus parasitizing gypsy moth larvae and tachinid eggs (Exorista larvarum and Parasetigena silvestris) on cuticle of gypsy moth larvae from collections before and after treatment with Dimilin ^{R} at St. Antoine Abbé, Quebec.

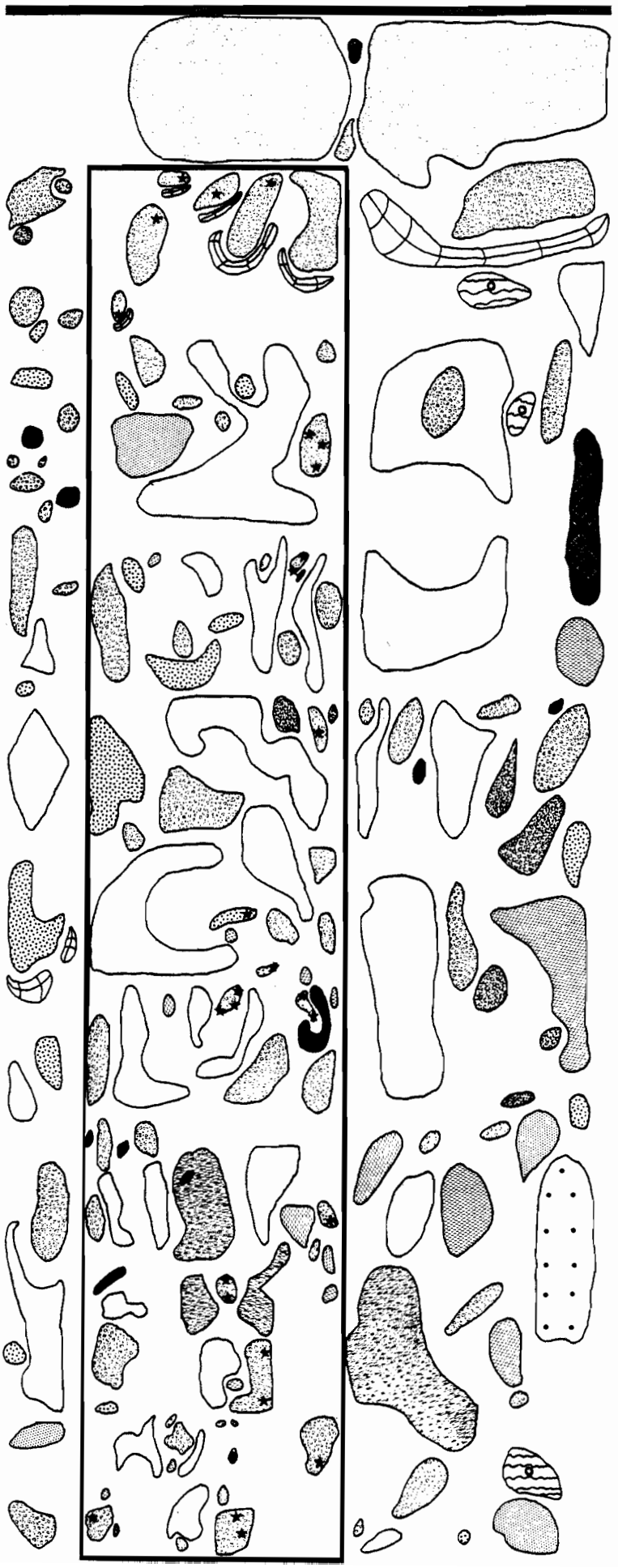
		Treated Area			Control Plot	
		Before Spray	After Spray 1 week	After Spray 2 week	Before Spray	After Spray
Gypsy moth larvae	alive	1749	813 (57.2)[1]	0	557	463
	dead	0	608 (42.8)	1421	0	0
A. melanoscelus	alive	83	13 (54.1)	5 (20.8)	25	10
	dead	0	11 (45.8)	19 (79.1)	0	0
Tachinids	alive	3	0	0	1	34
	dead	0	71	71	0	0

Numbers in brackets represent percentage values.

Table 30. Percentage mortality of A. melanoscelus collected under burlap traps, one week after spraying with Dimilin^{R} (St. Antoine Abbé, Quebec).

Burlap Trap No.	1	2	3	4	5	6	7	8	9	10	11	12	13	Total	Control
No. cocoons	1	6	12	20	6	8	10	2	12	1	1	1	7	87	63
Dead (no.)	0	2	7	15	4	4	5	1	11	1	0	1	6	57	0

Figure 28. Vegetation distribution. Control Plot. St. Antoine Abbé.



CONTROL PLOT
ST. ANTOINE ABBÉ
VEGETATION DISTRIBUTION

188

LEGEND

OVERSTORY

- WHITE PINE
- EASTERN HEMLOCK
- GRAY BIRCH
- SUGAR MAPLE
- AMERICAN BEECH

UNDERSTORY

- BRACKEN FERN
- OSTRICH FERN
- RASPBERRY
- RUSHES
- MEADOW

GROUND COVER

- GRASSES, MOSS & LILY OF THE VALLEY
- ROCK OUTCROP
- DEAD WOOD PILE

- FENCE
- BURLAP TRAP
- BOUNDARY OF STUDY AREA

N

SCALE 1cm = 1m

VIII. SUMMARY AND CONCLUSIONS

1. The gypsy moth is an economically important pest of hardwood trees, established recently in Canada (Quebec, Ontario and British Columbia).

2. Quebec populations of the gypsy moth are finding different climatic conditions, different food plant availability and fewer natural enemies, compared with Massachusetts populations.

3. In the region with a shorter growing season, hatching takes place as early as the date mentioned in the current literature for southern populations.

4. Larvae preferred birch to oak in food preference tests. This may suggest an adaptive change stimulated by the greater availability of birch over the primary host, oak.

5. Gypsy moth population dispersing towards the north, must have eggs that withstand increasingly severe temperatures in winter. Measurements of supercooling points of eggs can be used as an indicator of the insect's ability to expand northward. Low levels of winter mortality, even above snow cover, suggest the development of a more cold-hardy population.

6. Cold-resistance has been related to the presence of glycerol

and glycoproteins. The fully mature embryo of the gypsy moth contains both. Glycerol is found mainly in the embryo; the glycoproteins were obtained mainly from the external yolk surrounding the embryo.

7. Seven exotic species and three native species of parasitoids of the gypsy moth were recovered from both sampling sites. Only egg-parasites were not recovered. Introduction is recommended.

8. Three species of insect predators were found eating gypsy moth caterpillars. Fifteen species of birds were also identified as recognized gypsy moth predators.