



United States  
Department of  
Agriculture  
Forest Service  
Northeastern Forest  
Experiment Station  
General Technical  
Report NE-123



## PROCEEDINGS

# Lymantriidae: A Comparison of Features of New and Old World Tussock Moths



## FOREWORD

Tussock moths constitute the major forest pest throughout the world. While similarities in ecology, behavior, natural enemies, and means of control may be similar for different Lymantrid species, no previous effort had been made to synthesize this information.

These proceedings resulted from a five-day conference held in June 1988 at the Park Plaza Hotel in New Haven, CT. It offered scientists from Canada, the Soviet Union, the People's Republic of China, Great Britain, Switzerland, Japan, the Federal Republic of Germany, Denmark, Poland, the Netherlands, and the United States the unique opportunity to present research findings. Just as important, it provided a forum by which to discuss research issues and needs, clarify terminology and enhance international collaboration. The importance and timeliness of the conference was recognized by the USDA Forest Pest Sciences Competitive Grants Program, which provided funds for defraying travel expenses for invited foreign participants. The International Union of Forest Research Organizations (IUFRO) was the mechanism for identifying participants and, together with the Northeastern Forest Experiment Station which published these proceedings, co-sponsored the Conference.

The conference agenda allowed each participant 45 minutes for a presentation, followed by a 15-minute question and answer period. The comments that followed each presentation were recorded and are presented as a separate section at the end of the proceedings.

Most of the papers were submitted as camera ready copy. Some of the foreign authors requested that their papers be edited for clarity and retyped, and this has been done.

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## COVER

Elliptical projection of the world showing Lymantrid distribution, by Paul A. Gutwin, USDA Forest Service, retired.

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Northeastern Forest Experiment Station  
370 Reed Road, Broomall, PA 19008

March 1989

## **PROCEEDINGS**

### **Lymantriidae: A comparison of features of New and Old World tussock moths**

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June 26-July 1, 1988, New Haven, Connecticut

Technical Coordinators:

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Hamden, CT 06514

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Sponsored jointly by the  
Northeastern Forest Experiment Station and  
The International Union of Forest Research Organizations

### Welcoming Address

International cooperation on scientific issues  
of common interest

*The Honorable Bruce A. Morrison, Representative in Congress,  
Third Congressional District, Connecticut*

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E C O L O G I C A L   B A S I S   O F   T H E  
E V O L U T I O N   O F   H O S T  
R E L A T I O N S H I P S   I N   E U R A S I A N  
G Y P S Y   M O T H   P O P U L A T I O N S

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I N T R O D U C T I O N

Gypsy moth, *Lymantria dispar* L., is one of the most economically important pests of forests of boreal zones of the Holarctic. Despite numerous publications devoted to this species (Leonard, 1974; Vorontsov, 1977; Doane & McManus, 1981; Montgomery & Wallner, 1988) many aspects of its biology haven't been duly elucidated. Throughout its vast range, the gypsy moth inhabits many various biotopes whose ecological features have considerable influence on the biological properties of the species. One of the properties - intensity of gypsy moth migrations - has long been the focus of attention of forest entomologists.

In this work, I will summarize the literature data and our own observations on migrations in gypsy moth populations in northern Palearctic. There are many gypsy moth populations in this region where the females take flight (migrate) and populations where they do not fly. Thus, this is an excellent opportunity to make experimental comparisons of trophic adaptations of gypsy moth populations that differ in migration activity.

G Y P S Y   M O T H   M I G R A T I O N   A C T I V I T Y   A N D  
P R E D I C T A B I L I T Y   O F   H A B I T A T S

There is disagreement in the entomological literature on the flying abilities of gypsy moth females. Numerous records on forest entomology unambiguously state that the gypsy moth females are not capable of active flight. But there are quite opposite statements as well. For example, Yu. P. Kondakov (1963) disagrees with the statement of Ya. V. Chugunin (1949) about the flight passiveness of gypsy moth females. A.I. Vorontsov (1977) thinks that A.I. Ilyinsky (1954) also underestimated the flying abilities of this species. Those who believe that the females do not fly are located in Western, Central, or Southwestern Europe (Schedl, 1936; Chugunin, 1949; Ilyinsky, 1959; and others) while researchers in Siberia state that the females have active flight (Meinhardt, 1912; Kondakov, 1963; Zemkova, 1963, Terskov & Kolomiets, 1966; and others). The data, as a whole, show that as we move from eastern to western boundaries of the species range, the females gradually lose their flight ability (Fig. 1). In the centre of

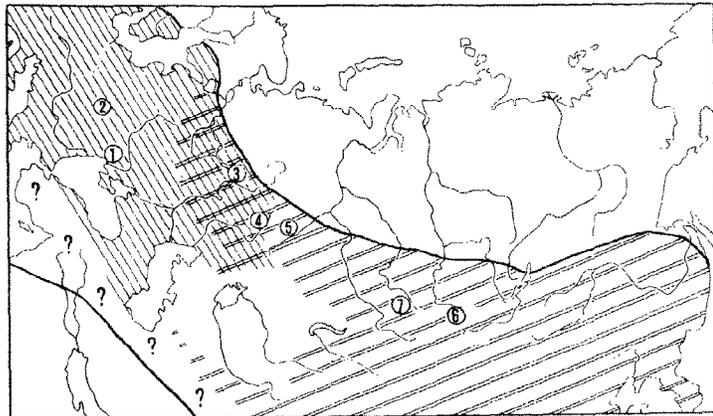


Figure 1. Zones of gypsy moth female flight ability in Eurasia. Double cross-hatching = zones of flying females; cross-hatching = zone of flightless females; overlapping = transition zone. Local gypsy moth populations: 1 - Ukraine-acacia; 2 - Karpats; 3 - Tataria; 4 - Baskhiria; 5 - Zauralje; 6 - Tuva; 7 - Altai. (See text.)

the species range, southeast Asia (Kozhanchikov, 1950), the gypsy moth females cover long distances on their wings. According to Yu. P. Kondakov (1963) their flights in Khakass region (southern part of Krasnoyarsk Territory) may be 4-7 km long. In our experiments in the Buryat Republik, marked females travel to light traps from a distance of 3.5 km. In the Krasnoyarsk and Amour regions (Terskov & Kolomiets, 1966), in the mountainous forests of the Western Sayan ridge (Zemkova, 1963), in Mongolian People's Republik (our unpublished observations), in Altai Mountains and in Northern Kasahstan (Guinenko, 1986), the females actively fly to ultraviolet light. There are reports of good flying performance of Chinese populations (Goldschmidt, 1934; Schaefer et al., 1984).

The transition zone of occasional female flights is situated in Eastern Europe (Fig. 1). The female moth here can fly well (Khanislamov et al., 1958; Benkevich, 1959; Andrianova, 1970), but active flights are relatively short and insects travel considerable distances only with moving air masses (Khanislamov et al., 1958; Mikkola, 1971).

In Western, Central, and South-Eastern Europe gypsy moth females don't fly (Schedl, 1938, Fig. 1). Nor do they fly in North America (Friend, 1945; Campbell, 1967; Beroza & Knipling, 1972). However, there are five cases of gypsy moth females gliding from trees in the USA that are described in detail (Forbush & Fernald, 1896; Sandquist et al., 1973). Inability of gypsy moth females from North American populations to fly is very demonstrative - the species was brought to

the USA in 1869 from France which was the western edge of its range (Goldschmidt, 1934).

The "east-west" reduction of the flying ability of the gypsy moth female is an example in favour of the rather poorly reasoned assumption of J.V. Kozhanchikov (1950) on eastern-Asian provenance of Lymantria dispar L. species. If we agree with the statement that in telomorphy function is first lost and then the organ (Schmalhausen, 1969), it is evident that inability of the European females to fly is a secondary phenomenon due to selection under new environmental conditions.

Peculiarities in migration activity of gypsy moth imagoes affect the role of the adult insects in the distribution strategy of individual populations. In Siberia the species spreads both by the flying females and by caterpillars of the first instar carried by the air streams (Kondakov, 1961, 1963). In the European part of the USSR, migrations are due mainly to the caterpillars (Ilyinsky, 1959), massive movements of the adult moths is a rare phenomenon there (Vorontsov, 1958; Mikkola, 1971). On the American continent, the species migrates only by the larvae carried in spring by the winds (Cameron et al., 1979).

There is a large body of literature on the ability of the species to distribute at the phase of the first instar caterpillar. Impressive figures are presented for the distance migrated - from 10 to 40 km (Collins, 1915; Chuganin, 1958; Kondakov, 1963) to 150 km (Ilyinsky, 1959). But verification of such migration abilities in the natural larval populations of the species was an enigma. Research carried out within a USA federal program in the 1970's showed that even in the knob topography with complicated air mass motion, as for example in the mountainous ridges in Pennsylvania, the caterpillars taken by the convection air stream from the trees on the tops of the hills are carried by the wind for only several kilometers (Mason & McManus, 1981). Recently, aerial sampling with airplane tow nets above ridge-valley terrain showed that caterpillars theoretically can be carried up to 16 km by air currents, but this would be only a very small percentage of the total population (Taylor & Reiling, 1986). In the valley forests, caterpillars actually don't intensively spread with the air streams. In oak and hickory stands where trees are 9-12 m high on the average, no more than 0.3% of the caterpillars of the first instar hatched on a tree were found more than 30 m from the trunk of this tree (Cameron et al., 1979; Mason & McManus, 1981). If the stand density decreases the possibility of distribution is higher, though it remains in rather modest limits. So, nearly 80% of the caterpillars taken by the wind do not fly farther than 75 m from the edge of the forest (Minott, 1922).

It is understood that migration abilities of European and Asian populations of gypsy moth differ considerably. These differences must affect substantially the rate and trends of the microevolution in the gypsy moth populations of these regions. In Siberia the migration process involves imago and larvae of the local populations. In the piedmont and mountainous landscape in the south of Siberia, these processes are of large scale. Each season there are two waves of migrations: in spring the caterpillars hatched in the rocky outcroppings of river valleys are carried away by the winds, and in summer when the females fly from the flood plain forests to the rocky

outcroppings to lay eggs. Although there is evidence of mass flights of females covering up to 100 km (Rozhkov & Vasilyeva, 1982) usually the movement of imagoes is limited by the topographic peculiarities of intermontane basins and seldom exceed 3-5 km. Because each gypsy moth micropopulation in Siberia annually changes its habitat two times, the possibility of the caterpillars of the filial generation feeding on the host species of the parents and the possibility of successive generations of gypsy moth developing in the same microhabitat is practically ruled out.

The females of most European populations of gypsy moth, on the contrary, usually lay eggs on or near the trunk of its food tree and the caterpillar, after hatching, goes up into the crown and starts feeding making attempts to leave the "native" tree only when the density of infestation is rather high (Semevsky, 1971). But in the valley forests, airborne dispersal by the caterpillars can result, at best, only in changing one tree for another, which in a one-species stand does not affect the course of trophic specilization of individuals. In contrast to many other species of Lepidoptera, gypsy moth chooses the food plant only at the larval stage. The ovipositing female isn't involved in it. Practically every regional record on the biology of gypsy moth has evidenced this, but to the best of my knowledge the evolutionary consequences of this on host relationships has never been considered in this respect.

Lack of rocky outcroppings in the habitats of Asian populations of gypsy moth has no effect on the pattern of laying eggs by the females. According to a number of authors (Kondakov, 1961; Alekseyeva, 1969; and others) and our own experience in the valley forests in Southcentral Siberia and in the Baikal region, the gypsy moth females, when in flight, concentrate at forest edges and on the periphery of single groups of trees giving preference to thicker trunks. Concentration of egg clusters has no relevance to the nutritional value of the plant for the gypsy moth caterpillars. Crucial in choosing the ovipositional site are the surface structure of the substrate and its temperature condition. Baranchikov & Kravtsov (1981) noted that the flight of gypsy moth females into the rocks in the habitats with mountainous topography is due to the temperature condition of the rocky outcroppings during the hours of migration activity of the moths. There is no reason to think that in the absence of rocky outcroppings there are other reasons for the females to choose large trunks but the peculiarities of their temperature condition. Our viewpoint is supported by the vertical distribution of egg clusters on pine trunks (Kondakov, 1963) in relation to the trunk temperature at various heights from the soil surface (Zyubina, 1965).

Migration of two life stages in Asian populations of gypsy moth is associated with the necessity to overcome insufficiency of total positive temperature required to complete egg embryogenesis during summer and autumn period (Baranchikov et al., 1987). This insufficiency is overcome by behavioural adaptation when eggs are placed in the optimal temperature conditions. Since climatic conditions in the European part of the species area are more favourable, migrations have little adaptive value and are not sustained by selection. This ecologically conditioned behaviour of imago is the primary reason for the differentiation of geographical populations of

gypsy moth which becomes crucial in forming the properties of their trophic adaptations.

The landscape and climatic properties of Central and Eastern Asia has fostered a double-stage migration biotype. The result is that the gypsy moth population mixes intensively over vast areas while the host plant relations of the populations are totally unpredictable. Migration of females into sites where the distribution of young caterpillars is most intense augments the unpredictability of the habitat of each sequential generation of gypsy moth. This reduces the possibility of the gypsy moth forming a specific relationship with one or even a few host plant species. Instead, these conditions seem to have brought about a superpolyphagous species inhabiting more than 600 species of plants.

Reduced migration abilities of the species in the forests of European valleys considerably increases the level of predictability of environment for the next generation of gypsy moth. With a less cold climate, the need to disperse from the host to better thermal substrates for oviposition is reduced; thus, regional host plant specialization is possible. Under such conditions, the phytophage can adapt more fully both to chemical and phenological properties of a limited range of food objects. The data available in literature support this assumption and one can see how European populations of gypsy moth, in the absence of migrations, trend to local trophic specialization, and time caterpillar hatching to the beginning of vegetation of the major food plant in the given habitat and how this results in chronological isolation of divergent groups (Kolybin & Zelinskaya, 1975; Kireyeva, 1983; Mamontova et al., 1983; Baranchikov, 1985).

#### HOST-PLANT ACCEPTABILITY AND SUITABILITY BY DIFFERENT POPULATIONS OF NEWLY ECLOSED FIRST INSTAR GYPSY MOTH LARVAE

There is numerous evidence of the peculiarities of gypsy moth larval development when feeding on a spectrum of food species. The host range of this species has been recorded for several regions in Europe (Kelus, 1939; Kurir, 1953; Edelman, 1956; Khanislamov et al., 1958; Zhigunova, 1967; Heskova, 1978), in Asia (Bey-Bienko, 1924; Kondakov, 1963, 1979), and in North America (Mosher, 1915). These and more recent reports (Vshivkova, 1983, 1984; Hough & Pimentel, 1978; Barbosa & Greenblatt, 1979; Rozkov & Vasilyeva 1982) support Vorontsov's (1963) statement that there is considerable variability of gypsy moth development (growth rate, mortality, weight of the pupae) in different regions feeding on the same host species. These differences are usually related to the diversity of feeding conditions and to biochemical and anatomical features of the peculiar species of plants in various parts of their areas (Vorontsov, 1963). These assumptions are supported repeatedly by experiments (Radkevich, 1980). We will first examine in detail regional distinctions in the ability of the individuals of some gypsy moth populations to feed on the foliage of one species of woody plant.

## Methods

### Gypsy Moth Populations

In our experiments we used caterpillars from geographically different gypsy moth populations. These populations are named below along with its location and the characteristics of its trophic relations citing the literary references. Populations are numbered as in Figure 1.

"Ukraine" (1) - insects were collected in three habitats along the Dnieper River in the Kherson region of the Ukrainian SSR: "Ukraine oak" - in the oak forests of the Black Sea Preserve; food species - oak, *Quercus robur* L.; "Ukraine-willow" in the *Salix alba* L. forests, and "Ukraine-acacia" in *Robinia pseudoacacia* L. plantations near Golaya Pristan settlement (Kireyeva, 1983; Mamontova et al., 1983).

"Karpats" (2) - near the city of Mukachevo of the Transkarpat region of the Ukrainian SSR. Food species - oak (Baganich, 1981).

"Tataria" (3) - the city of Zelenodolsk of Tatar, ASSR; the major food species - birch (Kondorsky, 1983, 1984).

"Bashkiria" (4) - the city of Blagoveschensk of Bashkirean ASSR; birch and oak (Idrisova, 1977).

"Zauralje" (5) - Chebarkul settlement of the Chelyabinsk region; birch (Rafes, 1980).

"Tuva" (6) - near Ishtii-Hem settlement of the Tuva ASSR. Food species: larch, birch, elm (Mashanov et al., 1981).

"Altai" (7) - near Chemal settlement of the Mountainous Altai Autonomous District of the Altai region. Food species: birch, elm, bird-cherry, willow (Benkevich, 1959).

Gypsy moths from the nine populations from the seven regions were collected as eggs and maintained in the laboratory for 1-2 generations on leaves of birch, *Betula pendula* Roth. Mating took place exclusively within the population groups. Eggs were collected in the years when all populations were latent.

### Acceptability and Suitability of Food Plants

To compare the initial preference of food species we used newly hatched first instar larvae from "Ukraine-acacia," "Transkarpat," "Bashkiria," and "Tuva" populations. The larvae, kept solitary in small petri dishes, were offered small (5 mm) circular pieces (leaf disks) cut from the leaves at the beginning of blossom of willow (*Salix viminalis* L.), birch (*Betula pendula* Roth.), bird-cherry (*Padus asiatica* Kont.), and several needles of larch (*Larix sibirica* Ledeb.). We carried out two test combinations of food: willow-birch-bird-cherry and willow-birch-larch. Each population was represented in every test by 50 larvae selected randomly from 15-20 egg clusters beginning to hatch. The dishes were observed daily and individuals starting to feed were removed. The remaining dishes were filled with fresh leaf disks. Experiments were observed in the red light.

Mortality of larvae from seven of the populations (Ukraine-acacia, Transkarpat, Tataria, Bashkiria, Zauralje, Tuva and Altai) was estimated by placing 250-350 newly hatched larvae of each population

into chambers with leaves or needles of the following food species: birch, bird-cherry, elm (Ulmus pumila L.), haw-thorn (Crataegus sanguinea Pall.), mountain ash tree (Sorbus sibirica Hedl.), larch, lime-tree (Tilia sibirica Fisch.) and acacia (Caragana arborescens Lam.). The leaves and needles were collected from the same trees near Krasnoyarsk. Each day the food was changed and dead insects removed. The number of molted second instar larvae was recorded.

### R e s u l t s

Irrespective of the main food plant of the local population - acacia, oak, birch or larch - the larvae of the Ukrainian, Transcarpathian, Bashkirian or Tuva population in the first variant of the experiment preferred, in decreasing order, willow-birch-bird cherry and in the second variant willow-birch-larch (Fig. 2). Distributions of larvae within each test showed difference in species selectivity: the value of Kolmogorov-Smirnov criterion  $\lambda$  in no case exceeded 0.85 ( $P > 0.2$ ). Only Ukrainian and Tuva populations differed in the number of larvae feeding and rejecting the food ( $\lambda = 1.5$ ;  $P < 0.05$ ), for the rest  $P > 0.05$ .

These results cast doubt upon the view of some authors that regional oligophagy owes its formation to conveyance of maternal effect on food acceptability of phytophagous insects (Konikov, 1978). They agree with other work (Fox & Morrow, 1981) disproving the so-called "Hopkins host selection principle" which connects the trophic selectivity of herbivore with the food plant of its parents.

The larvae of several European and Asian gypsy moth populations similar in trophic selectivity differ substantially in the ability to develop successfully on individual host species. Figure 3 compares the levels of mortality of the first instar larvae among seven gypsy moth populations grown en masse on the leaves and needles of nine plant species each of which is a potential host for this phytophagc. To make it more vivid, the results of each experiment are normalized relative to the mortality of the Ukrainian population.

Despite considerable variability in mortality within populations from each continent, the European populations of gypsy moth (Ukraine, Transcarpathia, Tataria) are clearly distinct from the Asian ones (Zauralje, Tuva, Altai). Elevated survival of the Asian populations is most obvious when the larvae are grown on the species of Sorbus, Larix, Pinus, Tilia, and Caragana which are, by Kozhanchikov (1950), not the most suitable host species for Lymantria dispar. In the preceding experiment the preference of the newly hatched larvae to representatives of Rosacea and Pinacea families was the least (Fig. 2). It is important to point out that the ancestors of the larvae participating in the experiment were fed birch leaves only for 1-2 generations. Thus, the revealed properties are related to the hereditary preadaptation level of European and Asian gypsy moth populations.

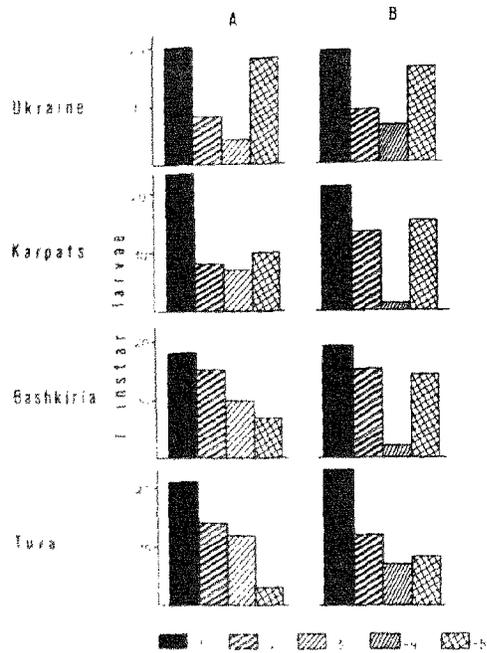


Figure 2. Distribution of newly eclosed larvae from four geographical gypsy moth populations on food plants. Tests: A - willow-birch-bird cherry; B - willow-larch-birch. Food selected: 1 - willow; 2 - birch; 3 - bird cherry; 4 - larch; 5 - the larvae weren't feeding.

#### FOOD UTILIZATION EFFICIENCY AND FEEDING BEHAVIOUR OF LARVAE FROM EUROPEAN AND ASIAN GYPSY MOTH POPULATIONS

The literature indicates that wherever *Larix* species coexist asymmetrically with gypsy moth they are usually a major food plant of the insect. This statement is valid not only for Western, Middle and Eastern Siberia, but for Eastern Asia - China (McFadden et al., 1981) and Japan (Furuta, 1982) as well. Feeding experiments show that larch needles are a superior food species for Transbaikal and Middle Siberian gypsy moth populations (Kondakov, 1963, 1979; Kondakov et al., 1967). Similar results were found in Tuva (Vshivkova, 1978) and South Baikal (Hoskey & Yantlova, 1982) populations. Larvae from the populations in

no-larch localities such as Voronezh region and Southern Urals, however, grew poorly and died when fed larch (Kelus, 1939; Amirkhanova, 1962). When grown in the laboratory on larch needles, the larvae of a number of West European and North American populations of gypsy moth were brought to imago (Mosher, 1915; Schedl, 1936; Jankovic, 1958), but these researchers never featured larch among the species most favourable for the gypsy moth.

The following experiment compares the growth, development, food utilization efficiency and feeding behaviour of the larvae from European and Asian gypsy moth populations on larch and on willow.

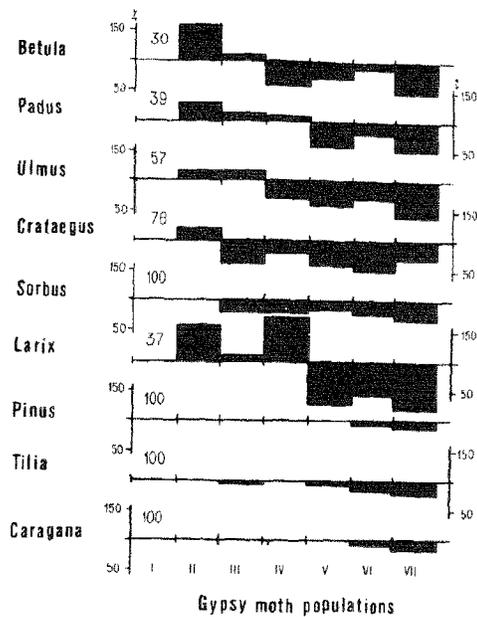


Figure 3. Relative indice of mortality of gypsy moth first instar larvae when growing on a number of food species. Gypsy moth populations: I - Ukraine; II - Karpats; III - Tataria; IV - Bashkiria; V - Zauralje; VI - Tuva; VII - Altai. Mortality of the "Ukraine" population is taken as 100%; the figures denote true indice of mortality, %.

## Methods

### Growth and Development

Larvae from the egg clusters of "Ukraine-oak," "Ukraine-willow," and "Ukraine-acacia" as well as Altai populations were used. We took 10 egg clusters from each locality. When about 70% of the eggs hatched, 10 larvae from each egg-cluster were placed into a glass chamber where they were grown to pupation, food was changed daily, mortality, number of instars, pupation time and weight of pupae were recorded. On the whole, 400 larvae were used in the experiment, 100 larvae (10 chambers) from each population. The larvae were fed needles of Siberian larch from five 20-year-old open-grown trees. Before feeding, the needles were thoroughly mixed.

Simultaneous to the start of the above experiment, 50 first instar larvae from the Altai and Ukraine-oak populations were placed into larger glass chambers in three replicates each. These larvae were fed with the leaves of willow (*Salix viminalis* L.). The food was changed every day, pupation time and weight of the pupae were recorded.

### Consumption and Utilization of Food

The feeding experiments were performed on fourth instar larvae from the Altai and Ukraine-oak populations that had been fed in the laboratory on larch needles from the first instar. Food consumption and utilization was estimated by a standard gravimetric technique (Waldbauer, 1968). Nutritional indices were calculated on the basis of the weight of leaves consumed (C), feces dropped (F) and larva body biomass gained (P):

$$\begin{aligned} \text{AD (approximate digestibility)} &= (C-F) \cdot C^{-1} \cdot 100, \% \\ \text{ECD (efficiency of conversion of digested food)} &= P \cdot (C-F)^{-1} \cdot 100, \% \\ \text{ECI (efficiency of conversion of ingested food)} &= P \cdot C^{-1} \cdot 100, \% \\ \text{RCR (relative consumption rate)} &= \text{mg consumed} \cdot (\text{mg mean larval biomass})^{-1} \cdot (\text{day})^{-1} \\ \text{RGR (relative growth rate)} &= \text{mg biomass gained} \cdot (\text{mean larval biomass})^{-1} \cdot (\text{day})^{-1} \end{aligned}$$

### Induced Feeding Preferences

Ability to induce feeding preference for first instar larvae of the Altai and Ukrainian populations was compared for larch. The preference tests were carried out immediately after hatching and after three and eight days of feeding on larch. Individual larvae were offered disks from leaves of *Salix viminalis* L. and larch needles. Feeding on each food or rejection were recorded for a day and the distribution of feeding on each food was analyzed between the populations by chi-square test. Each test had 100 larvae, 10 replications of 10 larvae each. Each larva was used only in one experiment.

## R e s u l t s

The experiment showed remarkable difference of the Altai population from the Ukrainian in the major parameters of growing and developing on larch trees. The results in Tables 1 and 2 are based on the data from 30 out of 40 chambers, because in four chambers with the "Ukraine-acacia" population and in six with "Ukraine-oak" population, most of the insects died from disease. As sex identification of the living larvae was not reliable, males and females in the data of Tables 1 and 2 are not differentiated.

Table 1. Development time and mortality of the gypsy moth I-V instar larvae from different geographical populations when feeding on Larix sibirica Ledeb.

Population	Development time, days	Mortality, %
Ukraine:		
Willow	38.4 ± 1.1 (34)+	66.0 ± 3.2 (10)++
Acacia	35.9 ± 1.0 (36)	40.0 ± 13.4 (6)
Oak	33.5 ± 0.6 (31)	22.5 ± 8.5 (4)
Altai	25.8 ± 0.4 (85)	14.0 ± 8.3 (10)

Note: in brackets + = number of larvae; ++ = number of chambers, 10 larvae in each.

Analysis of the material obtained shows that the Altai larvae are different from the Ukraine populations in the development time (Table 1, in all variants  $P < 0.05$ ). Mortality recorded in the Altai insects and the larvae from the "Ukraine-oak" and "Ukraine-acacia" populations were similar (Table 1,  $P > 0.05$ ); mortality differed most in "Altai" and "Ukraine-willow" populations (Table 1,  $P < 0.01$ ). The development time of all four populations coincided only in the first instar, the majority of other larval instars of the Ukrainian populations had a markedly prolonged time of development. The development of the Altai population was more synchronous.

The weight of the male and female pupae (Table 2) from the Altai was much greater ( $P < 0.05$ ) than any of the Ukraine populations which did not differ from each other ( $P > 0.05$ ). Since the moths of Asian gypsy moth populations are known to be larger than European ones (Vnukolsky, 1926), the superior growth of individuals from the Altai populations fed larch needles may be due to an inherited property of larger individual size rather than these larvae being better adapted to larch than larvae from the Ukraine. However, when larvae from Altai and "Ukraine-oak" populations were fed willow, the weights of the male and female pupae from the two populations were statistically insignificant (Table 3). Thus, the greater weight of Altai compared to Ukraine larvae fed larch is due to better adaptation to larch of the former.

There is evidence similar to these data in the literature. Amirkhanova (1962) and Idrisova (1983) both showed the mortality of the gypsy moth in the Bashkir ASSR (Europe) to be elevated when feeding on larch. When grown simultaneously on the leaves of *Betula pendula* Roth., the Bashkir gypsy moth differed little from the larvae of the Tuva population (Asia) in the rate of consumption and growth, time of development and the weight of the larvae and pupae (Vshivkova, 1982). Derevyanko et al. (1985), at my request, grew larvae of the Ukrainian and Siberian gypsy moth populations on oak leaves under the natural conditions in the Black Sea preserve in the Kherson region. The weight of the pupae from these populations did not differ (for males  $359.5 \pm 17.0$  mg, and  $969.8 \pm 26.5$  mg for females).

Table 2. Weight (mg) of the pupae of different gypsy moth populations grown on *Larix sibirica* Ledeb.

Population	Males	Females
Ukraine:		
Willow	$387.7 \pm 28.9$ (19)	$911.9 \pm 46.6$ (11)
Acacia	$378.8 \pm 24.8$ (21)	$918.8 \pm 29.9$ (15)
Oak	$362.8 \pm 45.8$ (11)	$936.5 \pm 89.4$ (13)
Altai	$521.6 \pm 35.1$ (32)	$1454.3 \pm 89.4$ (13)

Note: in brackets = number of larvae.

Thus, we find that all of the European and Asian gypsy moth populations feeding on different food species have similar success in developing on the species of *Betula*, *Quercus*, *Salix*, and *Padus*. These are hosts which I.V. Kozhanchikov (1950) regards as a sort of trophic standard for *Lymantria dispar* L. species. However, when gypsy moth larvae are exposed to food species that are somewhat outside the scope of the trophic standard, clear differences arise, usually with the more polytrophic Asian populations performing better.

The results of the experiment on comparing the efficiency of feeding of the larvae from the Altai population to that of the "Ukraine-oak" are given in Table 4. They enable us to argue that the earlier observed differences in the weight of the pupae from Ukrainian and Siberian gypsy moth populations are based on the significantly lower rate of growth of the Ukrainian larvae. The growth rate is, in its turn, limited by the lower consumption rate. The larvae of the Ukrainian and Altai gypsy moth populations had little difference in digestibility and efficiency of food conversion. This prompts us to

Table 3. Weight (mg) of pupae of different gypsy moth populations grown on Salix viminalis L.

Population	Males	Females
Ukraine	670.0 ± 21.5 (25)	1453.4 ± 83.9 (24)
Altai	687.6 ± 14.5 (51)	1666.1 ± 53.2 (27)
Difference:	P > 0.6	P = 0.05

Table 4. Indice of gypsy moth fourth instar larvae from different geographical populations feeding on Larix sibirica Ledeb.

Feeding indice	Populations		Significance of differences
	Altai	Ukraine	
AD, %	41.2 ± 4.4	33.6 ± 2.6	0.1 < P < 0.2
ECI, %	9.1 ± 0.7	8.2 ± 0.4	0.2 < P < 0.4
ECD, %	18.8 ± 1.7	26.8 ± 3.4	0.2 < P < 0.4
RCR	2.56 ± 0.25	1.40 ± 0.08	P < 0.01
mg/mg/day			
RGR	0.25 ± 0.05	0.11 ± 0.003	P < 0.01
mg/mg/day			

suspect the reason for differences in consumption rate is in differences in sensory system perception. Gypsy moths from the two geographical populations likely differ in their perception of food plants falling outside the scope of the trophic standard of the species.

As we are now unable to study directly the differences of the sensory input of the gypsy moth larvae, we attempted to do it indirectly - analyzing the features of their trophic behaviour. This was done by comparing the ability of first instar larvae from the Ukraine and Altai to develop induced feeding preference when growing on larch needles. This comparison (Table 5) showed no cardinal differences in the initial response of the caterpillars from the Altai and Ukraine to willow and larch. Though the ratio of the larvae from two populations feeding on willow and larch during the experiment differed ( $\chi^2 = 4.9$ ;  $P < 0.05$ ), willow enjoyed significant preference in both cases. However, after three days of feeding on larch needles, the larvae from the Altai showed some induction of larch preference ( $\chi^2 = 2.6$ ;  $P = 0.1$ ) and this was increased on the eighth day ( $\chi^2 = 10.1$ ;

$P < 0.01$ ). The larvae from the Ukraine, on the contrary, decreased larch preference significantly after 3 and 8 days ( $\chi^2 = 9.6$ ;  $P < 0.01$ ). Thus, the larvae of the Altai population showed clear induction preference for larch needles, while those from the Ukraine showed a learned aversion to larch.

The induction of preference for previously eaten food is known to come into action in the insects by lowering the sensitivity of the deterrent receptors by repeated feeding on a species of food plant (Schoonhoven, 1969). This results in increased intensity of feeding on previously consumed food. The sensory mechanism of the induction of aversion to previously eaten food isn't clear so far. This is to a great extent due to our poor knowledge of the modification mechanisms of the deterrent receptors.

The long-duration of larvae from the Ukrainian population on one host plant - oak - seems to have lowered the threshold of their

Table 5. Food selection by first instar larvae from the Ukrainian and Altai gypsy moth populations fed first on larch needles and then given a choice between larch (L) needles and willow (W) leaves

Percentage selecting	Days previous feeding on larch needles		
	0	3	8
Altai population			
L only	11.0 ± 3.1	24.0 ± 3.7	32.0 ± 3.3
L + W	22.0 ± 4.4	27.0 ± 4.2	36.0 ± 6.0
W only	53.0 ± 6.0	47.0 ± 3.7	30.0 ± 4.7
No feeding	12.7 ± 4.0	5.0 ± 2.2	2.0 ± 1.3
Ukrainian population			
L only	4.0 ± 1.6	0	0
L + W	12.0 ± 2.5	2.0 ± 1.9	5.0 ± 2.2
W only	65.0 ± 3.4	74.0 ± 4.0	90.0 ± 3.0
No feeding	19.0 ± 3.8	24.0 ± 7.6	5.0 ± 2.2

deterrent receptors, making them more sensitive to the biochemical features of new biologically active food - larch needles. The terpenoids of the conifers are known to lower the consumption rate of the larvae from a number of the European gypsy moth populations (Meisner & Skatulla, 1975). Inadequate sensory input information of the larvae from the Ukrainian gypsy moth population seems to lower the insect's consumption (and growth) rate and affect the direction of its feeding preference. Therefore, the local oligophages - the larvae from

the Ukrainian population - fed previously on larch needles lowered its consumption on subsequent days, while the considerably more polytrophic larvae of the Altai population showed increased preference for larch.

The material obtained proves that the intraspecific trophic differentiation of polyphagous Lepidoptera at the level of ecologically isolated populations does not affect an insect's ability to learn, but affects the ability of the larval sensory periphery to perceive or code information coming from the food plant. The ability to activate detoxication system gives any gypsy moth population the potential to be polyphagous. Long-duration feeding on one species of the food plant ensues in adapting the insect's physiological systems to more complete utilization of food (Kolybin & Zelinskaya, 1975), but simultaneously can reduce the possibility of successful development on other host-species. The latter can take place both owing to induced preference to the host-plant and to lowering the deterrent threshold of the sensory systems, affecting the intensity of feeding on new food.

#### CONCLUSION

This work has illustrated differences in the evolution strategy of European and Asian (Siberian) gypsy moth populations. Adaptations to climatic properties of the region caused the European populations to lose double-stage migration, resulting in intensive parapatric divergence of local phytophage populations. In Europe, selection results in the forming of local trophic specializations where larval hatching is timed to the beginning of bud-burst of the major host plant for the given locality and, hence, chronological isolation of the diverging groups.

Parapatric divergence is observed both in European and Asian populations of gypsy moth (Baranchikov, 1987), but with the latter it is hampered by high migration activity of the moths and larvae. The flight ability of the Asian gypsy moth females determines the majority of the specific properties of pest populations in the northeastern Palearctic. Unpredictable conditions of these localities are responsible for their high ecological elasticity: frost resistance of eggs, preadaptation to a wide range of food plants, morphologic, colour and physiological polymorphism. High variability of these characteristics is associated with elevated genetic polymorphism of the Asian populations compared to European and American ones (Harrison et al., 1983; Derevyanko et al., 1985).

Comparative study of geographical gypsy moth populations in northern Eurasia is just beginning. These investigations can be a fruitful foundation for revealing the role of ecological mechanisms in evolutionary transformations of herbivorous insect populations. The results of these studies can and will be applied to developing regional programmes of forest protection from gypsy moth.

## SUMMARY

Comparison of ecological properties of a number of geographical gypsy moth populations in Eurasia revealed differences in evolutionary strategy of European and Asian (mainly Siberian) populations of the species.

Adaptations to the milder climatic conditions of the region made European populations lose the double-stage migration habit, resulting in parapatric divergence of local polyphage populations, connected, in particular, to the local trophic specialization. Elevated polyphagy of Siberian populations was demonstrated by experiment. This is a consequence of adaptation to unpredictable conditions of habitats of this species in continental Asia. Local trophic specialization reduces successful development of gypsy moth larvae on a number of plant species, especially those falling out of the scope of the trophic standard of this phytophage species.

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## LITERATURE CITED

- ALEKSEJEVA, E.E. 1969. Gypsy moth, *Ocneria dispar* L. (Lepidoptera: Orgyidae) in Buryat ASSR. pp. 182-196 In: Glavneyshije vrediteli drevesnykh i kustranikovykh porod Zabaikalja. Ulan-Ude: BF SO AN SSSR. (In Russian)
- AMIRKHANOVA, S.N. 1962. Chemical aspect of plants and survival of gypsy moth. pp. 3-7 In: Voprosy massovykh razmnozhenii vrediteli lesa. Ufa: BF AN SSSR. (In Russian)
- ANDRIANOVA, N.S. 1970. Ecology of Insects. *Ekologiya nasekomykh*. Moskva:MGU. 153 p. (In Russian)
- BAGANICH, M.I. 1981. Insects-pests of oak foliage and its control in Transcarpathian region. pp. 6-9 In: Noveishie dostizheniya lesnoi entomologii. Vilnius:VEO. (In Russian)
- BARANCHIKOV, Yu.N. 1987. Trophic specialization of Lepidoptera. *Tropicheskaya specializatsia cheschuekrilich*. Krasnoyarsk: ILID SO AN SSSR. (In Russian). In press
- BARANCHIKOV, Yu.N., & KRARTSOV, B.A. 1981. An attempt of morphometric analysis of geographical gypsy moth populations in the totality of signs. pp. 96-112 In: Prostranstvennovmennaya struktura lesnykh biogeotsenozov. Novosibirsk: Nauka. (In Russian)
- BARANCHIKOV, Yu.N., RASPOPOV, P.M. & DEREVYANKO, N.M. 1987. Gypsy

- moth: development of trophic adaptations. Neparny shelkopryad: stanovleniye troficheskikh adaptatsii. Krasnoyarsk: ILID SO AN SSSR, 60 p. (In Russian)
- BARBOSA, P. & GREENBLATT, J. 1979. Suitability, digestibility and assimilation of various host plants of the gypsy moth, *Lymantria dispar* L. *Oecologia* 43: 111-119.
- BENKEVICH, V.I. 1959. Ultraviolet radiation in gypsy moth control. *Nauchnyye doklady vysshei shkoly. Biol. nauki* 3: 134-138. (In Russian)
- BEROZA, M. & KNIPLING, E. 1972. Gypsy moth control with the sex attractant pheromone. *Science* 177: 19-27.
- BEY-BIENKO, G.Y. 1924. Materials on gypsy moth biology in Altai. *Tr. Sibirskoi s.-kh. academi* 3: 134-141. (In Russian)
- CAMERON, E.A., MCMANUS, M.L. & MASON, C.J. 1979. Dispersal and its impact on the population dynamics of the gypsy moth in the United States of America. *Bull. Soc. Entom. Suisse* 52: 169-179.
- CHUGUNIN, Ya.V. 1949. Centre cycles of gypsy moth outbreaks. *Zool. zhurn.* 28: 967-975. (In Russian)
- DEREVYANKO, N.M., KOLYBIN, V.A. & SMIRNOVA, T.E. 1985. Ecological-biochemical properties of gypsy moth populations from different geographical zones of the USSR. pp. 173-174 In: *Sistema monitoringa v zashchite lesa. Krasnoyarsk: ILID SO AN SSR.* (In Russian)
- DOANE, C.C. & MCMANUS, M.L. (Eds.). 1981. *The Gypsy Moth: Research toward integrated pest management.* U.S. Dep. Agric. Tech. Bull. 1584. 757 p.
- EDELMAN, N.M. 1956. Biology of gypsy moth in the conditions of Kuba region of Azerbaijan SSR. *Zool. zhur.* 35: 572-583. (In Russian)
- FORBUSH, E.H. & FERNALD, C.H. 1896. *The gypsy moth.* Wright & Potter Co., Boston. 495 p.
- FOX, L.R., MORROW, P.L. 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.
- FRIEND, R.B. 1945. The gypsy moth in Connecticut. *Trans., Conn. Acad. Arts Sci.* 36: 607-629.
- FURUTA, K. 1982. Natural control of *Lymantria dispar* L. (Lep.: Lymantriidae) populations at low density levels in Hokkaido (Japan). *Z. ang. Ent.* 93: 425-429.
- GNINENKO, Yu.I. 1986. Elements of monitoring gypsy moth populations in Kazakhstan. *Lesovedeniye* 4:45-49. (In Russian)
- GOLDSCHMIDT, R. 1934. *Lymantria.* *Bib. Gen.* 11: 1-186.
- HARRISON, R.G., WINTERMEYER, S.F. & ODELL, T.M. 1983. Patterns of genetic variation within and among gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations. *Ann. Ent. Soc. Am.* 76: 652-656.
- HESKOVA, A. 1978. Influence of food change on the pathology of caterpillars of *Lymantria dispar* L. *Acta Insst. Forest Zvolensis* 5: 161-176.
- HOUGH, J.A. & PIMENTEL D. 1978. Influence of host foliage on development survival and fecundity of the gypsy moth. *Environ. Ent.* 7: 97-102.
- IDRISOVA, N.G. 1967. Biology, ecology and population dynamics of gypsy moth in Bashkiria. *Biologiya, ekologiya i dinamika chislennosti neparnogo shelkopryada v Bashkirii.* Avtoref. kand. diss. Moskva. 23 p. (In Russian)

- IDRISOVA, N.G. 1977. Materials on biology and ecology of gypsy moth in Bashkir ASSR. pp. 38-54 In: Nasekomye-vrediteli lesov Bashkirii. Ufa:BF AN SSSR. (In Russian)
- ILJINSKY, A.I. 1959. Gypsy moth and methods of its control. Neparny shelkopryad i mery borby s nim. Moskva: Goslesbumizdat. 63 p. (In Russian)
- JANKOVIC, L. 1958. Biljke hraniteljke gubara (*Lymantria dispar* L.) u prirodi u toku jedne gradacije. Bidiski Inst. N.R. Srbije. Zbornik radova 2: 1-15.
- KELUS, O.G. 1939. On the role of food plants in gypsy moth development. Zoolog. zhur. 18: 1010-1020. (In Russian)
- KHANISLANOV, M.G., GIRTANOVA, L.N. & YAFAYEVA, Z.Sh. 1958. Gypsy moth outbreaks in Bashkiria. pp. 4-45 In: Issledovaniye ochagov vreditel'ei lesa v Bashkirii. Ufa: BF AN SSSR. (In Russian)
- KIRFJEVA, I.M. 1983. Ecology and physiology of gypsy moth. Ekologiya i fiziologiya neparnogo shelkopryada. Kiev. Naukova Dumka. 128 p. (In Russian)
- KOLYBIN, V.A. & ZELINSKAYA, L.M. 1975. The role of behaviour in gypsy moth dynamics in the region of the lower Dniepr. pp. 75-82 In: Povedeniye nasckomykh kak osnova razrabotki mer borby s vreditel'nyami selskogo khozyaistva. Kiev. Naukova Dumka. (In Russian)
- KONDAKOV, Yu.P. 1961. Distribution of gypsy moth egg clusters in the forests of Krasnoyarsk territory. Uchen. zap. Krasnoyarsk gos. ped. in-t. 20: 34-42. (In Russian)
- KONDAKOV, Yu.P. 1963. Gypsy moth (*Ocneria dispar* L.) in the forests of Krasnoyarsk territory. pp. 30-77 In: Zashchita lesov Sibiri ot nasckomykh - vreditel'ei. Moskva: Izd-vo AN ASSR. (In Russian)
- KONDAKOV, Yu.P., ZEMKOVA, R.I. & NAKROKHINA, O.I. 1967. Experimental study of the effect of food base and population density on development and fecundity of gypsy moth. pp. 247-250 In: Itogi izucheniya lesov Dalnego Vostoka. Vladivostok: Kn.izd-vo. (In Russian)
- KONDORSKY, B.M. 1983. Index of degree of species preference by gypsy moth females in the process of egg laying. Nauchn. tr. MII. Moskva. 148: 213-218. (In Russian)
- KONIKOV, A.S. 1977. Regulators of forest insect populations. pp. 215-226 In: Problemy lesovedeniya Sibiri. Moskva: Nauka. (In Russian)
- KOZHANCHIKOV, I.V. 1950. Fauna of USSR. T.12. Volyanky (Oxyidae). Moskva-Leningrad: Izd-vo AN SSSR. (In Russian)
- KORTI, S. 1953. Die Frassenpflanzen des Schwamspinners (*Lymantria dispar* L.). Z. ang. Ent. 34: 543-586.
- MAMONTOVA, V.A., DEREVYANKO, N.M. & NIKITENKO, G.N. 1983. Structural functional properties of gypsy moth populations on different food plants. pp. 112-141 In: Rol vzaimootnoshenii rasteniye-nasekomoje v dinamie chislennosti lesnykh vreditel'ei. Krasnoyarsk: IZD SO AN SSSR. (In Russian)
- MAZHANGV, A.I., GUKASYAN, A.B., CHULIKOV, A.I. 1981. Microorganisms in forest protection. Microorganismy v zashite lesa. Novosibirsk: Nauka. 191 p. (In Russian)
- MASON, C.J. & MCMANUS, M.L. 1981. Larval dispersal of gypsy moth larvae. pp. 161-203 In: C.C. Doane & M.L. McManus (eds.). The

- Gypsy Moth: Research toward integrated pest management. U.S. Dep. Agric. Tech. Bull. 1584.
- MASON, C.J. & MCMANUS, M.L. 1979. The role of dispersal in the natural spread of the gypsy moth. pp. 94-115 In: Dispersal of forest insects: Evaluation, theory, and management implications. Washington State University Press.
- MCFADDEN, M.W., DAHLSTEN, D.L., BERISFORD, C.W. and others. 1981. Integrated pest management in China's forests. J. For. 79: 723-726.
- MEINHARDT, A.A. 1912. Review of entomological collections made in Western Sayan and on the Enisey from August 6 to September 8, 1903. Tomsk: Izd-vo Tomsk un-ta. 16 p. (In Russian)
- MEISNER, J. & SKATULIA, H. 1975. Laboratory experiments with antifeedants against larvae of the gypsy moth, *Porthetria dispar* L. Z. ang. Ent. 78: 317-320.
- MINOTT, C.W. 1922. The gypsy moth on cranberry bogs. U.S. Dep. Agric. Bull. 1093. 19 p.
- MIKKOLA, K. 1971. The migratory habit of *Lymantria dispar* (Lep.: Lymantriidae) adults of continental Eurasia in the light of a flight to Finland. Acta Ent. Fenn. 28: 107-120.
- MONTGOMERY, M.E. 1986. Gypsy moth host-plant relationships and population dynamics. pp. 67-82 In: Proc. 18th IUFRO World Congress. Div. 2, Vol. II. Ljublyana, Yugoslavia.
- MONTGOMERY, M.E. & WALLNER, W.E. 1988. The gypsy moth: A westward migrant. pp. 353-375 In: A.A. Berryman (Ed.). Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Press, New York.
- MOSHER, F.H. 1915. Food plants of the gypsy moth in America. U.S. Dep. Agric. Bull. 250. 39 p.
- RADKEVICH, V.A. 1980. Ecology of foliiferous insects. Ekologiya listogrzhushchikh hasekomykh. Minsk: Nauka i tekhnika. 239 p. (In Russian)
- RAFES, P.M. 1980. Biocenotic investigation of herbivorous forest insects. Biotsenoticheskiye issledovaniya rastitelnoyadnykh nasekomykh. Moskva: Nauka. 167 p. (In Russian)
- ROZKOV, A.S. & VASILJEVA, T.G. 1982. Gypsy moth in Middle and Eastern Siberia. pp. 4-19 In: Neparny shelkoprayd v Srednei i Vostochnoi Sibiri. Novosibirsk: Nauka. (In Russian)
- SANDQUIST, R.E., RICHERSON, J.V., & CAMERON, E.A. 1973. Flight of North American female gypsy moth. Environ. Ent. 2: 957-958.
- SCHAEFER, P.W., WESELOH, R.M., XILIN, SUN, WALLNER, W.E., & JINGJUN, YAN. 1984. Gypsy moth, *Lymantria (Ocnaria) dispar* (L.) (Lepidoptera: Lymantriidae) in the People's Republic of China. Environ. Ent. 13: 1535-1541.
- SCHEDL, K.E. 1936. Der Schwamspinner (*Porthetria dispar* L.) in Eurasia, Africa and Neuengland. Berlin: Parey. 242 p.
- SCHMALHAUSEN, I.I. 1968. Evolution factors. Faktory evolutsii. Moskva: Nauka. 451 p. (In Russian)
- SCHOONHOVEN, L.M. 1969. Sensitivity changes in some insect chemoreceptors and their effects on food selection behaviour. Proc. Kon. Ned. Acad. Wtsch. 72: 491-498.
- SEMEVSKY, F.N. 1971. Forest protection prognostication. Prognoz v zashchite lesa. Moskva: Lesn. promyshl. 71 p. (In Russian)
- TAYLOR, R.A.J. & RELING, D. 1986. Density/height profile and

- long-range dispersal of first instar gypsy moth (Lepidoptera: Lymantriidae). Environ. Ent. 15: 431-435.
- TERSNOV, I.A. & KOLOMIETS, N.G. 1966. Use of light traps in forest protection. Svetolovushki i ikh ispolzovaniye v zashchite lesa. Novosibirsk: Nauka. 124 p. (In Russian)
- VNIKOLSKY, V.V. 1926. New forms of gypsy moth in Siberia and Semirechje. Russk. entomol. obozr. 20: 42-49. (In Russian)
- VORONTSOV, A.I. 1958. Biology and control of gypsy moth. Vestnik s-kh. nauk 4: 31-39. (In Russian)
- VORONTSOV, A.I. 1963. Biological foundations of forest protection. Biologicheskie osnovy zashchity lesa. Moskva: Vyshaya shkola. 324 p. (In Russian)
- VORONTSOV, A.I. 1977. Some results in studying gypsy moth. pp. 5-21 In: Nasekomye - vrediteli lesov Bashkirii. Ufa: BF AN SSSR. (In Russian)
- VSHIVKOVA, T.A. 1978. Intensity of gypsy moth development on different food species. pp. 88-98 In: Ekologiya pitaniya lesnykh zhivotnykh. Novosibirsk: Nauka. (In Russian)
- VSHIVKOVA, T.A. 1983. Ecological and physiological parameters of the gypsy moth development on the main food plants in Siberia. pp. 127-138 In: The role of plant-insect relationships in population dynamics of forest pests. Krasnoyarsk: IFW Publ. (In Russian)
- VSHIVKOVA, T.A. 1984. Trophic conformity of gypsy moth larvae growth. Troficheskaja obuslovlennost rosta gusenits neparnogo shelkopryada. Avtoref. Kand. diss. Krasnoyarsk. 24 p. (In Russian)
- WALDBAUER, G.P. 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5: 254-288.
- ZEMKOVA, R.I. 1963. On possible use of light traps in finding pests in alpine forests of Western Sayan. pp. 78-85 In: Zhashchita lesov Sibiri ot nasekomykh - vreditel'ei. Moskva: Izd-vo AN SSSR. (In Russian)
- ZHIGUNOVA, A.S. 1967. On the problem of food preference and effect of some biochemical food components on growth and development of gypsy moth larvae. Uchen. zan. Kuybyshev. ped. inst. 50: 59-67. (In Russian)
- ZYURINA, V.I. 1965. Temperature of pine and birch trunks. pp. 100-106 In: Fisiologicheskiye kharakteristiki drevesnykh porod Srednei Sibiri. Krasnoyarsk: ILID SO AN SSSR. (In Russian)

RELATIONSHIPS BETWEEN FOLIAR  
CHEMISTRY AND SUSCEPTIBILITY  
TO LYMANTRIA DISPAR

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INTRODUCTION

An outstanding characteristic of the gypsy moth is its very broad host range and ability to adapt to novel hosts. The gypsy moth is by far the most polyphagous of the 40+ species of Lymantriidae in North America. It can utilize more than 60 host species, which exceeds by a factor of five the maximum diet breadth of 28 other major forest defoliators in North America (Northnagle & Schultz, 1987). In Europe, the gypsy moth attacks about half of the 185 native tree species (Kurir, 1953). Jankovic (1958) reported that 45 species of forest trees, 11 species of fruit trees, and 24 species of shrubs were completely defoliated during an outbreak in Yugoslavia. Although the gypsy moth has adapted to several novel tree genera in North America, e.g., Hamamelis, Liquidambar, Sassafras, and Carya (Lechowicz & Mauffette, 1986), it may be less polyphagous on that continent than in Europe. There are genera common to both continents (e.g., Juglans, Cornus, Celtis, and Ulmus) that do not seem to be to the gypsy moth's liking in North America, but are readily fed on in Europe. In North America, the native Robinia pseudoacacia is a poor host (Mosher, 1915), but in Europe it is fed on heavily by gypsy moth (Jankovic, 1958) and colonies may persist in robinia thickets for several successive years (Sidor & Jodal, 1983).

The more restricted host range and host adaptability of North American compared to European gypsy moth would be expected since the gypsy moth in North America apparently was derived from a single, small introduction from Western Europe 120 years ago (Forbush & Fernald, 1896). While some genetic variation in diet breadth has been reported for North American gypsy moth (Rossiter, 1987), this is not as striking as in Europe. For example, oak, willow, and robinia forests in the Ukraine each have distinctively colored gypsy moth biotypes (Kireeva, 1986). The greatest diversity in gypsy moth life history and color patterns, however, is in Eastern Asia (Goldschmidt, 1934). Baranchikov (this proceedings) presents strong evidence that the gypsy moth in Asia, where females fly, is more polyphagous than in Europe.

Although the gypsy moth has a broad host range and the ability to adapt to novel hosts, it generally avoids plants with a well-developed qualitative chemical defense such as alkaloids (Barbosa & Krischik, 1987). Plant families on which the gypsy moth prospers, such as Fagaceae and Betulaceae, seem to depend largely on quantitative defenses such as tannins. Quantitative defenses are not very toxic in small dosages and act by reducing digestion efficiency (Feeny, 1976).

These defenses may not present much of an evolutionary barrier to colonization, but they nevertheless may have considerable impact on an insect's population dynamics.

Tannins are widely distributed in vascular plants and can be divided into two major groups: the condensed tannins (proanthocyanidins), which are flavanol derivatives, and the hydrolyzable tannins, which are esters of glucose, usually with one or more gallic or hexahydroxydiphenic acids. The former are ubiquitous in woody plants while the hydrolyzable tannins are absent in some gypsy moth hosts such as *Populus deltoides* (Meyer & Montgomery, 1987) and *Acer macrophyllum* (Swain, 1979).

The significance of tannins in defense of plants against insect herbivores has been questioned from both an ecological (Bernays, 1981; Martin & Martin, 1983) and evolutionary (Beart et al. 1985; Scalbert and Haslam, 1987) perspective. Many Lepidoptera, including the gypsy moth, apparently are able to utilize leaves with high tannin content because they have surfactants and high pH in the midgut that inhibit tannin activity (Martin et al., 1985). However, to achieve a strongly alkaline midgut, considerable energy must be expended since leaves have pH values of 4.1-6.2 and are well buffered (Schultz & Lechowicz, 1986). Thus, the ecological activity of tannic acid could reside in its function as an organic acid rather than a protein precipitator. There also is evidence that the toxicity of tannins may not necessarily be due to the formation of insoluble protein complexes (Mole & Waterman, 1987; Blytt et al., 1988).

Regardless of the mode of action of tannins, it seems that any effect they have on the gypsy moth would be subtle and not the strong deterrent response that more species-specific defenses such as diterpenes (El Nager & Doskotch, 1980) have on the gypsy moth. Thus, in the following comparisons of foliar tannin content and insect performance, it is possible that a cause/effect relationship may be swamped by any of several other factors that determine the nutritional quality of foliage for gypsy moth. With this in mind, free sugar concentrations in the foliage will be examined with the larval performance variables.

Since there has been extensive research on the suitability of tree species as gypsy moth hosts, relationships will be examined between variation in foliar chemistry and larval performance for several species of trees. Variation in host chemistry and larval performance will be examined within a single species and within an individual tree. While larger differences in parameters are likely to be seen across species, the role of generally distributed secondary chemicals such as tannins may be detected more readily through intraspecific comparisons since qualitative variation in chemistry would be less and unidentified factors would be fewer.

Larval growth and feeding preference will be used to bioassay the quality of the foliage. Martinat & Barbosa (1987) found that the order of acceptability in choice tests was the same as the order of host suitability for gypsy moth growth. This implies that if tannins are deleterious, the gypsy moth should be able to directly taste or otherwise detect dietary tannin. Whether or not the gypsy moth can taste tannin is uncertain, however. Meisner & Skatulla (1975) reported that adding tannic acid at 0.2% dry weight to polystyrene lamellae containing ethanol extracts of *Quercus robur* did not reduce gypsy moth

feeding. The extract of *Q. robur* was highly phagostimulatory (it likely contained sugars and tannic acid). I have found that adding tannic acid or wattle condensed tannin at 0.1-5% to artificial diet has no effect on feeding rate, but adding 0.5% tannic acid to lettuce leaves increases feeding (unpublished). Feeding on several nonhosts, including potato, was increased if they were sprayed with tannic acid solutions (Gornitz, 1954). Dethier (1982) found that the gypsy moth does not have a receptor that fires in response to tannic acid, but that tannic acid does inhibit firing of sugar receptors. Thus, at the onset, it cannot be predicted whether tannin/growth relationships will complement tannin/preference relationships.

#### EXPERIMENTAL

##### Variation Between Species

**Methods.** Gypsy moth larvae were reared individually on excised foliage from fourth instar until pupation. Initial larval fresh weight ( $\times 0.16$  to convert to dry weight), development time, and dry pupal weight were recorded. The frass was collected and the nitrogen content of it and the larvae were determined by the Kjeldahl method and used to calculate nitrogen utilization efficiency (NUE) (Montgomery, 1982). Relative growth rates (RGR) were calculated as:  $\ln(W_f/W_i)/t$ , where  $W_f$  = weight final,  $W_i$  = weight initial, and  $t$  = days elapsed.

There were two series of tests, both of which were maintained at  $21 \pm 1^\circ\text{C}$  and 90-100% relative humidity. In Series I, larvae and leaves were placed in petri dishes. In Series II, larvae and leaves were placed in 0.4-liter paperboard containers with the leaf petiole inserted in a vial of water. Foliage was collected and renewed three times per week.

For chemical analyses, a subsample from each foliage collection was immediately frozen and weekly samples were pooled, freeze-dried, and ground to pass through a 0.2-mm mesh. Weighed samples ( $60 \pm 2$  mg) were extracted by stirring with 10 ml of 50% methanol for 2 hr at room temperature. After centrifugation (2,400 RCF), aliquots of the supernatant were taken for these tests: Total phenolics, Folin-Denis reagent with tannic acid as a reference (Rosenblatt & Peluso, 1941); condensed tannins, heated for 2 hr at  $95^\circ$  in butanol-5% hydrochloric acid with purified red oak tannin as standard; free sugars, gas chromatography after converting the sugars to oximes and then trimethylsilylethers (Method 18, Handbook and Catalog 1986-1987, Pierce Chemical Co., Rockford, Ill.). Nitrogen was determined on 0.5-gm of leaf powder by the Kjeldahl method using Kjeltac equipment.

**Results.** Table 1 shows that growth of late-stage gypsy moth larvae was best on foliage from Salicaceae species. Growth was not necessarily similar within a family or even a genus. This is seen most clearly with the *Betula*; good growth occurred on *B. populifolia* and poor growth on *B. lenta*. In the Series II tests, growth was better than expected on *Fagus grandifolia* and *Carya ovata*, which generally are not thought of as primary gypsy moth hosts. The data from both series

are for the last half of larval life and do not show that establishment and growth of young larvae on many of these hosts was poor compared to growth on oak.

Association of RGR with the other factors listed in Table 1 was tested using Spearman's coefficient of rank correlation ( $r_s$ ), which tests for monotonic functional relationships. This is more appropriate than Pearson's product-moment coefficient, which measures degree of linearity between two variables. Also, a nonparametric procedure should be used since species cannot be considered samples from a bivariate normal distribution. Within Series I, RGR was closely associated with NUE ( $r_s = 0.91$ ). This implies that something that affects nitrogen utilization, such as protein being bound by tannin, may have occurred. However, the relationship of condensed tannin with RGR was 0.56 ( $p < 0.05$ ) and with NUE was 0.30 ( $p < 0.05$ ). Only total phenolics were negatively associated with RGR (-0.46), though this too was not significant. Free sugar and nitrogen were poorly associated with RGR, 0.13 and 0.14, respectively. Series II species are too few to draw statistical correlations. However, these data seem to exhibit the same relationships observed with Series I species. Thus, although gypsy moth growth seems closely related to nitrogen utilization, growth could not be linked to any of the four chemical variables that could perhaps affect nitrogen utilization.

#### Variation within a Tree (Crown Position)

Methods. *Q. velutina* foliage was collected from outer branches located in the upper, middle, and lower thirds of the crown on two dates: 2 weeks and 6 weeks after bud opening. There were seven dominant trees ranging in height from 4-8 m in the test.

Part of each leaf sample (one from each tree/position on each date) was used for chemical and physical measurements. After freeze drying, the leaf lamina were weighed and area measured with a Li-Cor area meter. In addition to the chemicals reported for the species, hydrolyzable tannins were measured with Chinese gallotannin as a standard (Halsam, 1966).

Preferences for leaves were determined by giving larvae a choice between leaves from two areas within a tree crown. With 2-week-old leaves, whole leaves were used and with 6-week-old leaves, 2-cm-dia discs were cut and used. Both were placed in petri dishes on moistened filter paper and either five instar II larvae (2-week leaves) or a single instar IV larva (6-week leaves) were added and allowed to feed overnight. Leaf area consumed was measured and multiplied by the leaf specific weight to obtain dry weight consumed. Each choice-pair within a tree was replicated 8 times with differences in feeding on a choice-pair within a tree pooled. For statistical analysis, a randomized block design with trees as the blocking factor was used with each of the three choice-pairs for each leaf age tested against zero.

Results. Two weeks after bud opening, foliage in the lower part of the crown was preferred over foliage from higher levels in the crown (Table 3). This situation was reversed at 6 weeks after bud opening

Table 1. Relative growth rate (RGR) and nitrogen utilization (NUE) of female larvae reared from instar IV to pupation and the chemical contents of foliage used for rearing.

Host species	RGR (mg/mg/day)	NUE (%)	Total phenolics (%)	Condensed tannin (%)	Free sugar (%)	Total nitrogen (%)
Series I						
<i>Quercus rubra</i>	0.100d	27.0d	11.4bc	9.9c	3.1c	2.11de
<i>Q. alba</i>	0.104d	40.6bc	14.7ab	3.1e	3.8c	2.06e
<i>Q. prinus</i>	0.105d	35.5c	14.5ab	11.7b	3.5c	2.09e
Series II						
<i>Salix lucida</i>	0.131ab	43.7b	12.8bc	15.2a	5.1b	3.06a
<i>Populus deltoides</i>	0.127bc	47.0ab	11.5bc	3.5e	3.7c	2.68b
<i>P. grandidentata</i>	0.142a	49.5ab	11.6bc	15.0a	3.8c	2.41c
<i>P. tremuloides</i>	0.142a	55.6a	11.6bc	13.8ab	5.2b	2.19b
Series III						
<i>Betula lenta</i>	0.075e	17.7e	16.1a	3.0e	3.5c	2.34c
<i>B. populifolia</i>	0.119c	38.8bc	10.4c	11.0bc	3.0c	2.19d
<i>Carpinus caroliniana</i>	0.103d	24.8de	17.0a	15.2a	6.6ab	2.32c
<i>Alnus serrulata</i>	0.088e	30.4cd	16.5a	7.1d	8.0a	2.73b
Series IV						
<i>Quercus velutina</i>	0.096b	24.2e	14.2a	4.0c	5.2b	NM
<i>Fagus grandifolia</i>	0.111a	39.9a	14.4a	6.5b	5.7b	NM
<i>Carya ovata</i>	0.103ab	33.0b	8.6c	3.7c	7.0a	NM
<i>C. cordiformis</i>	0.091b	28.8c	11.0b	1.2d	5.2b	NM
<i>Robinia pseudoacacia</i>	0.074c	23.2e	10.6b	9.8a	0.9c	NM
<i>Tsuga canadensis</i>	0.068c	26.2ce	8.6c	0.9d	NM	NM

NM = not measured.

Values in columns within a series not followed by the same letter are significantly different ( $p < 0.05$ ), Bonferroni t-test was used for larval parameters because of unequal sizes ( $n = 3$  to 10), and Tukey's hsd for chemicals ( $n = 4$ ).

when upper crown foliage was preferred over lower crown foliage.

Table 2. Consumption by larvae given a choice between foliage from two crown strata of black oak.

Foliage age (weeks)	Crown strata choice-pair	Respective consumption mg dry wt/larva		Significance level <sup>1</sup>
Two	Top vs mid	0.70	1.16	0.006
Two	Mid vs low	0.96	1.45	0.008
Two	Top vs low	0.99	1.27	0.052
Six	Top vs mid	37.35	16.17	0.001
Six	Mid vs low	32.96	25.48	0.010
Six	Top vs low	37.50	20.01	0.001

<sup>1</sup> Analysis of variance on the difference in consumption for each pair tested against zero, df = 1, 12; see text for model.

Chemical composition of foliage from each third of the tree crown is given in Table 3. Total phenolics, hydrolyzable tannin, and condensed tannin were higher in lower canopy foliage at 2 weeks. At 6 weeks, however, total phenolics and condensed tannin were higher in the upper crown foliage. Free sugar also followed this pattern. Hydrolyzable tannin remained higher in the lower crown foliage. In this case, the gypsy moth chose to feed on leaves with the highest condensed tannin and free sugar contents.

#### E f f e c t s   o f   S t r e s s

##### ( D e f o l i a t i o n )

Methods. Black oak foliage was collected during the last 2 weeks of June when natural gypsy moth populations were in the fourth and fifth larval instars. A heavily defoliated stand was paired with an undefoliated stand of similar species composition and structure. In one case the stands were fairly close, within 2 km of each other. In the other case, the stands were 100 km distant. All sample leaves selected from the defoliated stand, where overall more than 75% of the foliage had been consumed, had some damage, but usually less than one-third of the leaf lamina had been eaten. Sample leaves from undefoliated stands had no damage and were from trees similar to the defoliated sample trees in size and in amount of solar radiation received. There were 10 trees selected from each stand. Leaves from each tree were analyzed chemically as detailed in the preceding sections.

Choice tests were conducted with fourth- or fifth-instar larvae that had been reared on *Q. rubra* foliage prior to use in the assays. Two 2.3-cm-dia discs from a defoliated tree were paired with two discs

Table 3. Chemistry (% dry wt.) of black oak foliage from each third of the tree crown at 2 and 6 weeks after budbreak.<sup>1</sup>

Crown strata	Total phenolics	Hydrolyzable tannin	Condensed tannin	Free sugars
Two-week foliage				
Upper	28.7a	15.5a	0.08a	0.68a
Middle	27.2a	15.7ab	0.19a	1.14a
Lower	34.2b	18.5b	1.03b	1.26a
Six-week foliage				
Upper	27.7b	5.9a	38.4b	8.20b
Middle	25.4ab	5.9a	31.4b	7.70b
Lower	23.4a	8.7b	12.4a	6.44a

<sup>1</sup> Different letters after chemicals in an age group indicate that they are different statistically at  $p < 0.05$ , Tukey's hsd test.

from an undefoliated tree in a petri dish. Each defoliated tree was tested once against each undefoliated tree (100 tests for each pair of stands). One larva was added to each dish in early evening when the larvae naturally begin to feed. Leaf area consumed was measured when about 50% of the discs were consumed.

**Results.** The three measures of phenolics usually were higher in the defoliated stand foliage, although only total phenolics were significantly different in both pairings (Table 4). Free sugars were much lower in defoliated than in undefoliated foliage in both pairs of stands. For both the nearby and remote stand pairs, larvae ate more foliage from the undefoliated stands than from the defoliated stands. These data suggest low levels of free sugars and high levels of condensed tannin as the most likely reasons for the rejection of leaves from defoliated trees.

#### DISCUSSION

Comparison of larval performance and foliar chemical parameters across several tree species showed a positive relationship between growth rate (RGR) and nitrogen utilization (NUE). This implies that the ability of the gypsy moth to digest and utilize dietary protein may be growth limiting. Since tannins are ubiquitous in gypsy moth hosts and have the potential to reduce digestion of proteins, it is reasonable to presume that tannins would affect foliage suitability. On the basis of Feeny's (1969) pioneering research, we would expect the condensed tannins to be more active than the hydrolyzable tannins because they are more effective at reducing digestion of protein at the highly alkaline pH that prevails in the midgut of caterpillars.

However, a positive association was observed between gypsy moth growth and condensed tannin across tree species in this study.

Table 4. Chemistry and larval choice of foliage from naturally defoliated and undefoliated black oak forests.

Choice-pairs	Foliar content (% dry wt.)				Larval choice (No.)
	Total phenolics	Hydrol. tannin	Cond. tannin	Free sugar	
<b>Nearby stands</b>					
Defoliated	12.9	15.3	21.0	3.0	32
Undefoliated <sub>1</sub>	11.1	18.1	11.4	5.1	57
Prob. level <sub>1</sub>	0.007	0.30	0.017	0.001	0.01
<b>Remote stands</b>					
Defoliated	15.4	14.6	22.0	2.7	12
Undefoliated <sub>1</sub>	12.5	8.6	19.0	7.4	52
Prob. level <sub>1</sub>	0.001	0.090	0.22	0.001	0.001

<sup>1</sup> Probability of incorrectly declaring that the defoliated and undefoliated stands are different, t-test for chemicals and chi-square for larval choice.

A study by Lechowicz (1983) examined the natural distribution of gypsy moth larvae and egg masses on several tree species in relation to foliar chemistry. Lechowicz's analysis suggested that gypsy moth larvae prefer trees with tough, dry leaves which also have high condensed tannin levels with preferences affected little by total phenolics or nitrogen. Similarly, levels of herbivory on tropical foliage were found by Coley (1983) to be most highly correlated with toughness, followed by fiber content. Phenolic measures were the least well correlated with herbivory. Feeny (1970), contrary to what the title of his paper implies, concluded that leaf toughness was the chief factor in deterring insect herbivores from feeding on mature oak foliage. The intimate association of condensed tannin with leaf toughness illustrates the difficulty in separating out which individual leaf traits are important determinants of foliage nutritional quality.

Another critical problem in attempting to establish the role of broadly distributed chemicals across several species of trees is that their role may be overshadowed by more potent species-specific secondary chemistry. Comparisons within a species or individual tree should better detect the influence of quantitative variation of a chemical because qualitative differences in foliar chemistry should be much less. Examination of foliage within a tree crown complimented the across-species findings, providing additional evidence of a positive relationship between gypsy moth host preferences and condensed tannin content. However, a similar relationship was found with free sugars, which were highly associated with condensed tannin ( $r_s = 0.88$ ). This illustrates the difficulty in attributing variation in insect

performance to levels of a single specific chemical. The upper crown leaves in this study were primarily sun leaves and the lower crown leaves were primarily shade leaves. A similar positive relationship was reported (Montgomery, 1986) between growth and total phenolics, condensed tannin, and free sugar of gypsy moth reared from the fourth instar to pupation on sun and shade leaves of *Q. rubra* and *Q. prinus*. Within unstressed oak trees, foliage preferences seem to be related to high sugar and high condensed tannin levels.

Variation in foliar chemistry associated with tree species and location in the tree crown are examples of constitutive chemistry. This chemistry can be changed or induced by stress such as defoliation. Defoliation-induced changes in chemistry are thought to be an active defensive response to reduce foliage quality in order to negatively impact the population dynamics of the herbivore. The strong nonpreference reported here for foliage from heavily defoliated trees implies that this foliage was lower in quality. That leaves from defoliated trees consistently had lower levels of free sugars and higher levels of total phenolics supports the contention that defoliated leaves are lower in quality; however, neither hydrolyzable nor condensed tannins were consistently connected with nonpreference for defoliated leaves. Schultz and Baldwin (1982) examined leaf traits of *Q. rubra* that were 50% defoliated by a gypsy moth outbreak and compared this to values from undefoliated trees on the other side of a small ravine. Condensed and hydrolyzable tannins were not measured, but ability to precipitate protein (tanning) was higher in leaves from the defoliated trees (54 vs. 37%). Leaves from defoliated trees also were tougher and had a slightly higher content of total phenolics (7.6 vs. 6.1%) than leaves from undefoliated trees.

One problem with such studies of natural defoliation is the selection of a nondefoliated control. Protecting trees from defoliation in an outbreak area by cages or pesticides risks altering foliar chemistry or affecting palatability. Selecting trees on a different, undefoliated site has the risk that differences in chemistry are due to constitutive differences between sites rather than to induction from defoliation. Conversely, in selecting leaves from a defoliated stand where most of the foliage already has been consumed, the remaining leaves that are selected for tests may not have been missed by the caterpillars due to chance, but may have been rejected because they were initially less palatable.

Studies that examine growth of gypsy moth on artificially defoliated trees remedy these ambiguities, though this technique also has inherent problems, such as how and when to defoliate artificially. Valentine et al. (1983) reported that artificial defoliation of *Q. velutina* reduced free-sugar levels in leaves and that this was correlated negatively with gypsy moth pupal weight. No relationship was found with several of the other factors measured (individual sugars, minerals, and amino acids), and no secondary chemicals were measured. The recent study by Rossiter et al. (1988) examined phenolics but not nutrients in artificially defoliated *Q. velutina*. Here, defoliation levels of 10-60% were correlated with total phenolics ( $r = 0.42$ ), hydrolyzable tannin ( $r = 0.43$ ), and tanning ( $r = 0.44$ ), but not with condensed tannin. Female but not male pupal weights were negatively correlated with the phenolic measures and percent defoliation. When all the measured phenolics were placed in a

regression model along with defoliation, less than 50% of the variation in pupal weights was accounted for. Thus, nonphenolic components of foliage chemistry also may have affected pupal weight in this study.

Although considerable variation in the chemistry of the host foliage can be identified and it can be established that the gypsy moth responds to variation in foliage quality, the ecological significance of specific foliar chemicals is difficult to define because variation of the chemicals often is correlated. It is particularly difficult to identify the effect of phenolics because the gypsy moth's response is paradoxical; i. e., phenolics seem to be positively correlated with the quality of the foliage when the variation is constitutive and negatively correlated when it is induced. Since all of the phenolic assays measure structural classes rather than molecular species, important changes in the "quality" of the phenolics may have been overlooked. The importance of molecular structure on protein binding and other biological functions of tannins has been discussed extensively (Zucker, 1983; Hagerman & Butler, 1981; Beart et al., 1985; Wisdom et al., 1987). It would seem that a prerequisite to the establishment of meaningful ecological relationships between dietary phenolics and the gypsy moth would be identification of the active chemicals and their mode of action.

#### LITERATURE CITED

- BARBOSA, P. & KRISCHIK, V.A.: 1987. Influence of alkaloids on feeding preference of eastern deciduous forest trees by the gypsy moth, *Lymantria dispar*. *Am. Nat.* 130: 53-69.
- BEART, J.E., LILLEY, T.H. & HASLAM, E.: 1985. Plant polyphenols--secondary metabolism and chemical defence: some observations. *Phytochemistry* 24: 33-38.
- BERNAYS, E.A.: 1981. Plant tannins and insect herbivores: an appraisal. *Ecol. Entomol.* 6: 353-360.
- BLYT, H.J., GUSCAR, T.K. & BUTLER, L.G.: 1988. Antinutritional effects and ecological significance of dietary condensed tannins may not be due to binding and inhibiting digestive enzymes. *J. Chem. Ecol.* 14: 1455-1465.
- DETHIER, V.G.: 1982. Mechanism of host-plant recognition. *Entomol. Exp. & Appl.* 31: 49-56.
- EL-NAGGAR, S.F., BOSKOTCH, R.W., ODELL, T.M. & GIRARD, L.: 1980. Antifeedant deterrence for the gypsy moth larvae from *Kalmia latifolia*: Isolation and characterization of ten grayanoids. *J. Nat. Prod.* 43: 617-631.
- FRENY, F.P.: 1969. Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. *Phytochemistry* 8: 2119-2126.
- FRENY, F.P.: 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.
- FRENY, F.P.: 1976. Plant apparency and chemical defense. *Rec. Adv. Phytochem.* 10: 1-40.
- FURBUSH, E.H. & FERNALD, C.H.: 1896. *The gypsy moth*. Wright and Potter, Boston.

- GOLDSCHMIDT, R. 1934. Lymantria. Bibliogr. Genet. 11: 1-185.
- GORNITZ, V.K. 1954. Feeding stimulants for polyphagous caterpillars that attack woody plants. (In German). Verhand. Gesell. Ang. Ent. 6: 38-47.
- HAGERMAN, A.E. & BUTLER, L.C. 1981. The specificity of proanthocyanidin-protein interactions. J. Biol. Chem. 256: 4494-4497.
- HALSAM, E. 1966. Chemistry of vegetable tannins. Academic Press, New York. 179 p.
- JANKOVIC, L. 1958. [Foster plants of the gypsy moth (Lymantria dispar L.) in the open in the course of a single gradation]. Zb. Rad. 2: 1-15.
- KIREEVA, I.M. 1986. Phenetic methods of investigating Lymantria dispar. (In Russian). Lesn. Khoz. 11: 50-52.
- KURIR, A. 1953. The host plants of the gypsy moth (Lymantria dispar L.). (In German). Z. Angew. Entomol. 34: 543-586.
- LECHOWICZ, M.J. 1983. Leaf quality and the host preferences of gypsy moth in the northern deciduous forest. p. 67-82 In: Talerico, R.L., & Montgomery, M.E. (eds.). Proceedings, Forest defoliator-host interactions: A comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. NE-85.
- LECHOWICZ, M.J. & MAUFFETTE, Y. 1986. Host preferences of the gypsy moth in eastern North American versus European forests. Rev. Entomol. Quebec 13: 43-51.
- MARTIN, M.M. & MARTIN, J.S. 1983. Tannin assay in ecological studies. Precipitation of ribulose-1,5, biophosphate carboxylase/oxygenase by tannic acid, quercetin, and oak foliage extracts. J. Chem Ecol. 9: 285-294.
- MARTIN, M.M., ROCKHOLM, D.C., & MARTIN, J.S. 1985. Effects of surfactants, pH, and certain cations on precipitation of proteins by tannins. J. Chem. Ecol. 11: 485-493.
- MARTINAT, P.J. & BARBOSA, P. 1987. Relationship between host-plant acceptability and suitability in newly eclosed first-instar gypsy moths, Lymantria dispar (L.) (Lepidoptera: Lymantriidae). Ann. Entomol. Soc. Am. 80: 141-147.
- MEISNER, J. & SKATULLA, U. 1975. Phagostimulation and phagodeterrence in the larva of the gypsy moth, Porthetria dispar L. Phytoparasitica 3: 19-26.
- MEYER, G.A. & MONTGOMERY, M.E. 1987. Relationships between leaf age and the food quality of cottonwood foliage for the gypsy moth, Lymantria dispar. Oecologia 72: 527-532.
- MOLE, S. & WATERMAN, P.G. 1987. Tannic acid and proteolytic enzymes: Enzyme inhibition or substrate deprivation? Phytochemistry 26: 99-102.
- MONTGOMERY, M.E. 1982. Life-cycle nitrogen budget for the gypsy moth Lymantria dispar, reared on artificial diet. J. Insect Physiol. 28: 437-442.
- MONTGOMERY, M.E. 1986. Gypsy moth host plant relationships and population dynamics. p. 743-754 In: Population dynamics of the gypsy moth in Yugoslavia; 1986 September 9-16; Ljubljana, Yugoslavia: Yugoslav IUFRO World Congress Organizing Committee.
- MOSHER, F.H. 1915. Food plants of the gypsy moth in America. Bull. 250. U.S. Dep. Agric., Bur. Entomol. Washington, D.C. 39 p.
- NOTHNAGLE, P.J. & SCHULTZ, J.C. 1987. What is a forest pest? pp. 59-80 In: Barbosa, P. & Schultz, J.C. (eds.). Insect outbreaks.

- Academic Press, San Diego.
- ROSENBLATT, M. & PELUSO, J.V. 1941. Determination of tannins by photocolormeter. *Assoc. Off. Agric. Chem.* 24: 170-181.
- ROSSITER, M.C. 1987. Genetic and phenotypic variation in diet breadth in a generalist herbivore. *Evol. Ecol.* 1: 272-282.
- ROSSITER, M.C., SCHULTZ, J.C. & BALDWIN, I.T. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69: 267-277.
- SCALBERT, A. & HASLAM, E. 1987. Polyphenols and chemical defence on the leaves of *Quercus robur*. *Phytochemistry* 26: 3191-3195.
- SCHULTZ, J.C. & BALDWIN, I.T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217: 149-151.
- SCHULTZ, J.C. & LECHOWICZ, M.J. 1986. Hostplant, larval age, and feeding behavior influence midgut pH in the gypsy moth (*Lymantria dispar*). *Oecologia* 71: 133-137.
- SIDON, C. & JODAL, I. 1983. A study on the physiological conditions of the gypsy moth (*Porthetria dispar* L.) in the acacia forest, "Bogromara." *Zast. Bilja* 34: 445-455.
- SWAIN, T. 1979. Tannins and Lignins. pp. 657-682 In: Rosenthal, G.A. & Janzen, D.H. (ds.). *Herbivores. Their interaction with secondary plant metabolites.* Academic Press, New York.
- VALENTINE, H.T., WALLNER, W.E. & WARGO, P.M. 1983. Nutritional changes in host foliage during and after defoliation, and their relation to the weight of gypsy moth pupae. *Oecologia* 57: 298-302.
- WISDOM, C.S., GONZALEZ-COLOMA, A. & RUNDEL, P.W. 1987. Ecological tannin assays. Evaluation of proanthocyanidins, protein binding assays and protein precipitating potential. *Oecologia* 72: 395-401.
- ZUCKER, W.F. 1983. Tannins: does structure determine function? An ecological perspective. *Am. Nat.* 121: 335-365.

DEVELOPMENT AND PHENOLOGY OF  
EGGS OF GYPSY MOTH, LYMANTRIA  
DISPAR (LEPIDOPTERA:  
LYMANTRIIDAE), IN ONTARIO

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INTRODUCTION

Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), was first observed in Ontario in 1969 (Sippell et al. 1970). During the 1980s, the species underwent dramatic increases in distribution and population levels, which peaked in 1985 at about  $246 \times 10^3$  ha of moderate-to-severe defoliation (Howse 1987). The insect is now distributed throughout the southeastern part of the province.

Several forms of biological control have been attempted against this insect. In the year following the peak of the infestation, approximately  $103 \times 10^3$  ha were treated with multiple aerial applications of the biological insecticide, *Bacillus thuringiensis* (Howse 1987). During the early 1980s, several releases of biological control agents, especially egg parasitoids, were made (Wallace 1987). As an aid to timing spray operations, to releasing biological control agents and to understanding gypsy moth population dynamics, we began to develop a process-oriented phenology model to describe development of gypsy moth near the northern distribution of its range.

Oviposition by gypsy moth occurs in summer on a variety of substrates on and around the host plants (Johnson et al. 1983). Larval development within the egg is completed shortly after egg deposition (Masaki 1956). Embryonated eggs are the overwintering stage. Diapause in the egg stage is obligatory (Leonard 1968a) and is terminated after a prolonged chill period (Masaki 1956). There are sexual differences in egg hatching times; the first larvae to eclose are predominately females (Leonard 1968b).

Egg developmental times at constant temperatures have been determined from European populations of gypsy moth (Rubtsov 1938, Pantyukhov 1962). The threshold for egg development has been estimated to be from 3 to 6°C and apparently varies with the length of the cold storage period (Rubtsov 1938). Relative humidity has little effect on development times (ibid.). The effect of temperature and exposure time on diapause termination was investigated by Masaki (1956). Johnson et al. (1983) presented a degree-day (DD) accumulation model for initial and mean egg eclosion. A mathematical

model of egg eclosion was presented by Waggoner (1984) wherein hatching was described as a Poisson process. Giese and Casagrande (1981) reviewed the literature on egg development.

The most difficult and critical stage for which to predict phenological events, for most insects, is the overwintering stage. This results in part from our inability to differentiate between diapause termination and morphogenesis (Rubtsov 1938), and the extreme variability of spring temperatures, especially in northern climates. Estimated threshold temperatures for development are also difficult to estimate (Rubtsov 1938, Campbell *et al.* 1974), as are development times for insects reared at low temperatures.

The purposes of this paper are to: (1) determine the effects of temperature on post-diapause development of an Ontario strain of gypsy moth eggs in the laboratory; (2) investigate variability in egg hatch at constant temperatures; (3) examine the effects of spatial distribution on development variability and survival; (4) compare egg microclimatic temperatures with the standards of conventional meteorology; (5) compare DD egg hatch predictions with actual hatch in the field and (6) develop and validate a simulation model for phenology of gypsy moth eggs under variable temperatures in the field.

## MATERIALS AND METHODS

### Laboratory Rearing

Gypsy moth egg masses were collected from six sites in southern Ontario (Perth, Queensborough, Kaladar, Rock Lake, Depot Lake and McLean) in September of 1986. The egg masses were initially stored in a chamber at 15°C for 4 d and then moved to a chamber at 6°C. The temperature was then reduced to 2°C, and the egg masses remained at that temperature throughout the winter. In mid-March the egg masses were removed from cold storage and surface sterilized by submersion in a 10% solution of formalin for 1 h followed by rinsing in tap water for 1 h. The egg masses were placed individually in 7-dram plastic snap-cap vials. Ten egg masses were placed in each of 11 constant temperature chambers (5.5, 8.0, 11.0, 13.6, 15.0, 18.5, 20.4, 24.1, 27.5, 31.4 and 32.7°C).

Two additional sets of 10 egg masses were placed in each of the three chambers with the lowest temperatures. One of the two sets was alternated daily between the three low temperatures and 18.5°C. The other sets were left at the three low temperatures for 27 d and then were moved to the chamber set at 18.5°C.

Additional egg masses were collected in April 1987 simultaneously from two locations (Castleton and Gordon Rapids, Ont.) and at two vertical strata (above or below 1 m) at each location. These egg masses were transported to the laboratory in cold storage where they were surface sterilized and placed in individual vials. Ten egg masses from each condition were reared at 27.5°C until the completion of hatch.

All egg masses were examined twice daily at about 0800 and 2000 hours until the completion of eclosion. Newly eclosed larvae were removed and counted.

#### Temperature-dependent Development

Development times and rates (1/time) were calculated for eggs hatching at each constant temperature. Estimated times ( $t_L$ ) for development of individuals at low temperatures were determined from the following:

$$t_L = t_H / [1 - (t_H / \bar{t}_H)] \quad [1]$$

where  $t_L$  = actual time spent at the low temperature (i.e., 22 d),  $t_H$  = the time individuals spent at 18.5°C prior to eclosion and  $\bar{t}_H$  = the average time required to complete development at 18.5°C.

A quadratic equation of the form  $r(T) = A + BT + CT^2$  and a linear function of the form  $r(T) = a + bT$  were used to describe development rates ( $r(T)$ ) of eggs as a function of temperature  $T$  (°C).

Individual development times at each temperature were normalized by division by the mean time for the respective temperatures.

Variation in hatch around the mean development times was described by means of a cumulative Weibull function (Eq. [2]) (Wagner *et al.* 1984):

$$F(x) = 1 - \exp(-((x - \gamma)/\eta)^\beta) \quad [2]$$

where  $F(x)$  = the proportion of the population that had completed development by normalized time  $x$ , and  $\gamma$ ,  $\eta$  and  $\beta$  are parameters estimated by nonlinear regression.

#### Field Development

In the fall of 1987, a Stevenson screen meteorological shelter (Atmospheric Environment Service, Environment Canada) was set up on a mown lawn in Tweed, Ontario. A data logger (Campbell Scientific Inc., Ogden Utah, Model CR-7) was connected to three copper-constantan thermocouples in the screen. Twenty egg masses were collected on 17 November 1987 from Frankford, Ontario and were placed in individual snap cap vials. One set of 10 vials was placed in an 18 by 13 by 11-cm plastic box in the Stevenson screen and another set was placed in a plastic box on the ground under the Stevenson screen. One thermocouple junction was placed in each of the plastic boxes while the third was suspended inside the Stevenson screen. The data logger was programmed to sample the thermocouples every 5 s and to output the average temperatures for every hour. On 7 April 1988 the box under the Stevenson screen was moved into the screen.

Twenty egg masses were marked in a hardwood stand 2.0 km ESE of the weather station and an additional 10 egg masses were marked in another stand 8.7 km ENE of the weather station prior to eclosion. A barrier of Tangletrap was placed around each egg mass to prevent the dispersal of newly eclosed larvae. These egg masses and the egg masses at the Stevenson screen were examined daily throughout the emergence period and newly eclosed larvae were counted and removed.

#### Bark Microclimate

Copper-constantan thermocouples (36-AWG) were taped to bark surfaces of trees within hardwood stands in which the egg masses were marked for examination of eclosion. The thermocouples were wired to a

data logger programmed as described previously. Bark temperatures were regressed as a linear function, after natural logarithmic transformation, of air temperature recorded at the remote weather station.

#### Degree-day Accumulations

To compare the prediction of Johnson *et al.* (1983) with observed field eclosion, DD above a threshold of 3.0°C were accumulated from 1 January until the end of egg eclosion from the hourly average temperatures recorded by thermocouples in the Stevenson screen and in the plastic boxes containing eggs. To determine the effect of threshold temperature ( $T_b$ ) on DD accumulations,  $T_b$  was varied between 3.0 and 5.0°C in 0.5°C increments for air temperatures recorded in the Stevenson screen.

#### Formulation of Model

The development model used by Lysyk and Axtell (1987) for development of house fly immatures was adapted to simulate gypsy moth egg hatch. Development rates, for each hour of the day, were determined from the temperature-dependent solution to the linear or quadratic rate equations. Average hourly temperatures recorded in the Stevenson screen were used as model inputs. Mean rates were accumulated and used to solve Eq. [2] to determine the proportion of the population that had completed development. Simulations for each model were run with 1 January, 1 February, 1 March and 1 April starting dates.

### RESULTS

#### Temperature-dependent Development

No eggs hatched at 5.5°C and a laboratory mishap prevented observation of hatch at 8.0°C. Development times and rates (1/days) for the other constant temperatures are listed in Table 1. For both development rates and times, coefficients of variation (CV) increased with increasing temperature (Table 1). Parameter estimates (SE) for the quadratic function (Fig. 1) relating development rate to temperature were  $A = -0.1079$  (0.0187),  $B = 0.0145$  (0.0019) and  $C = -0.0002$  ( $R^2 = 0.977$ ). This gives a development threshold of 8.4°C. For the linear relationship (Fig. 1) between development rate and temperature, parameters were  $a = -0.0143$  (0.0002) and  $b = 0.0044$  (0.00001) ( $r^2 = 0.855$ ), the two highest temperatures with apparent high temperature inhibition being omitted. A linear development rate function was constructed from the average median hatch data (i.e., 317.2 DD) and the 3.0°C development threshold provided by Johnson *et al.* (1987). This function,  $r(T) = -0.0096 + 0.0032 T$ , is also illustrated in Figure 1 for comparison.

Estimated development times and rates for eggs either alternated daily or moved after 22 d from low to high temperatures are listed in Table 2. Estimated times and rates for both treatments are similar for 5.5 and 8.0°C. However, the CVs for the treatments are

considerably different. Among samples for which mean times and rates were estimated at 11.0°C, the sample moved after 22 d came closest to the observed time and rate. Analysis of Eq. [1] yielded an interesting property of the relationship. As the individual times at the high temperature ( $t_H$ ) approach the mean time ( $\bar{t}_H$ ) at the high temperature (i.e., ratio  $t_H / \bar{t}_H \rightarrow 1$ ) the estimated time at low temperature ( $t_L$ ) becomes very unstable (Fig. 2). As a result of this instability, estimated rates were not used in the construction of temperature-dependent rate functions.

Eggs collected from heights less than 1 m on the boles of host trees survived considerably better than did eggs collected above 1 m on the boles (Table 3). There were small significant differences (t-test,  $\alpha = 0.05$ ) in development times for these eggs when they were reared in the laboratory at constant temperatures. Survival of the eggs did not affect variability of the eggs, as indicated by the values of the CVs (Table 3).

#### Variability in Development

Since the coefficients of variation for hatch times were temperature dependent, variability was described from the development times at the constant temperatures the insects were most likely to experience in the field. Consequently, a cumulative Weibull function (Eq. [2]) was fitted to normalized times for 11.0, 13.6, 15.0 and 18.5°C (Fig. 3). Parameter estimates (SE) for the cumulative function were  $\gamma = 0.7519$  (0.0125),  $\eta = 0.2704$  (0.0132) and  $\beta = 2.9442$  (0.1389) ( $R^2 = 0.961$ ).

A variance component procedure (SAS Institute 1985) was used to compare variability within and between egg masses. Normalized times were used so that egg masses exposed to each temperature could be pooled. The ratio of the between-egg mass variance component to the within-egg mass variance component was less than 1, an indication that most variation occurred within egg masses. The coefficients of variation for normalized hatch times for individual egg masses, when compared with pooled egg masses, increased only from 10.4 to 11.7%. Hence, if the effects of individual egg masses are ignored, only a small amount of variation remains unexplained.

#### Bark Microclimate

At higher temperatures, average bark temperatures were significantly higher than corresponding air temperatures recorded in the Stevenson screen. Bark temperature as a function of air temperature (Fig. 4) was:

$$y = 0.061 \text{ (SE = 0.030)} + 1.004 \text{ (SE = 0.011)} \times (r^2 = 0.935) \quad [3]$$

where  $y$  = natural log of bark temperature and  $x$  = natural log of air temperature.

#### Degree-day Accumulations

DD accumulated above a 3.0°C threshold were compared with egg hatch of natural populations and eggs housed in the Stevenson screen (Fig. 5). For natural eggs, 2.0 and 8.7 km from the Stevenson screen, air temperatures resulted in an accumulation of about 352 DD to the

Table 1. Mean development times (SE) and rates (SE) for gypsy moth eggs reared at constant temperatures.

Temp (°C)	n	Mean time (d)	CV (%)	Mean rate (1/d)	CV (%)
32.7	1283	10.0 (0.04)	13.83	0.1022 (0.0004)	13.21
31.4	1297	9.7 (0.04)	15.25	0.1056 (0.0004)	14.04
27.5	2124	9.0 (0.03)	16.47	0.1142 (0.0004)	14.84
24.1	2551	9.6 (0.02)	12.71	0.1052 (0.0002)	11.32
20.4	2837	12.7 (0.03)	12.68	0.0801 (0.0002)	10.98
18.5	2286	13.3 (0.04)	12.97	0.0763 (0.0002)	11.79
15.0	2259	17.5 (0.03)	9.17	0.0577 (0.0001)	8.34
13.6	2284	25.3 (0.05)	9.04	0.0398 (0.0001)	8.64
11.0	2732	41.4 (0.04)	7.72	0.0243 (0.0000)	7.13

Table 2. Mean observed development times (SE) and estimated development rates (Eq. [1]) for gypsy moth eggs moved between low temperatures and 18.5°C.

Temp (°C)	n	Mean time (d)	CV (%)	Estimated time (d)	Estimated rate (1/d)
11.0 <sup>a</sup>	2517	18.2 (0.03)	7.77	28.8	0.0347
8.0 <sup>a</sup>	2717	21.8 (0.05)	11.52	60.4	0.0166
5.5 <sup>a</sup>	2568	23.2 (0.05)	11.60	90.8	0.0110
11.0 <sup>b</sup>	2982	27.5 (0.02)	4.01	37.5	0.0267
8.0 <sup>b</sup>	2528	30.3 (0.02)	3.21	58.5	0.0171
5.5 <sup>b</sup>	3147	31.9 (0.02)	3.03	86.1	0.0116

<sup>a</sup> alternated daily between indicated temperature and 18.5°C

<sup>b</sup> moved to 18.5°C after 22 d at indicated temperature

Table 3. Proportion surviving and development times (SE) at 26.0°C for eggs collected at two heights on the boles.

Location	Height	n <sup>a</sup>	Survival (%)	Time (d)	CV (%)
Castleton	> 1 m	3643	6.2	8.2 (0.06)	10.70
	< 1 m	3933	79.1	7.5 (0.01)	10.33
Gordon Rapids	> 1 m	2577	15.0	7.0 (0.04)	10.07
	< 1 m	3055	61.9	6.7 (0.02)	10.70

<sup>a</sup> initial number of eggs

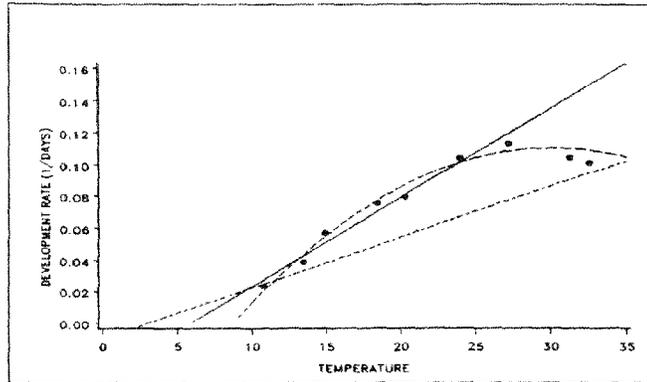


Fig. 1. Temperature-dependent development rates for eggs of the gypsy moth. Circles are observed mean rates, solid line is linear regression line, curve is quadratic regression line and dashed straight line is regression constructed from Johnson *et al.* (1983) data.

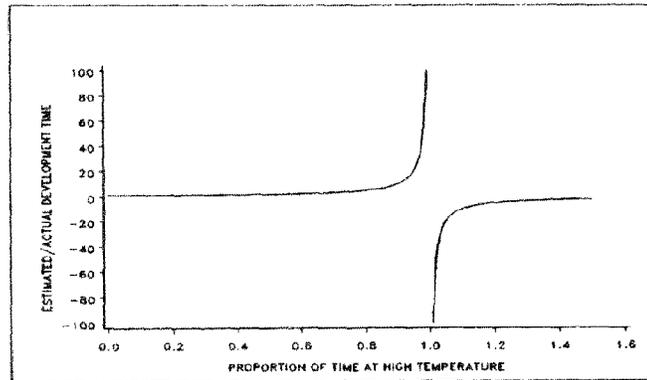


Fig. 2. Generalized proportion of estimated to actual development times from interpolation equation for varying values of the ratio  $t_H / \tau_H$ .

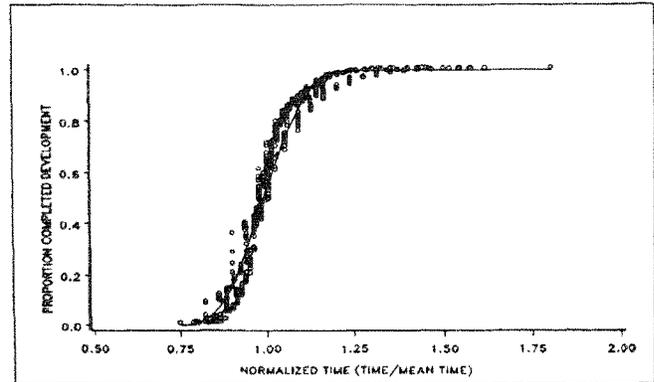


fig. 3. Cumulative frequency distribution of egg hatch as a function of normalized time. Circles are observed values and line is cumulative Weibull function fitted by nonlinear regression.

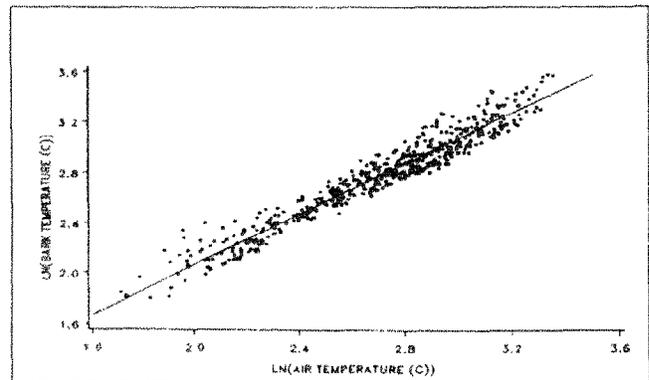


fig. 4. Linear relationship between natural logarithm of bark temperature and natural logarithm of air temperature recorded in Stevenson screen.

onset of hatch and a median hatch at about 380 DD. Eggs housed in and under the Stevenson screen began to hatch at about 428 and 408 DD and median hatch occurred at about 445 and 500 DD, respectively.

Correcting the air temperatures with the bark temperature function increased the number of DD to onset of hatch for field egg populations to about 385 and the median hatch to about 420. Some of the egg masses stored in and under the Stevenson screen got wet from snow melt in the spring, and low survival resulted. This may have accounted, in part, for the discrepancies in accumulated hatch as a function of DD between the natural and boxed egg masses.

Varying the development threshold from 3.0 to 5.0°C resulted in significant differences in accumulated DD by the time of larval eclosion from the eggs (Fig. 6).

#### Computer Simulations

Figure 7 shows the results of the computer simulations in which the three different rate equations were used. The four lines in each graph, from left to right, are the predicted eclosion for simulations beginning on 1 January, 1 February, 1 March and 1 April. For all three rate equations, the later the simulation starting date, the better the prediction. The linear model resulting from our constant-temperature rearing data deviated the most between predicted and observed for all starting dates. The linear model constructed from the temperature constant for median hatch and threshold provided by Johnson *et al.* (1983) was used in a successful prediction of egg hatch with a starting date of 1 April. When the model incorporating the quadratic function was used the onset of hatch was underestimated by only a couple of days for the same starting date. However, the model based on the quadratic function (Fig. 7C) was less sensitive to changes in the starting date than the models based on either linear rate. In all cases, our descriptions of variability seemed to reflect adequately the observed variability in egg hatch.

#### DISCUSSION

Development rate equations, derived from constant temperature rearings, coupled with a variability function, were used to construct rate summation models of phenology for gypsy moth eggs. Techniques similar to those employed by Lysyk and Axtell (1987) for house fly immatures and Casagrande *et al.* (1987) for modeling the development of the larval and pupal stages of the gypsy moth were used to predict the spring eclosion of gypsy moth from the egg.

Estimation of development times, and consequently rates, at low temperatures has been considered essential for predicting the development of overwintering stages of an insect. Although insects may develop at these low temperatures, the protracted development time required generally results in poor survival. To overcome this problem, development times at low temperatures can be estimated from insects moved between low and high temperatures (Régnière 1987). Utilization of this technique for gypsy moth eggs resulted in some negative estimated development times. This prompted us to analyze the procedure through the use of simulation techniques. As the ratio of

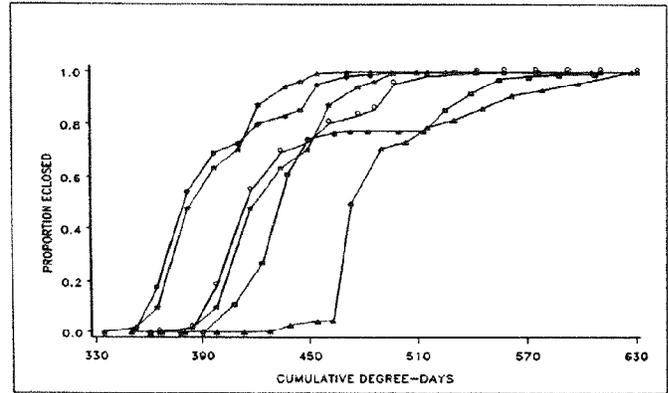


Fig. 5. Proportion of larvae that eclosed from gypsy moth egg masses in the field versus accumulated DD. Closed circles and stars are egg eclosion from sites 2.0 and 8.7 km from Stevenson screen, respectively. Open circles and stars are same data corrected with bark temperature correction function. Squares and triangles are egg masses kept in and below the Stevenson screen, respectively.

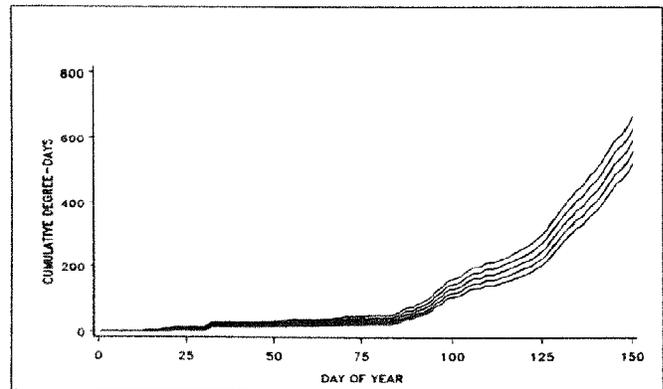


Fig. 6. DD accumulations from air temperature recorded in Stevenson screen. Lines from top to bottom represent 0.5°C changes in threshold between 3.0 and 5.0°C.

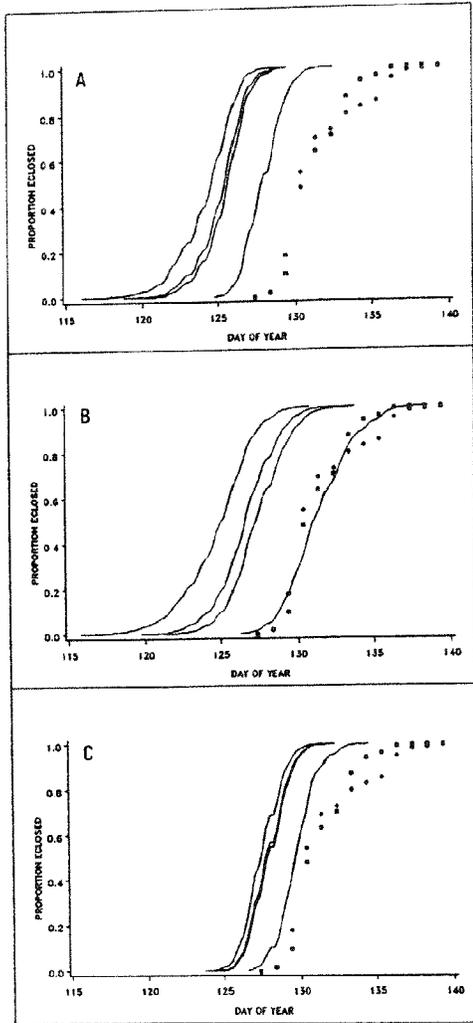


Fig. 7. Results of computer simulations with A) linear regression function, B) linear regression function from Johnson *et al.* (1983) and C) quadratic regression function. Solid lines, from left to right, in each graph represent 1 January, 1 February, 1 March and 1 April simulation starting dates.

time spent at the high temperature for completion of development, after movement from the low temperature, to the total development time required for complete development at the high temperature approached one, the relationship became very unstable. If individual development times were greater than the mean time required at the high temperature negative estimates resulted. Consequently, these estimated times were not employed in construction of temperature-dependent rate functions.

Most variability in egg eclosion times for gypsy moth eggs occurred within egg masses. Variability between egg masses only increased overall variability by a small amount. This suggests that small numbers of egg masses provide an adequate representation of variability and can be used in egg hatch investigations.

Low survival, in some years, of eggs well above the ground on the tree bole has been attributed to low winter temperatures (Leonard 1972). Eggs lower on the bole have a higher survival rate as a result of the insulating effects of snow cover. Campbell *et al.* (1974) suggested that low temperatures, resulting in mortality of insects, selectively kill individuals that cannot develop at low temperatures. Our observations indicate that when mortality caused by low temperatures occurs, the resulting variability of survivors is no different than that of egg masses that experience little or no mortality.

The use of normalized development times, pooled for all temperatures (Wagner 1984), is based on the assumption that variability is proportional to the mean development time for all temperatures. The observation made here that the coefficient of variation for development times of gypsy moth eggs varied with rearing temperature suggests that this assumption may not be valid for all insects and their stages. We conclude that normalized times derived from the constant temperatures within the range of average temperatures that the insects would experience in the field would be more appropriate.

Degree-day accumulations described by Johnson *et al.* (1983) were inadequate for predicting the onset or median of egg hatch observed in the present study. Degree-day accumulations were also extremely sensitive to small changes in threshold temperature and starting dates.

Considerable differences exist between the temperatures in the microenvironments in which insects dwell and the standards of conventional meteorology (Wellington 1950). Although these microclimatic differences have been investigated for the larval stages of gypsy moth (Anderson *et al.* 1987), such relationships have not been explored for the egg stage. Degree-day summations made by Johnson *et al.* (1983) for predicting egg hatch were based on daily maximum and minimum temperatures recorded at a weather station 2.0 m from the stand in which the eggs were collected. Empirical relationships presented here indicate that bark temperatures can be described as simple linear functions of meteorological standards. However, gypsy moth eggs are widely distributed throughout their habitat and occur in a variety of places; eggs are found at various heights on the tree, in different aspects with regard to solar radiation and on or under different substrates near the ground

(ibid.). These various microhabitats represent different microclimates in which the eggs undergo development. Nicolai (1986) has demonstrated that differences in temperature exist even between bark fissures and ridges in *Quercus* spp. A more thorough investigation of these relationships is required to predict gypsy moth egg hatch accurately.

The linear development rate equation, when incorporated into the rate summation model, was inadequate for predicting egg hatch regardless of the simulation starting date. The linear function constructed from Johnson et al. (1983) data permitted accurate prediction of the hatch date only for the simulation with a 1 April starting date. The quadratic function also enabled prediction of egg hatch within a couple of days of actual hatch and was less sensitive to starting date than the linear function-based models. That the quadratic function had a much higher threshold value (8.4°C) and was less sensitive to fluctuations of spring weather than were the linear models suggests that the threshold for development rate accumulation may not be as low as predicted with the aid of either linear function. For all models variability in egg hatch was well represented by the Weibull function.

Overwintering development of insects has been described as a biphasic process (Logan et al. 1979). The first phase consists of diapause development, while the second phase involves morphogenetic development. A portion of the population may complete diapause development and begin morphogenesis while the remainder of the population remains in diapause. This phenomenon may account for the discrepancies in reported development rates and thresholds, resulting from different storage treatments, that exist in the gypsy moth literature. Development rates for European eggs (Rubtsov 1938, Pantyukhov 1962) were much higher than the rates presented here. These higher rates probably reflect differences in storage temperatures and times rather than geographic differences. Eggs used in our development studies had probably completed diapause requirements and the 2°C storage temperature inhibited subsequent development. The late starting date of the accurate predictions suggests that a more complete knowledge of the temperature and time relationships for diapause termination in gypsy moth eggs may help us understand better the processes involved and may enhance our ability to predict this critical phenological event.

To predict gypsy moth phenology throughout the summer requires that spring development of the egg stage be accurately predicted. The model presented by Vaggoner (1984) is inadequate for predicting variability in egg hatch and does not lend itself well to conventional modeling techniques used to model phenology of other stages of gypsy moth (Casagrande et al. 1987). The model described here employs similar techniques and would be a suitable starting point for such a comprehensive model.

#### SUMMARY

Rate-summation modeling techniques, incorporating development variability, were used to predict eclosion from the egg by gypsy moth. A quadratic temperature-dependent rate function was compared

with two linear functions and proved to be less sensitive to changes in the simulation starting dates. Variability increased with increased rearing temperature. Consequently, variability was mathematically described from temperatures that eggs would experience in the field. The greatest amount of variability in hatch times occurred from within egg masses; between egg masses added only a small amount of variability. Reductions in survival resulting from spatial distribution of egg masses had no effect on variability. Techniques used to estimate development times of eggs at low temperatures proved to be inappropriate. Published DD summations, to onset and median egg hatch, above a 3.0°C threshold, were inadequate for predicting egg hatch for field populations. Degree-day techniques are shown to be very sensitive to changes in threshold value. Differences between microclimatic temperatures and the standards of meteorology also influenced DD predictions.

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#### LITERATURE CITED

- ANDERSON, D.E., D.R. MILLER, W.E. WALLNER, T.L. TAIGEN and J.J. SCHWARTZ. 1987. A numerical simulation of the microclimate of gypsy moth caterpillars in forest canopies. Proc. 8th Conf. Aero Bio-Meteorol. Am. Meteorol. Soc., Purdue Univ., W. Lafayette, Ind., 14-18 Sept., p. 353-355.
- CAMPBELL, A., B.D. FRAZER, N. GILBERT, A.P. GUTIERREZ and M. MACKAUER. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431-438.
- CASAGRANDE, R.A., P.A. LOGAN, and W.E. WALLNER. 1987. Phenological model for gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae and pupae. Environ. Entomol. 16: 556-562.
- GIESE, R.L. and R.A. CASAGRANDE. 1981. Egg development and diapause. p. 145-214 in C.C. DOANE and M.L. MCMANUS Ed. The gypsy moth: research toward integrated pest management. USDA For. Serv., Sci. Admin., Tech. Bull. 1584.
- HOWSE, G.M. 1987. Gypsy moth in Ontario. Gypsy Moth News. 15: 4-5.
- JOHNSON, P.C., D.P. MASON, S.L. RADKE, and K.T. TRACEWSKI. 1983. Gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. Environ. Entomol. 12: 929-932.
- LEONARD, D.E. 1968a. Diapause in the gypsy moth. J. Econ. Entomol. 61: 596-598.
- LEONARD, D.E. 1968b. Sexual differential in time of hatch of eggs of gypsy moth. J. Econ. Entomol. 61: 698-700.
- LEONARD, D.E. 1972. Survival in a gypsy moth population exposed to low winter temperatures. Environ. Entomol. 1: 549-554.
- LOGAN, J.A., R.E. STINNER, R.L. RABB and J.S. BACHELER. 1979. A descriptive model for predicting spring emergence of *Heliothis zea* populations in North Carolina. Environ. Entomol. 8: 141-146.
- LYSYK, T.J. and R.C. AXTELL. 1987. A simulation model of house fly (Diptera: Muscidae) development in poultry manure. Can. Entomol.

- 19: 427-437.
- MASAKI, S. 1956. The effect of temperature on the termination of diapause in the egg of Lymantria dispar Linne (Lepidoptera: Lymantriidae). Japan J. Appl. Zool. 21: 148-157.
- NICOLAI, V. 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia (Berlin) 69: 148-160.
- PANTYUKHOV, G.A. 1962. The effect of positive temperatures on different geographic populations of the European gold tail (Euproctis chrysorrhea L.) and the gypsy moth (Lymantria dispar L.-Lepidoptera, Orgyidae). Entomol. Rev. 41: 169-175.
- RÉGNIERE, J. 1987. Temperature-dependent development of eggs and larvae of Choristoneura fumiferana (Clem.) (Lepidoptera: Tortricidae) and simulation of its seasonal history. Can. Entomol. 119: 717-728.
- RUBTSOV, I.A. 1938. Effect of constant and variable temperatures on the development of the eggs of the gypsy moth (Porthetria dispar L.). Plant Prot. 17: 25-38.
- SAS INSTITUTE. 1985. SAS users' guide: statistics. SAS Inst. Inc., Cary, North Carolina.
- SIPPELL, W.L., A.H. ROSE and H.L. GROSS. 1970. Ontario Region. p. 52-71 in Annu. Rep. For. Insect Dis. Surv., 1969. Can. For. Serv., Ottawa, Ont.
- WAGGONER, P.E. 1984. The hatching of gypsy moth eggs, a phenological model. Agric. For. Meteorol. 33: 53-65.
- WAGNER, T.L., H. WU, P.J.H. SHARPE and R.N. COULSON. 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. Ann. Entomol. Soc. Am. 77: 475-487.
- WALLACE, D.R. 1987. Research at the Great Lakes Forestry Centre, Ontario. Gypsy Moth News 15: 5-6.
- WELLINGTON, W.G. 1950. Effects of radiation on the temperatures of insectan habitats. Sci. Agric. 30: 209-234.

NUTRITIONAL ECOLOGY: *LYMANTRIA*  
*DISPAR* AS A MODEL SYSTEM FOR  
 STUDY OF SERUM STORAGE PROTEINS

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The lepidopteran family Lymantriidae contains about 200 genera and about 2,500 described species, mostly from the Old World Tropics (DeWorms, 1983). Of the 46 recognized species and subspecies of Lymantriidae in North America, 30% are considered pests (Ferguson, 1978). The pest species include three introduced species which have become established in North America, the gypsy moth, *Lymantria dispar* (L.), the browntail moth, *Euproctis chrysorrhoea* L. and the satin moth, *Leucoma salicis* (L.). These exotic species are of particular interest to us because of their differing life history strategies and varying levels of success in North America. The satin moth is a minor pest of native and exotic species of poplar, but has on occasion defoliated aspen forests in North America. (Wagner & Leonard, 1979; 1980). The browntail moth is currently a refugial species in several maritime localities in eastern North America (Schaefer, 1974), but populations have recently rebounded (Leonard, 1988). The most successful of the invading Lymantriids is the gypsy moth, which continues to spread in North America.

With economically important species of Lymantriidae, a wide variation in the degree of polyphagy exists, from the rather narrow host ranges of the nun moth, *Lymantria monacha* L., the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McD.), and the satin moth, to the more catholic appetites of the gypsy moth and browntail moth.

Within the wide range of hosts that gypsy moth will feed upon, performance and fitness can vary between species of hosts (Barbosa & Greenblatt, 1981; Barbosa *et al.*, 1981). The quality of a tree host species will differ according to foliage age, location of foliage on the tree, and site conditions. (Wallner, 1987 and references therein.). Leaf quality can decline in response to grazing by gypsy moth larvae (Lance *et al.*, 1986; Schultz & Baldwin, 1982; Valentine *et al.*, 1983; Wallner & Walton, 1979).

There is considerable current interest in insect-host interactions encompassing the emerging field of nutritional ecology. As noted by Slansky and Scriber (1985), the amount, rate, and quality of food consumed influences growth rate, developmental time, weight, dispersal ability, and probability of survival; thus, the processes of food

consumption and utilization underlie and link the physiological, behavioral, ecological, and evolutionary aspects of insect life. Nutrient requirements for insects, reviewed by Dadd (1975), include protein and amino acids, carbohydrates, minerals, water-soluble growth factors including B vitamins, lipogenic factors, ascorbic acids, nucleic acids, and lipid growth factors including essential fatty acids, sterols, and fat soluble vitamins. Host-plant selection by feeding insects involves attraction to a potential food plant, arrest or cessation of locomotion, and stimulation or deterrence of feeding (Hanson, 1983). Allelochemical composition of food can influence performance of an insect feeding on a particular food, and often act in a negative, anti-biotic manner (Slansky & Scriber, 1985).

The complexities of biotic and abiotic factors relating to the nutritional ecology of insects have produced a large and growing literature (e.g. Slansky & Rodriguez, 1987; Slansky & Scriber, 1985; and references therein). As noted by our esteemed colleague, Professor Vincent Dethier (1987), "Knowledge of all these newly revealed capacities of plants and insects forces us to reexamine our ideas of ecological relationships and evolutionary hypotheses. We cannot fully comprehend what populations are doing without understanding individuals nor what individuals are doing without some understanding of relevant features of their physiology and behavior."

Our group is utilizing a unique approach to nutritional ecology by examining the major nutrient storage systems in insects: the serum, cuticular, and yolk storage proteins. Insect storage proteins are synthesized predominantly (c.f. Palli & Locke, 1987) by the larval fat body, accumulate primarily in the hemolymph, and their concentration increases enormously in the later larval instars (Levenbook, 1985). The existence and persistence of distinct groups of storage proteins suggests that they have important functional roles in the physiology of insects, and the absolute or relative amounts of these proteins would be diagnostic of the insects nutritional, developmental, and behavioral state.

We have focused our attention on proteins, rather than on carbohydrates and lipids. Nitrogen-containing compounds play an essential role in growth processes of insects; cellular growth, differentiation, internal and external structural components, enzymes, carrier molecules, pigments, and chromosomal material require and involve a large investment of nitrogen (Mullins & Cochran, 1983.). The female gypsy moth is remarkably efficient in utilizing nitrogen for egg production, incorporating nearly half of that assimilated by last stage larvae into eggs (Montgomery, 1982). Serum storage proteins are not only essential for development of larvae, pupae, and adults, but also serve as a nutritional link between generations. Yolk proteins are the primary nutrient resources in eggs (Kunkel

& Nordin, 1985) and the nutritional quality of eggs is important to survival during embryogenesis, diapause, and survival of pre-feeding neonates. The Lepidoptera in particular have a complicated set of yolk proteins which include vitellogenin, microvitellogenin, and egg specific protein (Irie & Yamashita, 1983; Kawooya *et al.*, 1986; Zhu *et al.*, 1986). This complexity of stored nutrient allows for a complex message between the maternal and offspring generation.

Animals are exposed to several thousand naturally occurring molecules in the food they ingest (Turunen, 1985). Our paradigm in studies of nutritional parameters is to examine how the nitrogenous compounds are utilized after being absorbed from the midgut of feeding larvae. From our perspective, the feeding gypsy moth larva is the ultimate biological filtering system, accomplishing the necessary steps in finding food, utilizing the appropriate behavioral and chemosensory repertoires required for ingestion, and in dealing with allelochemicals and other feeding-associated adaptations. Nitrogen-containing compounds absorbed through the midgut form the metabolic pool for biochemical and physiological processes necessary for development. From this pool the fat body will synthesize polypeptides and proteins and release them to the serum as storage proteins, the major internal pool of amino acid resource for development, growth and reproduction.

The gypsy moth is proving to be an excellent model system. The insect is readily cultured in the laboratory. Feeding and accumulation of nutrients occurs only in larvae, since adults are non-feeding. Reserves accumulated by the onset of the wandering stage in last instar larvae provide the store of amino acids and proteins for pupae, adults, and eggs. As perhaps the most studied of forest pests, field aspects of the biology and ecology of the gypsy moth are well documented, yet the underlying physiological and biochemical processes have received little attention.

#### PROTEINS ASSOCIATED WITH INSECT NUTRITION

##### Arylphorin (Ap).

The arylphorins are hexameric serum storage proteins which may also be stored in the fat body close to the time of metamorphosis (Tojo *et al.* 1978; 1980). Arylphorins have been described in several species of insects from several Orders, including an Ap isolated by our group from gypsy moth (Karpells, Leonard, & Kunkel, in ms). The Ap from gypsy moth is one of eight thus far described in lepidopteran species. The gypsy moth Ap is a native Mr

440,000 hexamer composed of nonidentical subunits of Mr 73,000 and 80,000. Ap has been suggested to supply the amino acids necessary for tissue remodeling during metamorphosis. Ap is high in aryl groups which may be related to the particular need by metamorphic stages for phenolic hard cuticle and tanning substrates (Munn & Greville, 1969; Levenbook, 1984). The greatest concentration of arylphorin occurs in hemolymph in the wandering stage, just prior to the prepupal stage. Ap may play a supportive role in supplying the conduit that amino acids must pass through in the hemolymph of the last stage larva in order to take part in the synthesis of vitellogenins in the fat body.

#### Female specific protein (FSP).

FSP is a hexameric storage protein described in five lepidopteran species. FSP, although structurally related to Ap, is compositionally distinct, lacking the high aryl content. FSP accumulates in the last larval instar and is cleared and stored prior to use in the fat body (Tojo *et al.*, 1981). FSP is more actively synthesized in females; in the best documented case, *Bombyx mori*, its disappearance from the hemolymph and fat body is correlated with the accumulation of vitellogenin (Tojo *et al.*, 1981). We are now reasonably certain that FSP is missing in *Lymantria dispar*. This absence is important, since lack of FSP puts more pressure on Ap as a storage vehicle for yolk protein synthesis.

#### Lipophorin (Lp).

Lipophorin is a major insect serum protein (Chino *et al.*, 1981) used to shuttle lipids and hydrophobic compounds between insect tissues. The level of Lp in insect serum is potentially important in the rate of supply of lipids to developing oocytes. Lp itself is taken up into oocytes in substantial enough amounts to be considered physiologically important within the oocyte (Kunkel & Nordin, 1985). Lp is also an important factor in transferring diglycerides to the developing oocytes, and substantial Lp is also itself incorporated into the oocytes of some species of insects (Kunkel & Nordin, 1985). It may be of nutritional and physiological value to the developing embryos as has been shown with *Bombyx mori* (Irie & Yamashita, 1980), and with *Musca domestica* (Agui *et al.*, 1985). Lp titer could also affect the physiology of male *L. dispar* moths as a transport of triglycerides required for flight.

#### Vitellogenin (Vg).

The vitellogenins are the maternal serum precursors of the major yolk proteins or vitellins (Vts), of the egg (Kunkel & Nordin, 1985). Vitellogenin is the generic name

for a unique group of proteins produced in the maternal fat body in most insects and transferred to the developing oocytes through the hemolymph (Hagedorn & Kunkel, 1979). Most often there are multiple immunologically distinct Vts in the egg (Storella *et al.*, 1985), and these may be used differentially during the embryonic development, such that one of them is being utilized by the embryo close to hatching (Kunkel & Nordin, 1985). Differential synthesis, or turnover, of one or multiple Vgs before storage in the egg could dramatically affect the nutritional supply by these proteins to the embryo or first instar larva. In lepidopterans which do not feed in the adult stage, such as the saturniid silk moths, Vgs are often synthesized starting in the late larval and the pupal stage (Pan *et al.*, 1969). With gypsy moth we have found that synthesis begins early in the ultimate stage of female larvae, with Vg appearing in the hemolymph in small amounts on day three. Vg accumulates most rapidly as Ap and FSP decline in the last instar or prepupae of *Bombyx mori*, suggesting that these proteins are the major potential sources or precursors for Vg synthesis (Izumi *et al.*, 1989). In *Bombyx mori*, Vt is not essential for embryonic development (Yamashita & Irie, 1980); however, Vt may be an important nutritional reserve for the pharate first instar larva (Indrasmith *et al.*, 1987).

#### Egg-specific protein (ESP).

ESP is a yolk protein produced within the ovary of lepidopterans. Its use during embryonic development has been correlated with the early phase of embryogeny. ESP is synthesized in the ovary and may rely on other serum storage proteins, such as FSP or Ap in *L. dispar* to be transported into the ovary and serve as an amino acid source for egg proteins (Ono *et al.*, 1975). The quantity of ESP in the egg may determine the size, vigor, and subtle behavior of the resultant larva since early embryonic development consumes the stored ESP of an egg. Surviving ESP levels may allow one to assess the nutritional state of egg masses.

### PROTEIN STUDIES OF GYPSY MOTH.

#### Production of antisera.

Antisera against purified proteins were obtained by immunizing male, white, New Zealand rabbits using a standard protocol (Kunkel, 1988). We have produced antisera for the storage proteins Ap, Ip, Vg, Vt, and for the ovarian protein, ESP.

#### Developmental profiles.

Profiles of Ap, Lp, and Vg have been developed for daily-staged larvae, and prepupae, using quantitative immunoelectrophoresis (QIEP) techniques outlined in Kunkel (1988). These profiles are based on individual animals reared at 24°C, 16:8 LD cycle, and fed *ad lib.* on the diet of Bell *et al.* (1982). Protein profiles of eggs have been determined by QIEP for Ap, Lp, and Vt and by gel electrophoresis for ESP using homogenates of individual eggs. For 1st and 2nd instar larvae we use whole tissue homogenates and for later stages we collect 1 ul of serum from a small puncture in a proleg. We sex larvae by dissecting and identifying testes or ovaries.

#### Maternal - egg profiles.

For correlations of maternal protein levels with those of their progeny, 1 ul of hemolymph from female prepupae is subjected to QIEP. The small puncture causes no apparent trauma, and we rear females to adulthood for mating and to obtain eggs to compare egg protein profiles with those of the maternal larva.

### PROTEIN PROFILES OF GYPSY MOTH

#### Arylphorin.

During each larval stadium, the concentration of Ap (mg/ml) in the hemolymph shows a gradual increase, reaching the highest concentration at early apolysis. As apolysis progresses, Ap is rapidly cleared from the hemolymph, providing an amino acid source for the newly forming larval tissues. Newly molted larvae contain very low levels of Ap. The titers of Ap in male and female larvae of instars III and IV are similar until the metamorphic instar, V in males and VI in females. These stadia are longer in duration, and more Ap accumulates, reaching a level of 26.2 mg/ml in males and 44.8 mg/ml in females. The extra larval instar in females results in a substantially greater absolute amount of Ap accumulation than in males. The titer of Ap in eggs is low.

#### Lipophorin.

Lipophorin also displays some of the same cycling as seen with Ap, but the concentration of Lp is much lower, and remains at constitutive levels throughout development. Lp reaches its highest concentration of about 5 mg/ml in female prepupae and 4 mg/ml in prepupal males (Karpells, Leonard & Kunkel, in prep.) with the higher concentrations

as a function of the longer duration of the ultimate instars. Concentration of Lp in eggs is highest in newly-laid eggs.

#### Vitellogenin.

Vitellogenin appears in the hemolymph in low levels at day three, and accumulates rapidly during the later third of the ultimate instar of females. In wandering stage larvae, Vg levels are ca. 25 mg/ml, and increase to ca. 30 mg/ml in prepupae. Vt levels in eggs are highest in newly oviposited eggs, and our preliminary studies show about 1/2 of the Vt is utilized during embryogenesis, and about 90% is utilized by the time of eclosion of neonates.

#### Egg Specific Protein.

Titers of ESP are highest after eggs are deposited. At completion of embryonation ESP is completely utilized.

### IMPACT OF NUTRITIONAL STRESS ON PROTEIN LEVELS

The raising of antisera to Ap, Lp, Vg and ESP and determination of their titer on daily stage animals fed *ad lib.* provides us with the opportunity to compare the base line levels of serum proteins of healthy animals with levels in animals that have been stressed in the laboratory or in field populations. These studies are just beginning but our initial results show that various nutritional stress factors affect concentrations of proteins in serum and chorionated eggs.

Defoliation-induced changes in leaf quality have been shown to affect the population quality of the gypsy moth (e. g. Capinera & Barbosa 1976, 1977; Lance *et al.*, 1986; Rossiter *et al.*, 1988; Schultz, 1983; Schultz & Baldwin, 1982; Valentin *et al.*, 1983; Wallner & Walton, 1979). Lance *et al.* (1986) found that the addition of tannin at 2.5% of the total dry weight of the diet fed to third and fourth stage gypsy moth larvae could induce behavioral changes that approximated those observed during the shift in diel periodicity in dense field populations of the gypsy moth. In our studies (Leonard, Montgomery & Kunkel, unpubl.) larvae fed continuously on 0.5% (wt/wt) diet with tannin until apolysis of instar IV had 3 to 4% of the amount of Ap found in larvae fed normal diet, levels too low for molting to occur. Larvae switched from control to tannin diet at stage IV and bled at apolysis IV had reductions in Ap and Lp of ca. 30% and 20% respectively of that in control-fed larvae.

Mid- and late-stage larvae show a reduction in Ap and Lp levels in the serum after a two day period of food

deprivation. In ultimate stage female larvae, starvation after day four causes about a one-third reduction in the level of Vg in hemolymph of prepupae.

Leonard (summarized in 1974; 1981) described a series of qualitative changes in the gypsy moth, including variation in the rate of development, supernumerary molts, coloration (phase polymorphism), fecundity, and size and quality of eggs associated, in part, with nutrition. Nutritional stress will be manifested in the amount and quality of nutritional components (proteins) biosynthesized for the egg by late-stage female larvae of the previous generation. While the amount of storage proteins could clearly be a factor in determining the number of eggs produced by the female, it is our hypothesis that the absolute and/or relative amounts of the storage proteins may be causal or at least be correlated with the quality of the eggs of gypsy moth such that a different behavior is exhibited by the next larval generation.

We have initiated studies to determine protein profiles of metamorphic female larvae in the wandering or early prepupal stage after feeding has been completed, to correlate maternal reserves with fecundity and partitioning of Vt, ESP, and Lp in eggs. The role of vitellin reserves in newly hatched larvae relative to dispersal of neonates is of particular interest to us. Mason & McManus (1981) summarized their studies on dispersal, reviewed the research of others, and note that dispersal is an important process in the population dynamics of the gypsy moth and is still a subject of much controversy. The gate for dispersal is narrow. McManus (1973) considered dispersal as an innate tendency that larvae must satisfy before feeding. Collections of dispersing larvae show that they produce frass with little or no leaf constituents (Leonard, 1970a; 1971). Mason & McManus (1981) suggest that the "turnoff mechanism" for dispersal is likely associated with the expending of energy reserves, the inability to produce silk, and starvation. We believe that the tendency of a 1st instar larva to disperse greatly affects its reproductive fitness in a given population level, and that this propensity is reflected by both physiological and behavioral adaptations. These factors would logically be influenced by the amount, quality, and utilization of nutritive reserves in the egg and in newly hatched larvae to sustain it during dispersal. The parameters relating to the nutritive condition of eggs are: (1) a function of synthesis storage proteins during late instars of female larvae since adults do not feed; (2) the quality and quantity of proteins available to the developing oocyte, and (3) the utilization of proteins during the egg stage.

The role of yolk reserves and dispersal of neonates remains to be resolved. Large gypsy moth eggs contain about twice the yolk content of small eggs (Capinera *et al.*, 1977, Capinera & Barbosa (1967), Greenblatt & Barbosa (1979), Campbell (1981) and Lance & Barbosa (1981) consider

that larvae from larger eggs have a higher tendency to disperse, whereas Leonard (1970) suggested that larvae from smaller eggs or larvae that had depleted yolk reserves were more active and dispersed more readily. McManus & Mason (1983) suggest that physical factors probably exert greater control of the extent of dispersal than size and quality of individuals. Our technique of using QIEP to quantify protein levels in individual animals provides an opportunity to examine the nutritional status of dispersing larvae. Using the wind tunnel of Carde & Hageman (1979) to induce dispersal behavior of neonates, we have begun making direct measurements of  $Vt$  of larvae which disperse as well as those that remain on the platform in the airstream.

#### SUMMARY

We are utilizing a unique approach to examine the influence of nutritive parameters on the population biology of the gypsy moth by examining the major nutrient storage system in insects, the serum and yolk storage proteins. By development of specific antibodies for the major serum storage proteins, vitellogenin, lipophorin, and arylphorin, and the ovarian-produced egg-specific protein, we can examine changes in the titer and the profiles of these proteins during development, and determine the influence of stress factors such as the change in diel periodicity of larvae, and influence of leaf polyphenols such as tannin, on the quantity and quality of these proteins. One of the advantageous features of our study is the ability to obtain hemolymph samples for analyses of storage proteins without sacrificing the insect. This allows us to compare the profiles of prepupae of the previous generation which are diagnostic of the major pool of nutrient reserves available to the progeny via the egg. This approach will permit an examination of the influence of events occurring in the previous generation on fitness (nutritional) factors which are important in the survival, dispersal, and the dynamics of the succeeding generation. Interest in the identification of serum storage proteins is growing. Relatively few have been identified from a limited number of insect species, but our efforts will add at least five from the gypsy moth. We know of no other research group, however, that has begun an intensive study of the role of storage proteins in biological and behavioral parameters relating to population quality or population trends. The gypsy moth lends itself as an excellent model for such a study, because of the importance of nutritional status as it relates to behavior, dispersal, and host anti-herbivore responses. Equally exciting to us is the potential of using data generated from immunoelectrophoresis to develop discriminant functions to predict population trends.

Discriminant function analysis of biochemical parameters has not yet been applied to assess a physiological behavioral class in insects.

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#### LITERATURE CITED

- AGUI, N., M. TAKAHASHI, S. IZUMI & S. TOMINO. 1985. The relation between nutrition, vitellogenin, vitellin and ovarian development in the housefly, *Musca domestica*. *J. Insect Physiol.* 31: 715-722.
- BARBOSA, P. & W. BALTEMSWEILER. 1987. Phenotypic Plasticity and Herbivore Outbreaks. In: P. Barbosa and J. C. Schultz (Eds.), *Insect Outbreaks*. Academic Press, NY. Pp. 469-503.
- BARBOSA, P. & J. A. GREENBLATT. 1979. Suitability, digestibility and assimilation of various host plants of the gypsy moth, *Lymantria dispar* (L.). *Oecologia* 43: 111-119.
- BARBOSA, P., P. MARTINAT & M. WALDVOGEL. 1986. Effects of multiple plant species diets on the development and reproduction of the gypsy moth *Lymantria dispar* (L.). *Ecol. Ent.* 11: 1-6.
- CAPINERA, J. L. & P. BARBOSA. 1976. Dispersal of first instar gypsy moth larvae in relation to population quality. *Oecologia* 26: 53-60.
- CAPINERA, J. L. & P. BARBOSA. 1977. Influence of natural diets and larval density on gypsy moth, *Lymantria dispar* (Lepidoptera: Orgyiidae) egg mass characteristics. *Can. Entomol.* 109: 1313-1318.
- CAPINERA, J. L., P. BARBOSA & H. H. HAGEDORN. 1977. Food and volk depletion of gypsy moth eggs: Implications for population quality. *Ann. Entomol. Soc. Amer.* 70: 40-42.
- CARDE, R. T. & T. E. HAGAMAN. 1979. Behavioral response of the gypsy moth in a wind tunnel to air-borne enantiomers of disparlure. *Env. Entomol.* 8: 475-484.

- CHINO, H. R., G. H. DOWNER, G. R. WYATT & L. I. GILBERT. 1981. Lipophorins, a major class of lipoproteins of insect hemolymph. *Insect Biochem.* 11: 491.
- DADD, R. H. 1985. Nutrition: Organisms. In: G. A. Kerkut and L. I. Gilbert (Eds.). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Vol. 4. Pergamon, Oxford. Pp. 313-390.
- DETHIER V. G. 1987. Concluding Remarks. In: V. Labeyrie, G. Fabres & D. Lachaise (Eds.). *Insects-Plants. Proc. 6th Int. Symp. Insect-Plant Relationships (Pau 1986)*. Junk Publ., Dordrecht. Pp. 429-435.
- DE WORMS, C. G. M. 1983. Lymantriidae. In: J. Heath & A. M. Emmett (Eds.). *The Moths and Butterflies of Great Britain and Ireland*. Harley, Essex. Pp. 66-78.
- FERGUSON, C. C. 1978. The Moths of America North of Mexico. Fasc. 22.2. Noctuiodea, Lymantriidae. E. W. Classey Ltd., London, and the Wedge Entomological Research Foundation. 110 pp.
- HAGEDORN, H. H. & J. G. KUNKEL. 1979. Vitellogenin and vitellin in insects. *Annu. Rev. Ent.* 24: 475-505.
- HANSON, F. E. 1983. The Behavior and Neurophysiological Basis of Food Plant Selection by Lepidopterous Larvae. In: S. Amhad (Ed.). *Herbivorous Insects*. Academic Press, NY. Pp. 3-23.
- INDRASMITH, L. S., T. FURUSAWA, M. SHIKATA & O. YAMASHITA. 1987. Limited degradation of vitellin and egg-specific protein in *Bombyx* eggs during embryogenesis. *Insect Biochem.* 17: 539-545.
- IRIE, K. & O. YAMASHITA. 1980. Changes in vitellin and other yolk proteins during embryonic development in the silkworm *Bombyx mori*. *J. Insect Physiol.* 26: 811-817.
- IRIE, K. & O. YAMASHITA. 1983. Egg-specific protein in the silkworm *Bombyx mori*: Purification, properties, localization and titre changes during oogenesis and embryogenesis. *Insect Biochem.* 13: 71-80.
- ISUME, S., S. TOMINO & H. CHINO. 1980. Purification and molecular properties of vitellin from the silkworm, *Bombyx mori*. *Insect Biochem.* 10: 199-208.
- KAWOYIA, J. K., E. O. OSIR & J. H. LAW. 1986. Physical and chemical properties of microvitellin, a protein from the egg of the tobacco hornworm, *Manduca sexta*. *J. Biol. Chem.* 261: 10844-10849.
- KUNKEL, J. G. 1988. Analytical Immunological Techniques. In: L. I. Gilbert & T. A. Miller (Eds.). *Immunological Techniques: Arthropods*. Springer Verlag. In press.
- KUNKEL, J. G. & J. H. NORDIN. 1985. Yolk Proteins. In: G. A. Kerkut & L. I. Gilbert (Eds.). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Vol. 1. Pergamon, Oxford. Pp. 83-111.
- LANCE, D. & P. BARBOSA. 1981. Host tree influences on the dispersal of first instar gypsy moths, *Lymantria dispar*. *Ecol. Ent.* 6: 411-416.

- LANCE, D. R., J. S. ELKINTON & C. P. SCHWALBE. 1986. Feeding rhythms of gypsy moth larvae: effect of food quality during outbreaks. *Ecology* 67: 1630-1654.
- LECHOWICZ, M. J. & Y. MAUFFETTE. 1986. Host preferences of the gypsy moth in eastern North American versus European forests. *Rev. Entom. Quebec* 32: 43-51.
- LEONARD, D. E. 1970a. Effects of starvation on behavior, number of larval instars, and developmental rate of *Porthetria dispar*. *J. Insect Physiol.* 16: 25-31.
- LEONARD, D. E. 1980b. Intrinsic factors causing qualitative changes in populations of *Porthetria dispar* (Lepidoptera: Lymantriidae). *Can. Ent.* 102: 239-249.
- LEONARD, D. E. 1971. Air-borne dispersal of larvae of the gypsy moth and its influence on concepts of control. *J. Econ. Entomol.* 64: 638-41.
- LEONARD, D. E. 1974. Recent developments in ecology and control of the gypsy moth. *Annu. Rev. Ent.* 19: 197-229.
- LEONARD, D. E. 1981. Bioecology of the gypsy moth. In: C. C. Doane and M. L. McManus (eds.). *The Gypsy Moth: Research Toward Integrated Pest Management*. US Dept. Agric. Tech. Bull. 1584. Pp. 9-29.
- LEONARD, D. E. 1988. The browntail-moth, *Euproctis chryorrhoea* (Lepidoptera: Lymantriidae) on Cape Cod, Massachusetts. In: *Ecology and Management of Exotic Species*. U. S. Dept. Interior, George Wright Soc. In press.
- LEVRNBOOK, L. 1985. Insect Storage Proteins. In: G. A. Kerkut & L. I. Gilbert (Eds.). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Vol. 10. Pergamon, Oxford. Pp. 307-346.
- MASON, C. J. & M. L. MCMANUS. 1981. Larval dispersal of the gypsy moth. In: C. C. Doane and M. L. McManus, (Eds.). *The Gypsy Moth: Research toward Integrated Pest Management*. Chapt. 4. US Dept. Agric. Tech. Bull. 1584: Pp. 161-202.
- MCMANUS, M. L. 1973. The role of behavior in the dispersal of newly hatch gypsy moth larvae. US Dept. Agric. For. Serv. Res. Pap. NE 267. 10 p.
- MCMANUS, M. L. & C. J. MASON. 1983. Determination of the settling velocity and its significance of larval dispersal of the gypsy moth. *Env. Entomol.* 12: 270-272.
- MONTGOMERY, M. E. 1982. Life-cycle nitrogen budget for the gypsy moth, *Lymantria dispar*, reared on artificial diet. *J. Insect Physiol.* 28: 437-442.
- MULLINS, D. E. & D. G. COCHRAN. 1983. Nitrogen Metabolism. In: R. G. H. Downer and H. Laufer (Eds.). *Invertebrate Endocrinology*. Volume I. Liss, NY. Pp. 451-464.
- MUNN, E. A. & G. D. GREVILLE. 1969. The soluble proteins of developing *Calliphora erythrocephala*, particularly calliphorin and similar proteins in other insects. *J. Insect Physiol.* 15: 1935-1950.

- ONO, S.-E., H. NAGAYAMA & K. SHIMURA. 1975. The occurrence and synthesis of female- and egg-specific proteins in the silkworm, *Bombyx mori*. *Insect Biochem.* 5: 313-329.
- PALLI, S. R. & M. LOCKE. 1987. Purification and characterization of three major hemolymph proteins of an insect, *Calpodus ethlius* (Lepidoptera: Hesperidae). *Arch. Ins. Bioch. Physiol.* 5: 233-244.
- PAN, N. L., W. J. BELL & W. TELFER. 1969. Vitellogenic blood protein synthesis by insect fat body. *Science* 164: 393.
- ROSSITER, M. D., J. C. SCHULTZ & I. T. BALDWIN. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69: 267-277.
- SCHAEFER, P. W. 1974. Population ecology of the brown-tail moth (*Euproctis chrysorrhoea* L., Lepidoptera: Lymantriidae) in North America. PhD Dissertation, University of Maine, Orono, 249 pp.
- SCHULTZ, F. C. & I. T. BALDWIN. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217: 149-151.
- SLANSKY, F. JR. & J. G. RODRIGUEZ. 1987. Nutritional Ecology of Insects, Mites, Spider, and Related Invertebrates: An Overview. In: F. Slansky, Jr. & J. R. Rodriguez (Eds.). *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*. Wiley & Sons, NY. Pp. 1-69.
- SLANSKY, F. JR. & J. M. SCRIBER. 1985. Food Consumption and Utilization. In: G. A. Kerkut & L. I. Gilbert (Eds.). *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*. Vol. 4. Pergamon, Oxford. Pp. 87-163.
- STORELLA, J. R., D. M. WOJCHOWSKI & J. G. KUNKEL. 1985. Structure and embryonic degradation of two native vitellins in the cockroach, *Periplaneta americana*. *Insect Biochem.* 15: 259-275.
- TOJO, S., T. BETCHAKU, V. J. ZICCARDI & G. R. WYATT. 1979. Fat body protein granules and storage proteins in the silkmoth *Hylophora cercropis*: Comparisons with calliphorin and manducin. *Insect Biochem.* 13: 601-613.
- TOJO, S., M. NATAGA & M. KOBAYASHI. 1980. Storage proteins in the silkworm *Bombyx mori*. *Insect Biochem.* 10: 284-303.
- TURUNEN, S. 1985. Absorption. In: G. A. Kerkut & L. I. Gilbert (Eds.). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Volume 4. Pergamon, Oxford. Pp. 241-278.
- VALENTINE, H. T., W. E. WALLNER & P. M. WARGO. 1983. Nutritional changes in host foliage during and after defoliation, and their relation to the weight of gypsy moth pupae. *Oecologia* 57: 298-301.

- WAGNER, T. L. & D. E. LEONARD. 1979. The effects of parental and progeny diet on development, weight gain, and survival of pre-diapause larvae of the satin moth, *Leucoma salicis* (Lepidoptera: Lymantriidae). Can. Ent. 111: 721-729.
- WAGNER, T. L. & D. E. LEONARD. 1979. Aspects of mating, oviposition, and flight in the satin moth, *Leucoma salicis* (Lepidoptera: Lymantriidae). Can. Ent. 111: 833-840.
- WAGNER, T. L. & D. E. LEONARD. 1980. Mortality factors of satin moth, *Leucoma salicis* (Lep.: Lymantriidae) in aspen forests in Maine. Entomophaga 25: 7-16.
- WALLNER, W. E. 1987. Factors affecting insect population dynamics: Differences between outbreak and non-outbreak species. Annu. Rev. Entomol 32: 317-340.
- WALLNER, W. E. & G. S. WALTON. 1979. Host defoliation: A possible determinant of gypsy moth population quality. Ann. Entomol. Soc. Amer. 72: 62-67.
- YAMASHITA, O. & K. IRIE. 1980. Larval hatching from vitellin-deficient eggs developed in male hosts of the silkworm. Nature 283: 385-386.
- ZHU, J., L. S. INDRASMITH & O. YAMASHITA. 1986. Characterization of vitellin, egg-specific protein and 30-k dalton protein from *Bombyx* eggs and their fates during oogenesis and embryogenesis. Bioch. Biophys. Acta. 882: 427-436.

SPATIAL RELATIONSHIPS OF DOUGLAS-FIR  
TUSSOCK MOTH DEFOLIATION WITHIN  
HABITAT AND CLIMATIC ZONES

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INTRODUCTION

The distribution and abundance of organisms are two resultants of the same dispersal process; changes in density over time are related to changes in distribution over time (Andrewartha and Birch 1954). Studies in population dynamics are often based on detailed changes in survival over time with a view to determining the regulatory factors of density. An alternate but just as valid approach may be to study the changes in spatial distribution over time. Comparing outbreak patterns with various environmental patterns could also provide information on regulatory factors. An important advantage of this approach is that regulatory factors detected through pattern comparisons can be tested experimentally through population introductions or changes in host species distributions within different habitat types. A second practical consideration is that modifications of the environment or host species may be indicated to reduce pest impact. The purpose of this study is to determine frequency of defoliation caused by Douglas-fir tussock moth, (Orgyia pseudotsugata (McDunnough), in British Columbia within Biogeoclimatic subzones, zones of climatic moisture deficit/surplus, and zones of growing degree days.

Differences between areas in soils, topography, climate, etc. result in new opportunities for organisms to become established and compete. Over time, a climax plant community develops which is characteristic for that area or site. In Europe, ecozones characterized by basic groups of coinhabiting plants are termed plant associations (Braun-Blanquet 1932), in western U.S.A. they are called habitat types (Daubenmire 1968), and in British Columbia they are called biogeoclimatic subzones (Krajina 1965, Pojar et al. 1987). Where topography is relatively smooth or gently rolling, environmental factors tend to change gradually. Habitat types and plant species form a gradient of change without distinct boundaries (Curtis and McIntosh 1951). In mountainous topography, environmental factors change rapidly and habitat types are distinct with narrow ecotones or boundaries. The forests of southern British Columbia fall into the latter situation and an ecosystem classification characterized by plant communities has proven quite useful in forest and land management.

The differences between habitat types also affect the next trophic level, i.e. the insect grazers, which are dependent for their

survival and well-being upon finding the correct species of host plants within a suitable climate. The fidelity of insects to specific habitat types varies considerably, just as the specificity of plants to certain habitat types varies from species to species. This habitat specificity which often applies to the distribution of species, also may apply to the distribution of outbreaks and result in a unique defoliation pattern (Shepherd 1977).

A complicating factor in determining the correspondence between defoliation and environmental patterns is the insect's ability to disperse. We assume that there is not a mass transport of insects which are capable, in themselves, of causing defoliation; i.e. there must be local build up in a favourable environment before defoliation can take place. This assumption is particularly valid for Douglas-fir tussock moth as the female moths are flightless and dispersal is restricted to short-distance travel by silk-drifting larvae (Mitchell 1979).

The best historical records of outbreak patterns of a forest insect in British Columbia are for Douglas-fir tussock moth. Outbreaks of this insect have, on the average, occurred somewhere in British Columbia at about nine-year intervals. High larval densities and the resultant defoliation usually lasts 1 to 4 years, then the population disappears until the next outbreak period. Defoliation, primarily on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in British Columbia, is at the northern limit of outbreaks for this insect which extends south through western United States into Arizona and New Mexico (Shepherd et al. in press). The spatial relationships between these outbreak and various environmental patterns can now be studied relatively easily because of recent developments in geographic information systems. Computer mapping analysis provides rapid quantification and integration of complex shapes from various map overlays.

#### LITERATURE REVIEW

Research on the relation between Lymantrid pests and climatic and habitat types has been carried out using many approaches, all different from those used in this paper for the tussock moth. In California, outbreaks of Douglas-fir tussock moth on white fir occurred more frequently in open stands on poor sites or ridge tops (Williams et al. 1979). Similar outbreak patterns of tussock moth occurred in the grand fir host type of Idaho (Stoszek et al. 1981) where, again, defoliation was greater on ridgetop sites with shallow soils. Stoszek theorized that high densities of biomass on poorer sites created a stress in the trees to which populations responded. Clendenen (1975) found some significant correlations between various climatic factors and population changes but did not establish any cause-effect relationships to explain the correlations.

The nun moth, *Lymantria monacha* L., is one of the worst defoliators of European forests. The longest period of time studied was that of Cramer (1962) for the Schwetzingen forest of West Germany beginning in 1844, comparing 3-year averages of temperature and

rainfall during critical insect activity periods. Outbreaks usually occurred when mean monthly temperatures during May and June for the preceding 3 years were above 32.6°C and total May precipitation during the same years averaged less than 8 mm. Only 22 years had these characteristics. Eight were build-up years and 11 were outbreak years leaving only three cases when an outbreak did not follow.

In a study of climate during a 20-year period of nun moth population build up within Moravia, Czechoslovakia, Svestka (1971, 1973, 1982) found that warm dry weather for 2 to 3 years during the insects active periods preceded outbreaks. Once underway, 1 year of cool wet weather was not enough to deter the outbreak. Populations were differentially affected because of differences in temperature and precipitation at different elevations. Many of the outbreaks were in Norway spruce, *Picea abies* (L.), stands of uniform age on dry southerly exposed soils. In Denmark, Bejer (1985) and Jensen (1985) also found outbreaks on spruce following a period of warm dry summers; the outbreaks only occurred in forests growing on dry sandy soils. Soil type was more important than the species of conifer present. Similar patterns occurred in the Netherlands with outbreaks starting on poor sandy soils after one or two hot summers (Grijpma et al. 1986). The collapse of the population in the Netherlands was attributed, in part, to asynchrony between nun moth larval emergence and bud burst of host trees (Steijlen et al. 1987). Svestka (1971) also stressed the importance of the bud burst/larval emergence synchrony.

Analysis of weather patterns in eight different areas of Russia (Benkevich 1964) and in Romania (Marcu 1970) led to the conclusion that gypsy moth, *Lymantria dispar* L., outbreaks occurred following cold winters and warm dry springs. A study of 35 years of records for New York city indicated a correlation between warm summer temperatures and upward population trends (Watt 1968). Heavy precipitation adversely affected infestations in Wisconsin (Braham and Witter 1978). In contrast, population fluctuations still occurred in Spain and Morocco even though the weather was favourable all the time (Romanyk 1973, Fraval 1986). Predictive equations from a climatic study of New England populations, when applied in Wisconsin, showed significant divergence between the projected and recorded patterns (Biging et al. 1980). A number of authors have emphasized that this insect is rather adaptable (Kyryeyeva 1973) and each population responds differently to a local climatic pattern (Kolybin et al. 1974) thus making correlation analysis among many populations difficult.

Site characteristics of outbreak and non-outbreak areas of gypsy moth were extensively studied in New England by Houston and Valentine and were previously reviewed (Houston 1981). In brief, susceptible sites are characterized by the following conditions: hot dry climates; excessively drained soils; open ridge tops or other exposed physiography; and open, scattered stands caused by logging, fires, storm drainage, etc., which allow for increased stand temperatures. In such conditions height growth is poor and crowns sparse and open. In contrast, resistant stands occur on good, moist sites with vigorous well-stocked stands of many species. The species of host trees in the stand are of less importance than the ecological conditions. Stand disturbances, which open up the crown, increase temperatures and

of areas within any designated zone and also areas of overlap and non-overlap between superimposed zones from 2 or more maps. The proportion of ecological or climatic zones which had sustained outbreaks were thus determined. During the analysis, more than 600 overlays, intersections, unions or subtractions of map polygons were made and areas of the unique polygons were determined to the nearest hectare. The percentage of the area defoliated was determined individually for each zone based on the total area available in that zone and histograms were prepared. No defoliation estimate was made unless there was at least 100 ha present per zone. A subsample of 586,913 ha was analyzed for cross comparisons and percentage defoliated was calculated based on the area falling within each cell. Circle diagrams of relative percentage were prepared by assigning a value of 100 to the cell with the highest percentage defoliated and values for other cells were calculated relative to the maximum.

#### RESULTS & DISCUSSION

A preliminary subsample of 23,466 ha was selected to test the usefulness of including forest composition information in the study. The area selected had the most detailed and recent defoliation information and was expected to result in the best correspondence between forest composition and percentage defoliated. A broad approach was initially taken (Table 1) but no consistent relationships could be determined from this analysis. A second, more detailed approach, was attempted in which the percentage of Douglas-fir present, in 20 or 30% classes, was compared to the percentage of area defoliated (Table 2). Again no differences were evident except where Douglas-fir was less than 20% or where lodgepole pine was dominant. The latter class only occurred at higher elevations above stands normally defoliated by tussock moth. The results of this initial analysis illustrated the problems which arose when two surveys were compared which had been mapped at different resolutions. The forest cover maps were made from aerial photographs and each small stand is detailed. In contrast, the defoliation maps only indicated blocks of forest within which there was some defoliation; defoliation history of each stand was not identified. As no consistent relationships could be found between defoliated area and forest composition, as depicted by the scale of maps available, this variable was deleted from further analysis.

Each outbreak period was initially recorded separately. It was thought that multiple outbreaks might be a better indicator of susceptibility than single outbreaks. When compared to a random distribution of expected frequency of outbreaks (Table 3), there was a significant difference. There were more stands with two outbreaks and fewer with only one outbreak than would be expected due to random chance; this indicated that some stands were more susceptible than others. However, the distribution between biogeoclimatic subzones and climatic zones were essentially the same for both one and two periods. As an example, the distribution between growing degree zones is given in Figure 2. Therefore, subsequent analysis was carried out

Table 1. Percentage of area defoliated and non-defoliated in stands in which the presence or absence of Douglas-fir was indicated on forest cover maps within Douglas-fir and Ponderosa pine Biogeoclimatic Zones

Biogeoclimatic zone	Douglas-fir >20%		Douglas-fir <20%	
	Defoliated	Non defoliated	Defoliated	Non defoliated
Interior Douglas-fir	16	44	8	32
Ponderosa Pine Bunch Grass	10	12	17	61

Table 2. Percentage of area defoliated within stands of different composition

Stand Composition	Area ha	Defoliated ha	Defoliated %
D.-fir <sup>1</sup> >80%	5099	1149	23
D.-fir 50-80%, P. pine 20-50%	1602	456	28
P. pine >50-80%, D. fir 20-50%	2034	484	24
L. pine 50-80%, D. fir 20-50%	670	1	0
D.-fir <20%	14227	1811	13
	23632		

<sup>1</sup> D.-fir = Douglas-fir, P. pine = Ponderosa pine, L. pine = Lodgepole pine.

Table 3. Comparison of the frequency of outbreaks of the Douglas-fir tussock moth

Number of periods in which outbreaks occurred within each 100-ha unit	Expected frequency by random chance. # of 100-ha units	Observed number which occurred. # of 100-ha units
0	4332	4345
1	457	432
2	24	36
3	9	11
$\chi^2 = 7.81, p_2 = .027$		

using one overlay amalgamated from all outbreaks as this provided a much bigger sample base. Any stand that had been defoliated in one or more periods was considered to have sustained an outbreak. Of the total defoliated area, 90% had been defoliated once, 8% defoliated twice, and 2% defoliated three times. Even though multiple outbreaks had been recorded in a region with the same place name, exact geographical overlaps were not common.

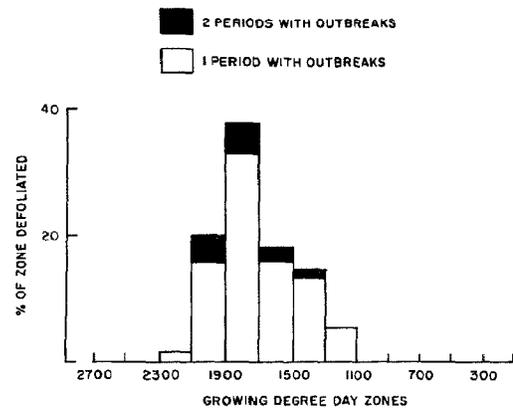


Figure 2. Percentage of stands defoliated within zones of accumulated degree-days above 5°C during the growing season. Stands defoliated in one and two separate outbreak periods are illustrated.

The biogeoclimatic subzones had been subdivided on the maps into variants and subvariants. These were initially kept separate, but the reduction in data for any one subdivision was too great to retain confidence in the sample. Therefore, the data was accumulated to the subzone level. An example of an overlay of outbreaks for one

biogeoclimatic map is presented in Figure 3.

The percent area of each biogeoclimatic subzone defoliated during at least 1 outbreak period is given in Table 4. The order of listing in this table follows a progression from the cool moist forests of the Engelmann Spruce Subalpine Fir subzone (ESSF) down to the hottest and driest Ponderosa Pine Bunch Grass subzone (PPBG) at valley bottom. The PPBGa subzone is essentially a grassland with small clumps of Ponderosa pine mixed with lesser amounts of Douglas-fir. Of the total area, 4.8% had been defoliated, but because Douglas-fir makes up so little of the area, a much larger proportion of the Douglas-fir present was probably defoliated (Table 4).

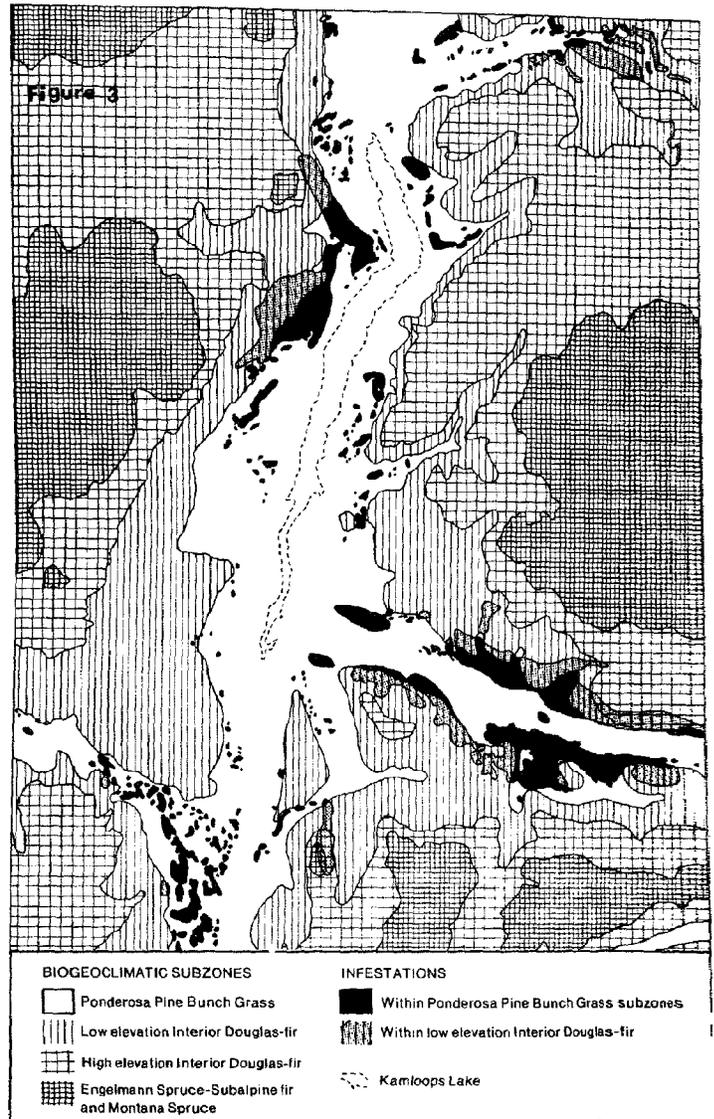
Table 4. Percentage of area defoliated within biogeoclimatic subzones

Biogeoclimatic subzone	% Defoliated	Number of 100 ha units
Cool and Moist Subalpine		
ESSF <sub>e to p</sub>	0 d <sup>1</sup>	458
ESSF <sub>d</sub>	.2 d	222
MS <sub>b</sub>	0 d	450
MS <sub>c</sub>	.2 d	1244
ICH	0 d	184
IDF <sub>b</sub>	.9 d	2081
IDF <sub>d</sub>	.5 d	432
IDF <sub>j</sub>	1.6 d	325
IDF <sub>a</sub>	8.6 b	1824
IDF <sub>c</sub>	12.7 b	144
PPBG <sub>d</sub>	20.3 a	974
PPBG <sub>a</sub>	4.8 c	902
Hot and Dry Valley Bottom		

<sup>1</sup>Values with the same letter are not significantly different,  $p \leq .05$ .

The largest percentage defoliated occurred in the next subzone, PPBGd. This subzone consists of more forest than grassland but, Douglas-fir is still not the dominant species. A defoliated area of 20.3% means that a high proportion of Douglas-fir had again suffered defoliation. The difference in percentage defoliated between PPBGa and PPBGd may reflect the amount of Douglas-fir present; the susceptibility to defoliation may be equally high in both subzones.

At elevations above the ponderosa pine forest are many Interior Douglas-fir subzones. They make up the largest block of forest within these valleys, but it is only the lowest stands which have had significant area defoliated (IDFa and IDFc). Above those stands, only an insignificant amount of defoliation has occurred and some of these records probably reflect earlier mapping inaccuracies. The standard



error of proportion is indicated by a vertical bracket on the histogram of percentage of area defoliated within biogeoclimatic subzones (Fig. 4).

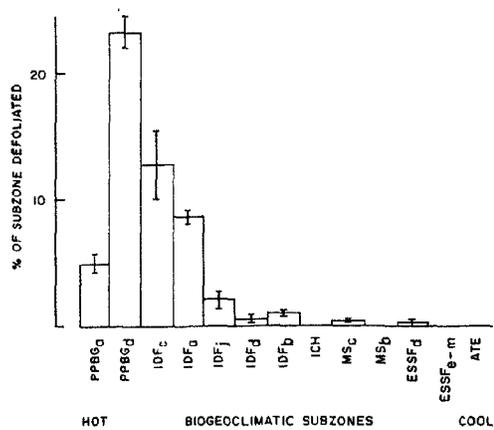


Figure 4. Histogram of percent area defoliated within biogeoclimatic subzones. Brackets indicate standard errors of proportion.

The percentage defoliated for each climatic moisture deficit zone is illustrated in Figure 5. About 1% of the area in the driest zone (-500 to -400 mm) was defoliated. This zone covers about the same area as PPBGa and probably also had a low percentage defoliated because of the lack of Douglas-fir. The highest amount defoliated occurred in the next zone (-400 to -300 mm); the percentage gradually decreased with succeeding zones. There was almost no defoliation in zones with a positive water balance.

The percentage defoliated for each zone of growing degree days is illustrated in Figure 6. The distribution of percentage defoliated among zones was nearly symmetrical with the peak being in the 1700 D° zone. The histograms of Figures 5 to 7 were based on an identical land base and therefore covered the same range of

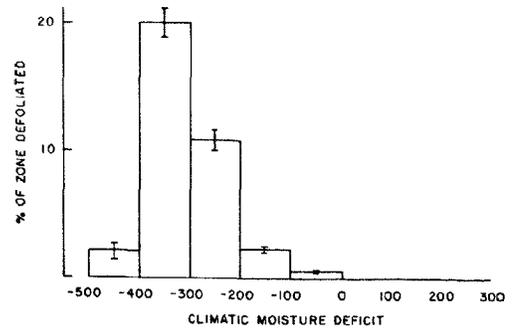


Figure 5. Histogram of percent area defoliated within climatic moisture deficit zones. Brackets indicate standard errors of proportion.

environmental conditions. Choices of class sizes by the different cartographers made direct comparison of these histograms difficult and statistical tests invalid.

Cross comparisons of the relative percentage defoliated by two ecological or climatic classifications are illustrated by circle diagrams in Figures 7 to 9. These showed that the PPBCd and IDFa zones had the greatest amount defoliated and, within those zones, the percentage increased with increasing climatic moisture deficits to -300 to -400 mm. In contrast, when the PPECa zone was divided into growing degree day zones, the maximum defoliated was not in the hottest zone but in the moderate 1500 to 1700 and 1700 to 1900 D° zones. Above 2300 or below 1100 D° outbreaks rarely occurred. Distribution of outbreak incidence was significantly different from the average for central cells (Figs. 8 and 9) of both the climatic moisture deficit and growing degree day cross classifications within biogeoclimatic subzones ( $\chi^2$  test,  $p < .001$ ). This indicates that the Douglas fir tussock moth usually rises to outbreak levels within moderate temperature zones, but within a moisture gradient, outbreaks occur most frequently in the driest zone available which contains Douglas fir.

This study provides information of the environmental requirements and limitations for outbreaks of this pest species in British Columbia. It would be useful to compare these results with similar studies carried out where this insect defoliates different host species and

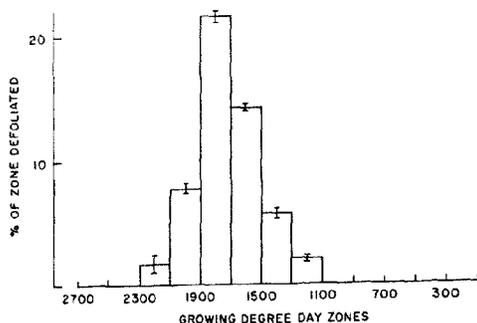
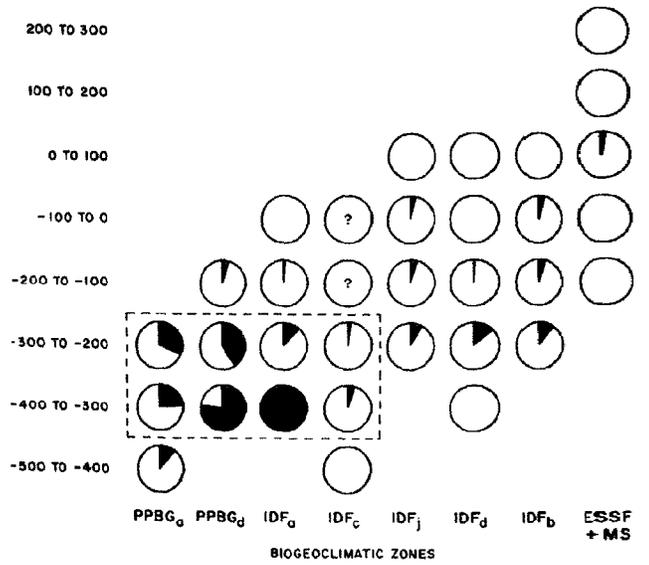


Figure 6. Histogram of percent area defoliated within zones of accumulated degree-days during the growing season. Brackets indicate standard errors of proportion.

where the frequency and synchrony of outbreak cycles is different (Shepherd, in press). It also provides a hypothesis for experimental testing of survival rates of seeded populations.

An understanding of the role of temperature and moisture in the regulation of population trends and in the location of outbreaks provides the basis for predictions of population changes and damage which can be expected following climatic shifts because of atmospheric pollution or possible greenhouse effects. Such an understanding is also useful when making forest management decisions regarding which tree species to plant, which spacing densities to use, the expected need for pest control applications, and other silvicultural treatments (Shepherd and Otvos 1986).

A practical outcome of this study is that a relatively small climatic zone within the range of Douglas-fir has been identified as being susceptible to outbreaks; this zone can be defined on maps and recognized in the field through the plant communities present. This is an important step in a pest management system now operating in British Columbia (Shepherd and Otvos 1986) which provides for the early detection of rising populations by monitoring with pheromone traps within the susceptible zone. An early treatment of threatening populations with an effective specific virus can then be applied to prevent outbreaks from reaching damaging levels.



. Cross comparison of the incidence of defoliation between biogeoclimatic zones and climatic moisture deficits. Maximum area of defoliation was assigned a value of 100 and those for other cells were assigned relative to the maximum. Sample base: 586,913 ha. Box highlights cells used in  $\chi^2$  test. "?" indicates data not usable.

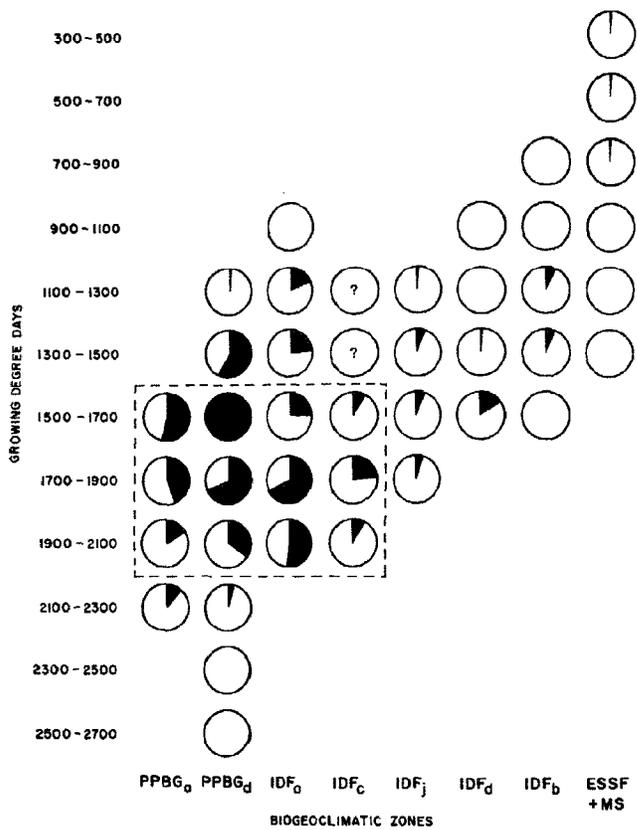


Figure 8. Cross comparison of the incidence of defoliation between biogeoclimatic zones and accumulated growing degree-days. Maximum area defoliated was assigned a value of 100 and those for other cells were calculated relative to the maximum. Sample base: 586,913 ha. Box indicates cells used in  $\chi^2$  test. "?" indicates data not usable.

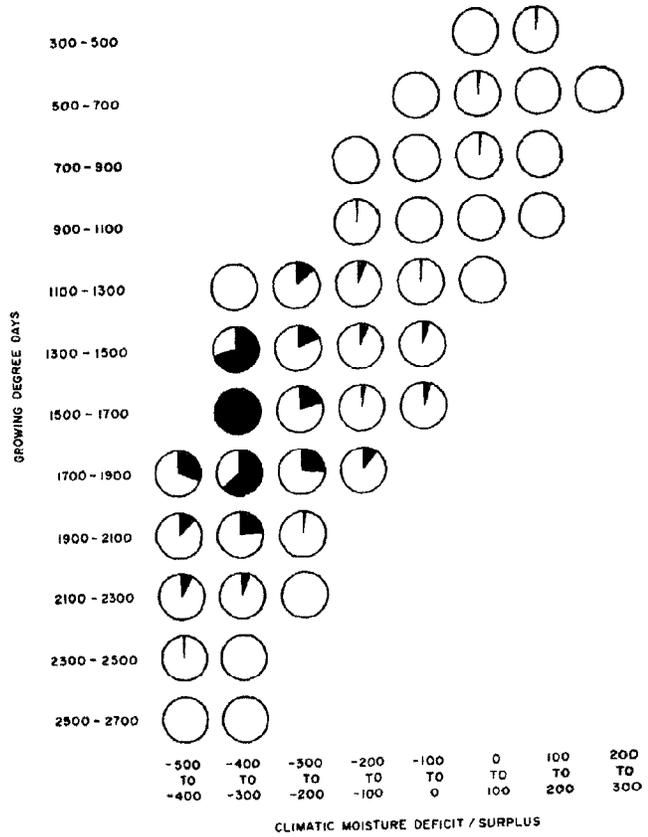


Figure 9. Cross comparison of the incidence of defoliation between zones of climatic moisture deficit and accumulated growing degree days. Maximum area defoliated was assigned a value of 100 and those for other cells were calculated relative to the maximum. Sample base: 586,913 ha.

## SUMMARY

Six outbreaks of Douglas-fir tussock moth mapped in British Columbia were overlaid on forest habitat and climatic maps to determine correspondence between defoliated areas and different ecozones. Analysis using a geographic information system indicated that outbreaks occurred most frequently in the Ponderosa-Pine Bunch grass a and d Subzones and the Interior Douglas-fir a and c Subzones. Within these stands, defoliation most often occurred where temperatures were moderate (1500 to 1900 accumulated degree-days per growing season) and where climatic moisture deficits were extreme (-300 to -500 mm per growing season). Identification of susceptible forest communities is useful for pheromone trap monitoring to detect rising populations. Knowledge of climatic conditions most prone to outbreaks is useful to understand the dynamics of the pest and to predict where and when defoliation may occur under current or future modified stand and climatic conditions.

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## LITERATURE CITED

- ANDREWARTHA, H.G. and BIRCH, L.C. 1954. The distribution and abundance of animals. Univ. Chicago Press. 782 p.
- BEJER, B. 1985. Nun moth (*Lymantria monacha* L.) outbreaks in Denmark and their association with site factors and climate. *in* Bevan, D. and Stoakley, J.T. Site characteristics and population dynamics of lepidopteran and hymenopteran forest pests. Proceed. IUFRO Conf., Dornock Scotland 1-7 Sept. 1980.
- BENKEVICH, V.I. 1964. Information on the forecast of the widespread appearance of *Ocueria dispar* (Lepidoptera, Liparidae). VIII The widespread appearance of *Ocueria dispar* and their forecast in the forests of Altai Krai in eastern Kazakhstan. [In Russian]. Tr Orekhovo-Zuevskogo Pedagog Inst. 3: 83-95.
- BESS, H.A., SPURR, S.H. and LITTLEFIELD, E.V. 1947. Forest site conditions and the gypsy moth. Harvard Forest Bull. 22: 1-56.
- BIGING, G.S., GIESE, R.L. and NORDHEIM, E.V. 1980. Gypsy moth, *Lymantria dispar*, population simulation for Wisconsin, U.S.A. For. Sci. 26: 710-724.
- BRAHAM, R.R. and WITTER, J.A. 1978. Consumption of foliage of juvenile and mature red oak trees by late instar gypsy moth larvae. J. Econ. Ent. 71: 425-426.

- BRAUN-BLANQUET, J. 1932. Plant sociology, the study of plant communities (Translated by G.D. Fuller and H.S. Conrad). McGraw-Hill, New York. 439 p.
- CLENDENEN, B. 1975. Tussock moth, Orgyia pseudotsugata (McD), outbreaks and climatic factors: a correlation analysis. USDA For. Serv. Coop Aid Agreement. Coll. For., Univ. Wash., Seattle, Prelim. Rep. 60 p.
- CURTIS, J.T. and MACINTOSH, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.
- CRAMER, H.H. 1962. The possibility of forecasting outbreaks of forest pests with the aid of meteorological data [In German] Publications of the Forestry Department of Albert Ludwig University, Freiburg in Breisgau p. 238-245.
- DAUBENMIRE, R. 1968. Plant communities. Harper and Row. New York. 300 pp.
- FORRESTER, M.W. and VANDERWALL, K. 1987. Implementation of a GIS on a national forest: operation realities. p. 187-195. In second annual international conference on geographic information systems. San Francisco, Calif. Oct. 26-30, 1987.
- FRAVAL, A. 1986. Population dynamics of Lymantria dispar L. (Lep., Lymantriidae) in cork oak forests of western Morocco: influencing factors of climate, entomophagous organisms and of man. [In French]. Zeitschrift fuer Angewandte Entomologia 102: 38-52.
- GOLUBEV, A.V. and SEMEVSKY, F.N. 1969. Distribution of an endemic population of the gypsy moth. [in Russian]. Zool. Zhur. 48: 850-859.
- GRIJMA, P., REYBROEK, P.A.F.M., RAAYMAKERS, P.A.W.M. and VLAK, J.M. 1986. The nun moth in 1984 and 1985; outbreak, control and research [in Dutch]. Nederlands Bosbouw tijdschrift 58: 58-67.
- HARRIS, J.W.E., DAWSON, A.F. and BROWN, R.G. 1985. The Douglas-fir tussock moth in British Columbia. Can. For. Serv., Pac. For. Cent., Inf. Rep. BC-X-268. 16 pp.
- HOUSTON, D.R. 1981. Forest stand relationships. in Doane, C.C. and M.L. McManus. The gypsy moth: research toward integrated pest management. U.S.D.A., Forest Service Tech. Bull. 1584. pp. 267-297.
- JENSEN, T.S. 1985. Outbreak and latency populations of nun moth, Lymantria monacha L. Mitteilungen der Deutschen Gesellschaft fur Allgemeine and Angewandte Entomologie 41: 240-243.

- KOLYBIN, V.A., KIREEVA, I.M. and ZELMSKAYA, L.M. 1974. Biological bases of population dynamics of the gypsy moth Porthetria dispar Part 1 Fecundity. [In Russian]. Vestn Zool. 2: 61-65.
- KRAJINA, V.J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecol. West. N. Am.: 1-17.
- KYRYEYEVA, I. 1973. Some characteristics of the Porthetria dispar population in the Kherson and transcarpathian regions. Dopov Akad Nauk UKR RSR Ser B. Heol Heofig Khim Biol 35: 565-568.
- MARCU, O. 1970. The role of climatic factors in the distribution and epidemiology of Lymantria dispar. [In German] Bulstinul Institutului Politehnic Brasov, B12: 111-116.
- MITCHELL, R.G. 1979. Dispersal of early instars of the Douglas-fir tussock moth. Ann. Ent. Soc. Amer. 72: 291-297.
- PARKS, B.D., SIMMONS, G.A. and GAGE, S.H. 1987. Assessing statewide risks of gypsy moth infestation using a geographic information system (GIS). p. 50-55. In Michigan Forest Pest Report: 1985-86. Mich. Cooperative Forest Pest Manage. Prog. Annual Rept. 87-1.
- PATOCKA, J. and CAPEK, M. 1971. Population changes of certain oak defoliators in Slovakia. Acta Inst. Forest Zvolen 1971, 461-485.
- POJAR, J., KLINKA, K. and MEIDINGER, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119-154.
- ROMANYK, M. 1973. Gradations of Lymantria dispar L. in Spain. [In French]. Zastita Bilja 24: 285-288.
- SHEPHERD, R.F. 1977. A classification of western Canadian defoliating insects by outbreak spread characteristics and habitat restriction. in Kulman, H.M. and H.C. Chiang. Insect ecology. Univ. of Minnesota, Agric. Exp. Station Tech. Bull. 310. p. 80-88.
- SHEPHERD, R.F. and OTVOS, I.S. 1986. Pest management of Douglas-fir tussock moth: procedures for insect monitoring, problem evaluation and control actions. Can. For. Serv., Pacific Forestry Centre, Inf. Rpt. BC-X-270. 14 p.
- SHEPHERD, R.F., BENNETT, D.D., DALE, J.W., TUNNOCK, S., DOLPH, R.F. and THIER, R.W. (in press). Evidence for synchronized cycles in outbreak patterns of Douglas-fir tussock moth, Oryzia pseudotsugata (McDunnough), (Lepidoptera: Lymantriidae). Can. Ent.
- STEIJLEN, I.M., SCHURING, W. and GRIJPMAN, P. 1987. Collapse of the nun moth outbreak in 1986; an analysis of possible causes [In Dutch]. Nederlands Bosbouwtijschrift 59: 5-12.

- STOSZEK, K.J., MIKA, P.G., MOORE, J.A. and OSBORNE, H.I. 1981. Relationships of Douglas-fir tussock moth defoliation to site and stand characteristics in northern Idaho. *Forest Science* 27: 431-442.
- SVESTKA, M. 1971. The influence of climatic factors and natural enemies in the spring of 1967 on the population dynamics of Lymantria monacha in Norway Spruce stands in SW Moravia. [In Czechoslovakian]. *Prace Uyakumneho Ustavu Lesniho Hospodarstvi a Myslivosti* 40: 17-34.
- SVESTKA, M. 1973. Influence of weather on the population dynamics of nun moth and application of meteorological data in forecasting its occurrence [In Czechoslovakian]. *Inst. for Scientific and Tech. Inf., Czechoslovakian Academy of Agriculture* 19: 1131-1150.
- SVESTKA, M. 1982. Evaluation of the changes in numbers of the nun moth (Lymantria monacha L.) in the framework of the biogeosystem with regard to climatic conditions. *Prace Uyakumneho Ustavu Lesniho Hospodarstvi a Myslivosti* 61: 195-212.
- WATT, K.E.F. 1968. *Ecology and resource management*. McGraw-Hill, New York. 450 pp.
- WILLIAMS, C.B. Jr., WENZ, J.M. DAHLSTEN, D.L. and NORICK, N.K. 1979. Relation of forest site and stand characteristics to Douglas-fir tussock moth (Lepidoptera: Lymantriidae) outbreaks in California. *Bull. Soc. Ent. Suisse* 52: 297-307.