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# Spatial Relationships between Western Blackheaded Budworm (*Acleris gloverana)* (Lepidoptera: Tortricidae) Defoliation Patterns and Habitat Zones on Vancouver Island, British Columbia

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ABSTRACT The western blackheaded budworm (*Acleris gloverana* (Walshingham)) is a cyclic defoliator of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). At least seven blackheaded budworm outbreaks have occurred in British Columbia and severe defoliation has been recorded during five of these outbreaks on Vancouver Island. Spatial patterns of past blackheaded budworm outbreaks on the Island were examined by overlaying them with biogeoclimatic units, elevation, and climate data to identify and rate stands susceptible to outbreaks. Three variants of the Coastal Western Hemlock biogeoclimatic zone, in decreasing order of susceptibility, were CWHvm1, CWHvm2, and CWHvh1. In addition, small areas of the Mountain Hemlock zone (MHmm1) were also defoliated. Only a small area on the northern tip of Vancouver Island was defoliated during three of the four outbreaks. Based on these results, we recommend locating permanent sentinel pheromone monitoring traps in the repeatedly defoliated area on northern Vancouver Island. We also recommend conducting additional larval sampling in the CWHvm1, CWHvm2, and CWHvh1 biogeoclimatic units to confirm rising pest populations based on pheromone trap catches so that control options may be examined prior to serious damage to the stands.

THE WESTERN BLACKHEADED budworm (*Acleris gloverana* (Walshingham)) is a cyclic defoliator of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) in southern Alaska, British Columbia, and Washington State. Other hosts, such as amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Forbes), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), white spruce (*Picea glauca* (Moench) Voss), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), can also be attacked and defoliated when large-scale outbreaks occur in mixed stands with western hemlock (Furniss and Carolin 1977). Periodic outbreaks of this budworm result in severe defoliation in the western hemlock zones of North America. At least seven blackheaded budworm outbreaks have occurred in British Columbia this century. Severe defoliation has been recorded and mapped during five of these outbreaks on Vancouver Island (Anonymous 1972). Examining spatial patterns of past outbreaks and overlaying them with biogeoclimatic units (Krajina 1965, Pojar et al. 1987), elevation, and available climate data will help to identify and rate susceptible habitats (Shepherd 1977, Borecky and Otvos 2000). Researchers can then identify areas where outbreaks are most likely to occur. It is in these stands that permanent pheromone trap sites can be established during low budworm population densities. Monitoring these trap catches will allow the detection of increasing insect populations before

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defoliation occurs. This is an essential component in the development of a pest management system for this species (Shepherd 1994) and is similar to one developed for the Douglas-fir tussock moth (Shepherd and Otvos 1986, Shepherd et al. 1989).

## Methods

Annual pest surveys conducted by the Forest Insect and Disease Survey (FIDS) of the Canadian Forestry Service (CFS), from the time it was established in 1936 until its dissolution in 1996, used a variety of methods to determine the presence and extent of insect and disease outbreaks. Prior to the 1960s, surveys were conducted in British Columbia (B.C.) using boat and ground patrols, and sporadically by aircraft. From the 1960s onward, insect defoliation was mapped annually, first by using fixed-wing aircraft, then later using a combination of fixed- and rotary wing aircraft. Outbreaks were later checked on the ground to verify the causal agents. Outlines of infestations were traced onto 1:250,000 scale topographic maps, producing an accurate assessment of pest activity from year to year.

The historical FIDS pest outbreak survey maps were digitized and compiled into a database for the entire Province of British Columbia. The digitizing and analysis was conducted using Environmental System Research Institute's (ESRI) geographic information system (GIS) software Arc/Info. Registration accuracy via root means squared (rms) was limited to under 0.005 for the electronic capture of historical survey maps. The initial map projection was Universal Transverse Mercator (UTM). As coverages from each 1:250,000 mapsheet were added together for each year, they were re-projected into the CFS-Pacific Region's standard Lambert Conformal Conic Projection. For this paper, we used historic maps from the Vancouver Island western blackheaded budworm outbreak database from 1941 to 1998.

There are some known gaps in this database and there are recognized limitations in obtaining and utilizing this digital information. Digitizing captures data with much higher positional precision than can be accurately obtained by manual mapping of insect infestations from the air. Surveys may also have gaps in infestation information because aerial mapping could not be carried out or because earlier outbreaks could have occurred in areas that were not accessible by road or water. Generalized infestation locations were indicated on maps, as happened for the 1955-1960 outbreak, and are not detailed enough for comparison with today's habitat, climatic or ecological maps (Fig. 1). Therefore, we restricted our studies to four of the five outbreaks on Vancouver Island by excluding the 1955-1960 outbreak from the analysis because of its lack of detail.

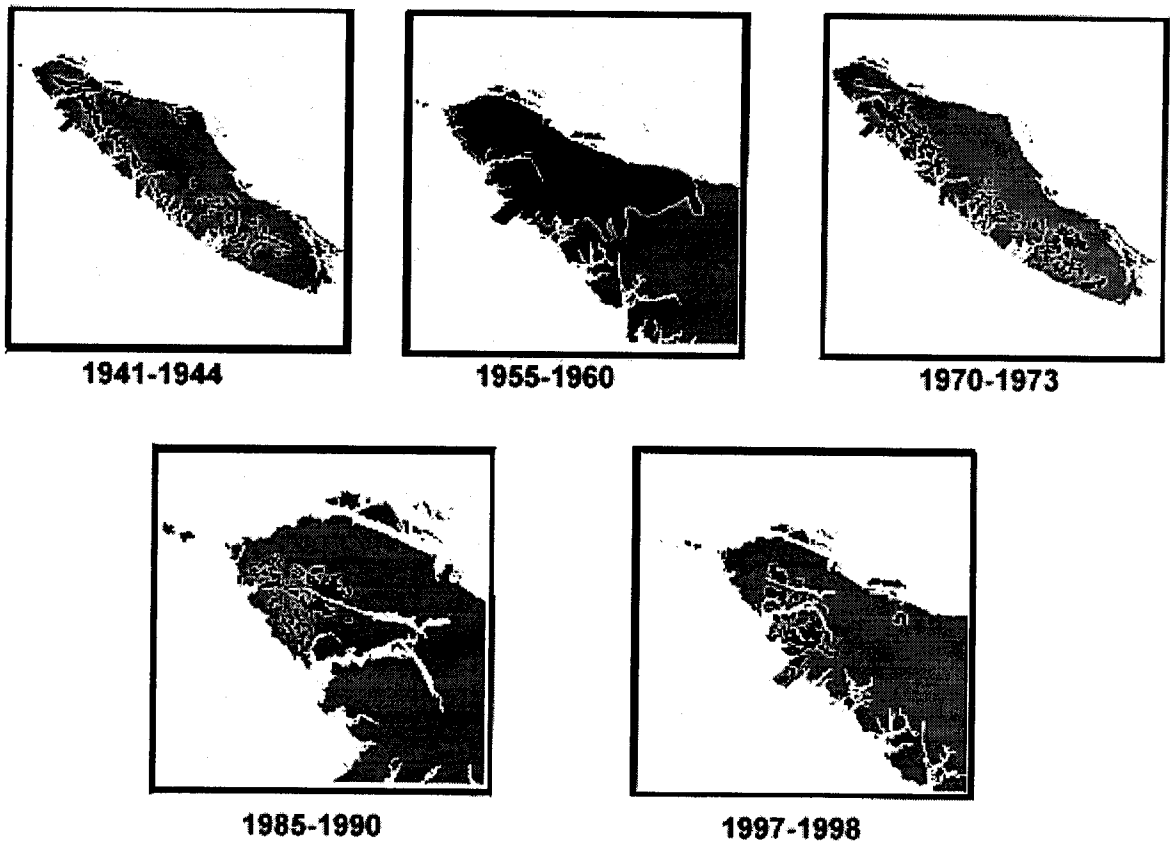


**Figure 1. Outbreaks of the western blackheaded budworm on Vancouver Island (1941 to 1998).**

The 1941-1944 and 1970-1973 outbreak data are less accurate than the data collected for the last two outbreaks; however, eliminating these would leave comparisons only for northern Vancouver Island and ignore the potential relationships with central and southern environments. Thus, the database we accepted may be less precise, but it is also less biased in comparison with the total range of environments on Vancouver Island that are capable of supporting outbreaks. The negative aspect of this approach is that generalization may lead to the inclusion of some areas or regions in the data set that have never experienced outbreaks. Although inferences cannot be accurately drawn at a small scale, we feel confident about making observations of the broader trends that are apparent.

The outbreaks were digitally compared with biogeoclimatic units on Vancouver Island, yielding a data set that summarizes defoliation for each zone. The biogeoclimatic zone classification system was developed by Krajina in the 1960s (Krajina 1965) and present zonal designations are based on the work of Pojar et al. (1987). This hierarchical system classifies the landscape into zones, sub-zones, and variants. The system integrates climate, soils, and vegetation to classify all of British Columbia's landscape. This classification is at a relatively fine scale and is closely related to the vegetation and climate of the Island. It also defines the habitats available to insect herbivores, and by comparing these zones to outbreak patterns, we can determine their susceptibility or risk of outbreak. The most recently released version of these biogeoclimatic zones (B.C. Ministry of Environment, Lands and Parks, ca. 1998/06/17) was adopted for this study and re-projected for the purposes of analysis. Biogeoclimatic zone codes are described in Table 1.

**Table 1. Description of biogeoclimatic zone codes**

| Code | Zone | Sub-zone and Variant |
|---|---|---|
| AT p | Alpine Tundra | Park |
| CWH xm1 | Coastal Western Hemlock | Eastern Very Dry Maritime |
| CWH xm2 | Coastal Western Hemlock | Western Very Dry Maritime |
| MH mm1 | Mountain Hemlock | Windward Moist Maritime |
| CWH mm1 | Coastal Western Hemlock | Sub-montane Moist Maritime |
| CWH mm2 | Coastal Western Hemlock | Montane Moist Maritime |
| **CWH vm1** | Coastal Western Hemlock | Sub-montane Very Wet Maritime |
| **CWH vm2** | Coastal Western Hemlock | Montane Very Wet Maritime |
| **CWH vh1** | Coastal Western Hemlock | Southern Very Wet Hyper-maritime |

## Results and Discussion

At least five western blackheaded budworm outbreaks are known to have occurred on Vancouver Island (Fig. 1). When maps of four of these outbreaks were prepared and compared by biogeoclimatic unit, an interesting trend emerged (Table 2).

**Table 2. Summary of western blackheaded budworm defoliation during four outbreaks on Vancouver Island by biogeoclimatic unit**

| Unit | 1941-1944 | | | 1970-1973 | | | 1985-1990 | | | 1997-1998 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Defoliated Area (ha) | % of Total Defoliation | % of Unit | Defoliated Area (ha) | % of Total Defoliation | % of Unit | Defoliated Area (ha) | % of Total Defoliation | % of Unit | Defoliated Area (ha) | % of Total Defoliation | % of Unit |
| AT p | 258 | 0.2 | 0.38 | 698 | 0.4 | 1.04 | 0 | 0.0 | 0.00 | 27 | 0.1 | 0.04 |
| CWHxm1 | 349 | 0.2 | 0.15 | 17 | 0.0 | 0.01 | 0 | 0.0 | 0.00 | 0 | 0.0 | 0.00 |
| CWHxm2 | 11,222 | 7.4 | 2.50 | 1,946 | 1.2 | 0.43 | 0 | 0.0 | 0.00 | 0 | 0.0 | 0.00 |
| MHmm1 | 8,703 | 5.7 | 2.50 | 17,506 | 10.7 | 5.03 | 0 | 0.0 | 0.00 | 235 | 0.5 | 0.07 |
| CWHmm1 | 2,275 | 1.5 | 1.61 | 4,242 | 2.6 | 3.00 | 0 | 0.0 | 0.00 | 0 | 0.0 | 0.00 |
| CWHmm2 | 6,073 | 4.0 | 2.65 | 15,207 | 9.3 | 6.64 | 0 | 0.0 | 0.00 | 0 | 0.0 | 0.00 |
| **CWHvm1** | **97,348** | **64.3** | **9.82** | **79,470** | **48.6** | **8.02** | **7,365** | **72.3** | **0.74** | **20,063** | **46.7** | **2.02** |
| **CWHvm2** | **20,248** | **13.4** | **5.25** | **43,577** | **26.6** | **11.30** | **241** | **2.4** | **0.06** | **8,043** | **18.7** | **2.09** |
| **CWHvh1** | **4,945** | **3.3** | **1.45** | **878** | **0.5** | **0.26** | **2,585** | **25.4** | **0.76** | **14,627** | **34.0** | **4.29** |
| Total | 151,421 | | | 163,540 | | | 10,191 | | | 42,995 | | |

During two of the outbreaks (1941 to 1944 and 1970 to 1973), defoliation occurred throughout the Island, including southern and central Vancouver Island, whereas the remaining two outbreaks (1985 to 1990 and 1997 to 1998) were restricted to the northern part of Vancouver Island. Furthermore, a fifth outbreak (1955 to 1960) was also restricted to the northern part of the Island, but for reasons given earlier, was excluded from the study.

There are several interesting points that are apparent when the four outbreaks and their distributions within biogeoclimatic units are compared. The two outbreaks (1941 to 1944 and 1970 to 1973) that occurred over the length of Vancouver Island were about the same size and, when combined, were about six times the size of the last two outbreaks combined (1985 to 1990 and 1997 to 1998) that occurred only on the northern tip of Vancouver Island (Table 2). There is a gradual increase in elevation of the Island going from North to South. The middle portion of the Island is generally higher and has a more varied biogeoclimatic unit distribution than the northern part of the Island (Fig. 2). Of the total area on Vancouver Island (approximately 3,190,000 ha), 313,173 ha (9.8%) has been defoliated at least once during the four outbreaks studied.

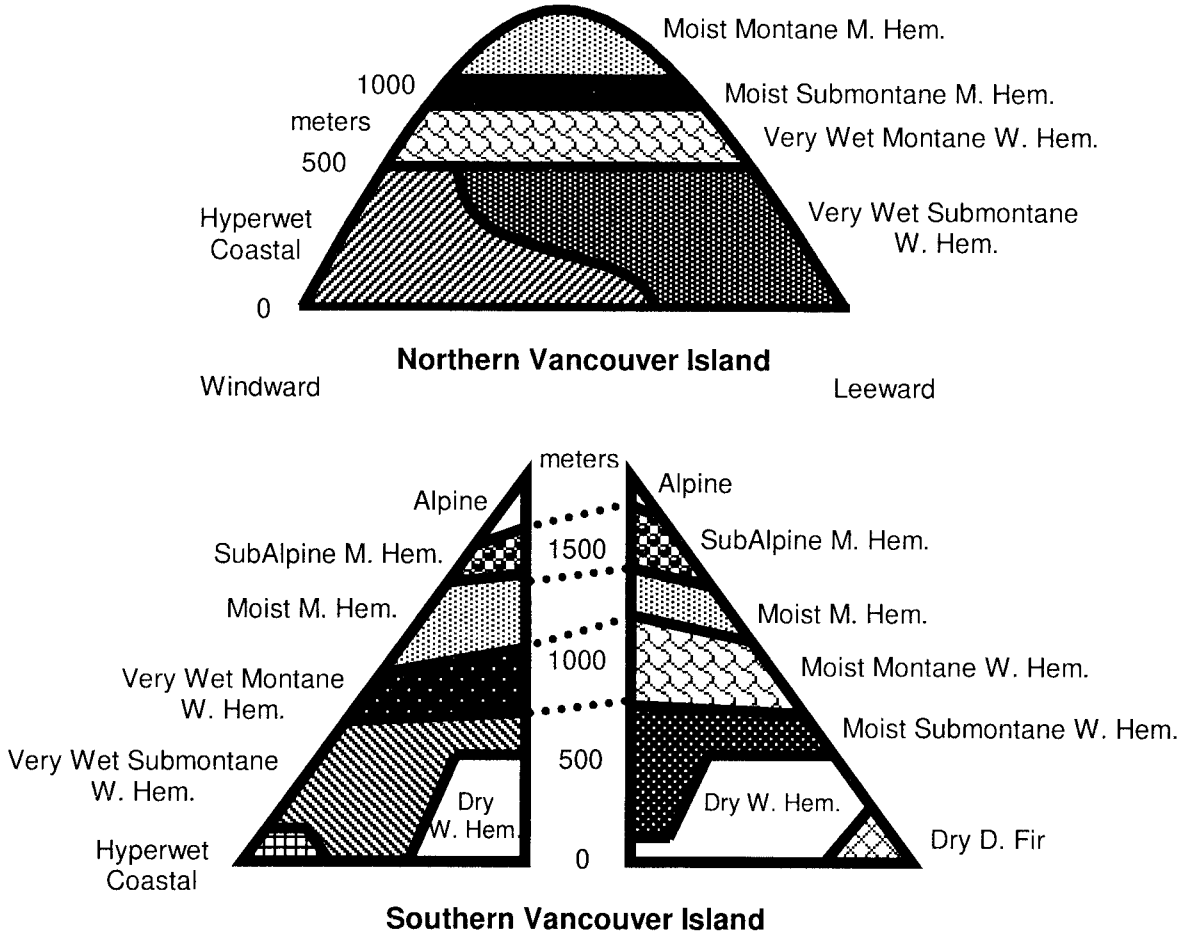


**Figure 2. Elevation and distribution of biogeoclimatic units on Vancouver Island.**

About 92% of all blackheaded budworm defoliation occurred in the Coastal Western Hemlock biogeoclimatic zone (CWH) with the remaining 8% in the windward moist maritime Mountain Hemlock zone (MHmm1) (Table 3, Fig. 3). Although the table shows that about 0.3% of the total outbreak area occurred in the Alpine Tundra biogeoclimatic zone, this is likely due to mapping error during aerial surveys as well as complications associated with broad ecotones between some biogeoclimatic zones. The distribution of defoliated stands within biogeoclimatic sub-zones was similar regardless of whether the outbreak occurred along the length of the Island or only on the northern tip of the Island. During the two outbreaks that covered the length of the Island, approximately 64% and 49% of the defoliation was in the CWHvm1 sub-zone during the 1941-1944 and 1970-1973 outbreaks, respectively (Table 2). Thirteen percent and 27% of the defoliation was in the CWHvm2 sub-zone during the same two outbreaks, respectively (Table 2).

**Table 3. Frequency and area (ha) of western blackheaded budworm outbreak occurrence by biogeoclimatic unit on Vancouver Island**

| Unit | N=1* (ha) | % of 1 Outbreak | N=2* (ha) | % of 2 Outbreaks | N=3* (ha) | % of 3 Outbreaks | N=4* (ha) | % of 4 Outbreaks | Cumulative Defoliation (ha) | % of Unit | % of Total Defoliated Area |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AT p | 843 | 0.30 | 70 | 0.23 | 0 | 0.00 | 0 | 0.0 | 913 | 1.36 | 0.3 |
| CWHxm1 | 365 | 0.13 | 0 | 0.00 | 0 | 0.00 | 0 | 0.0 | 365 | 0.15 | 0.1 |
| CWHxm2 | 12,146 | 4.33 | 511 | 1.67 | 0 | 0.00 | 0 | 0.0 | 12,658 | 2.82 | 4.0 |
| MHmm1 | 22,843 | 8.13 | 1,905 | 6.20 | 0 | 0.00 | 0 | 0.0 | 24,748 | 7.11 | 7.9 |
| CWHmm1 | 5,985 | 2.13 | 266 | 0.87 | 0 | 0.00 | 0 | 0.0 | 6,251 | 4.42 | 2.0 |
| CWHmm2 | 19,218 | 6.84 | 1,054 | 3.43 | 0 | 0.00 | 0 | 0.0 | 20,272 | 8.85 | 6.5 |
| **CWHvm1** | **138,766** | **49.41** | **19,619** | **63.88** | **1,158** | **93.63** | **366** | **92.8** | **159,909** | **16.14** | **51.1** |
| **CWHvm2** | **57,678** | **20.54** | **7,261** | **23.64** | **79** | **6.37** | **28** | **7.2** | **65,046** | **16.87** | **20.8** |
| **CWHvh1** | **22,985** | **8.18** | **26** | **0.08** | **0** | **0.00** | **0** | **0.0** | **23,011** | **6.74** | **7.3** |
| Grand Total | 280,829 | | 30,712 | | 1,237 | | 395 | | 313,173 | | |

* N = cumulative number of outbreaks

When these two earlier outbreaks were combined, 76% of the defoliation occurred in these two biogeoclimatic units (CWHvm1 and CWHvm2) compared with 67% of the defoliation in the two later outbreaks (Table 4). The main difference between the four outbreaks is that defoliation occurred in only three biogeoclimatic units on northern Vancouver Island (CWHvm1, CWHvm2, and CWHvh1) in the two later outbreaks. This is in contrast to the two earlier outbreaks where defoliation was distributed over several additional biogeoclimatic units that appear over the more mountainous central and southern Vancouver Island region, including one dominated by mountain hemlock (MH) (Table 4).

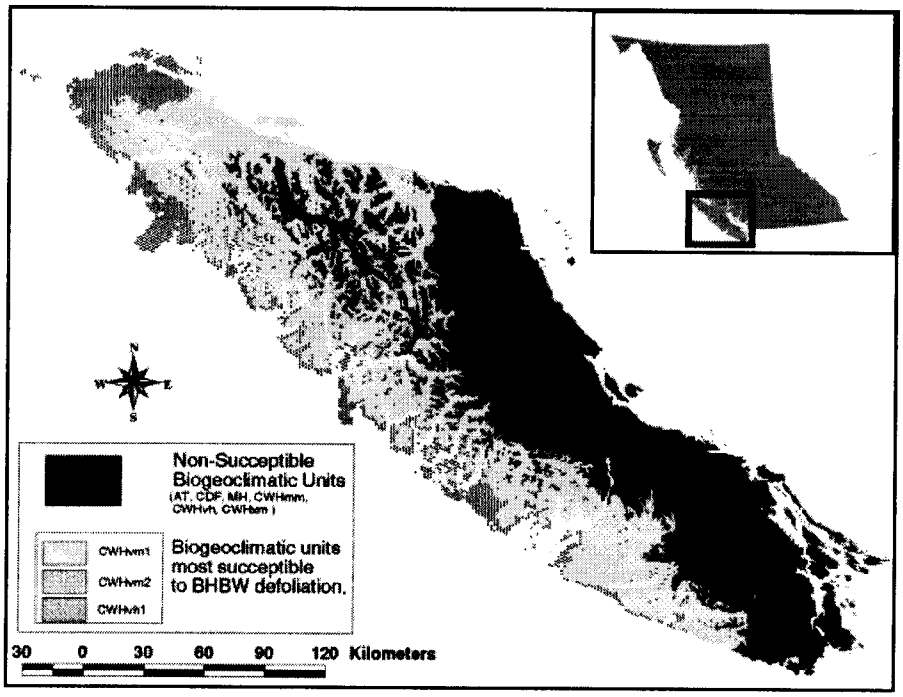


**Figure 3. Biogeoclimatic units most susceptible to western blackheaded budworm outbreak on Vancouver Island.**

**Table 4. Comparison of early and recent western blackheaded budworm outbreaks on Vancouver Island by biogeoclimatic unit**

| Unit | Total Unit Area (ha) | 1941-1944 and 1970-1973 | | | 1985-1990 and 1997-1998 | | |
|---|---|---|---|---|---|---|---|
| | | Defoliated Area (ha) | % of Outbreak | % of Unit | Defoliated Area (ha) | % of Outbreak | % of Unit |
| AT p | 67,372 | 956 | 0.3 | 1.4 | 27 | 0.1 | 0.0 |
| CWHxm1 | 238,690 | 365 | 0.1 | 0.2 | 0 | 0.0 | 0.0 |
| CWHxm2 | 448,247 | 13,168 | 4.2 | 2.9 | 0 | 0.0 | 0.0 |
| MHmm1 | 348,007 | 26,208 | 8.3 | 7.5 | 235 | 0.4 | 0.1 |
| CWHmm1 | 141,301 | 6,517 | 2.1 | 4.6 | 0 | 0.0 | 0.0 |
| CWHmm2 | 228,939 | 21,280 | 6.8 | 9.3 | 0 | 0.0 | 0.0 |
| CWHvm1 | 990,897 | 176,818 | 56.1 | 17.8 | 27,427 | 51.6 | 2.8 |
| CWHvm2 | 385,512 | 63,825 | 20.3 | 16.6 | 8,284 | 15.6 | 2.1 |
| CWHvh1 | 341,240 | 5,824 | 1.8 | 1.7 | 17,213 | 32.4 | 5.0 |
| Total | | 314,961 | | | 53,186 | | |

The largest proportion of the four outbreaks occurred in the sub-montane (vm1) variant and was similar both in the earlier Island-wide outbreaks and the two later outbreaks (about 56% and 52% of the outbreak area, respectively) (Table 4). The second largest portion of the defoliation for the two earlier outbreaks (20%) occurred in the montane (vm2) variant of the Coastal Western Hemlock zone, whereas in the two later outbreaks, approximately 16% of the defoliation occurred in this variant. In the two later outbreaks, the second largest portion of the defoliation (32%) occurred in the southern very wet hyper-maritime sub-zone of the Coastal Western Hemlock zone (CWHvh1), whereas only about 2% of the defoliation occurred in this unit during the two earlier outbreaks (Table 4). When the frequency of defoliation during the four outbreaks is examined, only two biogeoclimatic units (CWHvm1 and CWHvm2) were defoliated in all four outbreaks (Table 3). CWHvm1 was defoliated the most with 49%, 64%, 94%, and 93% of the defoliated area being within this unit during one, two, three, and four outbreaks, respectively. The proportion of defoliated area within the second biogeoclimatic unit, CWHvm2, was 21%, 24%, 6%, and 7% over the same four outbreaks. Four other biogeoclimatic units were defoliated during the two earlier outbreaks only. These four are arranged in decreasing proportion of defoliated area: MHmm1 (8.1% and 6.2%), CWHmm2 (6.8% and 3.4%), CWHxm2 (4.3% and 1.7%), and CWHvh1 (8.2% and 0.1%) (Table 3).

Based on synthesis of the data from the four outbreaks, we list the following biogeoclimatic units in decreasing order of susceptibility to defoliation from the western blackheaded budworm on Vancouver Island: CWHvm1, CWHvm2, and CWHvh1, followed by MHmm1 and then CWHmm2, CWHxm2, CWHmm1, and CWHxm1 (Figures 3 and 4).

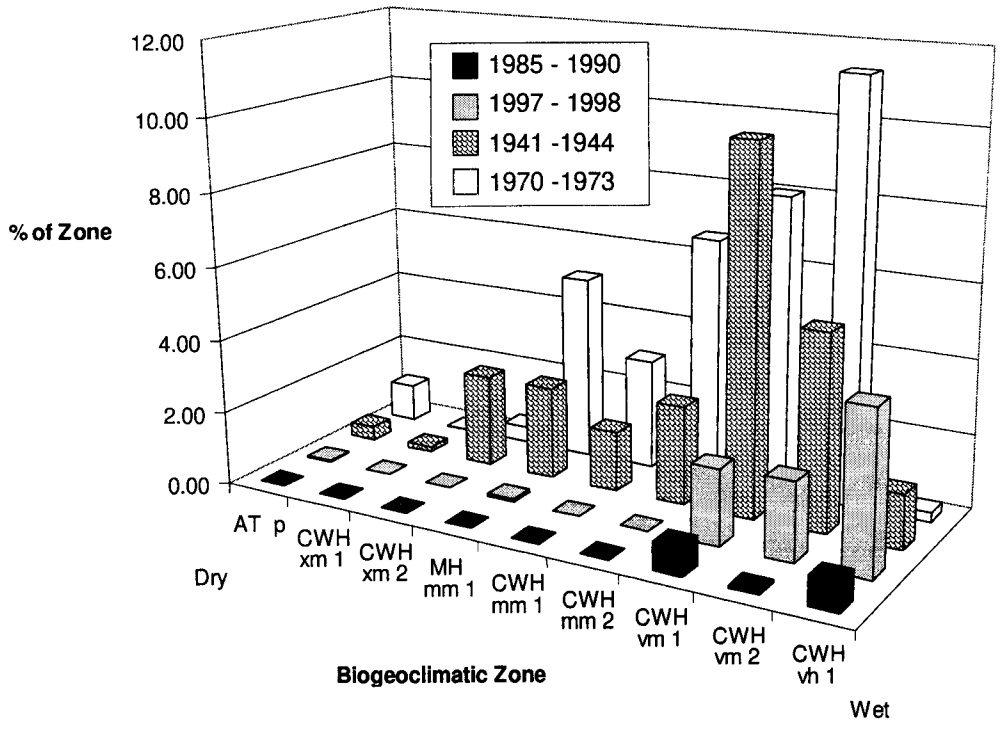


**Figure 4. Comparison of the proportion of biogeoclimatic units defoliated by the western blackheaded budworm in four separate Vancouver Island outbreaks.**

When the proportions of each biogeoclimatic unit defoliated during the four blackheaded budworm outbreaks are compared and the units are arranged from wet to dry, an interesting trend is revealed. The two most recent outbreaks have occurred almost exclusively in the three wettest sub-zones of the Coastal Western Hemlock zone (CWHvm1, CWHvm2, and CWHvh1) (Fig. 4). Although the two earlier outbreaks also occurred in these three sub-zones, they also occurred in the drier parts of the Coastal Western Hemlock zone. In addition, small areas in the windward moist maritime variant (MHmm1) of the Mountain Hemlock zone were also defoliated in the two earlier outbreaks (Fig. 4).

When the locations of areas defoliated during these four outbreaks on the Island are overlaid on top of each other, the only area defoliated during all four outbreaks is restricted to a small area on the northern tip of Vancouver Island (Fig. 5, Table 3). This area was also

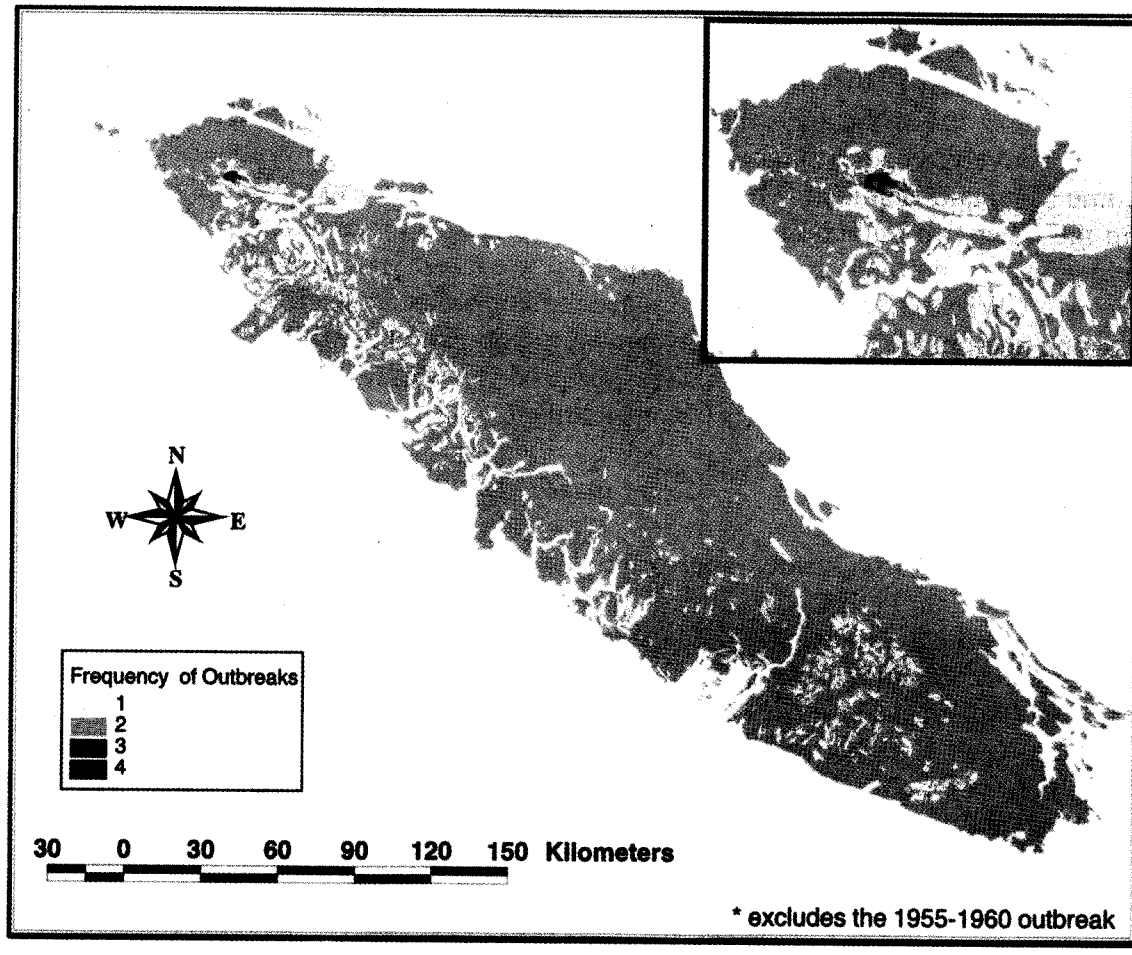


**Figure 5. Outbreak frequency of the western blackheaded budworm on Vancouver Island (1941 to 1998*).**

likely defoliated in the 1955-1960 outbreak, thus receiving five successive outbreaks of western blackheaded budworm defoliation. The areas defoliated during three out of the four outbreaks analyzed in detail only occurred in the area immediately surrounding this hot spot. Therefore, in order to monitor blackheaded budworm population build-up, we recommend that pheromone traps should initially be set up in these areas. If this area around the northern end of Holberg Inlet was monitored annually with a low trap density detection system, we believe population build-up could be followed into the next outbreak and appropriate control measures could then be taken to prevent or minimize severe defoliation and damage when warranted.

## Conclusions

Three units or variants of the Coastal Western Hemlock biogeoclimatic zone are most susceptible to western blackheaded budworm attacks. In decreasing order of susceptibility, these are CWHvm1, CWHvm2, and CWHvh1. During four outbreaks on Vancouver Island, 51%, 21%, and 7% of the areas that were defoliated were within these three biogeoclimatic units, respectively. The next highest proportion of defoliated area was about 8% in the moist maritime Mountain Hemlock (MHmm1) biogeoclimatic unit during two of the outbreaks and 0% in the other two outbreaks. Based on these results, we recommend pre-outbreak larval sampling at the northern tip of Holberg Inlet to detect rising pest populations in the CWHvm1, CWHvm2, and CWHvh1 biogeoclimatic units in addition to establishing and monitoring pheromone traps during low budworm population densities. Preference should be given to locations where outbreaks have occurred repeatedly, particularly in the northern portion of the Island in the CWHvm1 biogeoclimatic unit.

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# The Relationship between Biogeoclimatic Zones and Defoliation by the Two-Year Cycle Spruce Budworm in Central British Columbia

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**ABSTRACT** The two-year cycle spruce budworm (*Choristoneura biennis* (Freeman)) (Lepidoptera: Tortricidae) is a major defoliator of Engelmann spruce (*Picea engelmannii* (Parry)), white Spruce (*P. glauca* (Moench) Voss), an Engelmann-white spruce hybrid, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the interior of British Columbia, Canada. Repeated defoliation causes top kill, tree mortality, and a loss of timber volume. A Geographic Information System analysis of the biogeoclimatic ecosystem classifications, leading tree species, and stand ages associated with budworm defoliation was used to investigate environmental and stand characteristics associated with susceptibility to outbreaks of this budworm. The biogeoclimatic designation of the stand was an important indicator of susceptibility to two-year cycle budworm defoliation. Stands that experienced repeated defoliation were predominantly in the wet, cool Sub-Boreal Spruce and moist, very cold Engelmann Spruce-Subalpine Fir biogeoclimatic classifications. Within these susceptible biogeoclimatic designations, those forest stands leading in the host species were the most likely to experience defoliation.

THE TWO-YEAR CYCLE spruce budworm (*Choristoneura biennis* (Freeman)) (Lepidoptera: Tortricidae) is a major defoliator of Engelmann spruce (*Picea engelmannii* (Parry)), white spruce (*P. glauca* (Moench) Voss), an Engelmann-white spruce hybrid, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the interior of British Columbia. Its recorded range includes the subalpine spruce-fir forest of the Rocky Mountains, the Interior Plateau, the Queen Charlotte Islands, and the southwest Yukon (Stehr 1967, Unger 1984, Shepherd et al. 1995). The current outbreak of this defoliator in the Fort St. James and Mackenzie Forest Districts started in the late 1980s. Repeated defoliation causes top kill, tree mortality, and a loss of growth increment. Alfaro et al. (1982) related mortality to levels of defoliation for the related western spruce budworm (*Choristoneura occidentalis* (Freeman)). This budworm and the defoliation it causes are a component of the natural ecology in this region. Defoliation episodes in this area have occurred roughly every 30 years over the last 300 years. Defoliation episodes last for about 10 years (Alfaro and Zhang, in press).

The two-year cycle budworm was named as a new species (*Choristoneura biennis*) in 1967 (Freeman 1967). The two-year life cycle is distinctive in *C. biennis* and was recognized and described as early as 1932 (Mathers 1932) and was concisely described by Unger (1984). Moths emerge from mid July to early August, mate, oviposit, and die within 2 weeks. Females each deposit about 150 eggs in several flattened, shingle-like masses on the underside of needles. Eggs hatch within 2 weeks and newly emerged larvae seek shelter, spin

Pages 144-151 in Liebhold, A.M.; McManus, M.L.; Otvos, I.S.; Fosbroke, S.L.C., eds. 2001. **Proceedings: integrated management and dynamics of forest defoliating insects**; 1999 August 15-19; Victoria, BC. Gen. Tech. Rep. NE-277. Newtown Square, PA; U.S. Department of Agriculture, Forest Service, Northeastern Research Station.

hibernacula, and overwinter as second instar larvae. Following overwintering, larvae become active in late May to early June, mining needles and buds for 3 to 4 weeks, then spin hibernacula and overwinter as fourth instar larvae. Larval development is completed during the spring of the second year when the greatest amount of feeding occurs. A short pupation period in July precedes the emergence of adults.

Past investigations have shown a relationship between budworm defoliation and stand ecology. Shepherd (1959) made a comprehensive investigation of the relationships between soil, plant, and climate characteristics of stands inhabited by the two-year cycle budworm and outbreak severity. Outbreak areas were found to be drier, poorer sites with a more open canopy than non-outbreak stands. Alfaro et al. (in press) demonstrated that defoliation by the closely related eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) was related to stand age, site quality, and crown closure. Susceptibility to outbreaks of *C. fumiferana* has also been related to stand species composition in eastern Canada, with balsam fir defoliated more than white spruce; greater defoliation also occurred on better drained, richer sites (MacLean and MacKinnon 1997). Studies in Quebec (Dupont et al. 1991) with eastern spruce budworm on balsam fir showed greater mortality on drier sites.

The British Columbia biogeoclimatic ecosystem classification describes the biotic and abiotic characteristics of the ecosystems in this province. It consists of a hierarchical system that integrates climate, vegetation, and site classifications at a broad landscape level. The zonal or regional climate, reflected by vegetation and soil relationships, defines the basic biogeoclimatic unit, the subzone. These units are grouped into zones and subdivided into variants based on finer differences between temperature and moisture regimes (Pojar et al. 1987, Meidinger and Pojar 1991).

The purpose of this investigation was to (1) compare stand characteristics of defoliated and undefoliated stands in order to aid in the prediction of stand susceptibility and vulnerability to budworm defoliation, (2) analyze areas recently defoliated by the two-year cycle budworm in central British Columbia in relation to their biogeoclimatic ecosystem classification, and (3) determine the conditions associated with budworm susceptibility. Stand attributes such as the tree species leading in percent composition, stand age, and site index were examined.

## Materials and Methods

The study area was 27,776 square kilometers in size and located north of Prince George, British Columbia; of the total study area, 4,274 square kilometers were defoliated between 1989 and 1997 (Fig. 1).

Digitized information on defoliation was obtained from aerial overview surveys made by the Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service (CFS) from 1985 to 1994 and the British Columbia Ministry of Forests (BCMoF) from 1995 to 1997. Defoliated areas were originally hand drawn at a scale of 1:100,000 or 1:250,000 during aerial observations. Digitized forest cover data were obtained from BCMoF Forest Inventory Polygon (FIP and FC1) files, mapped at a scale of 1:20,000. The study area consisted of 200 mapsheets that contained 126,340 forest cover polygons. Forest stand attributes included tree species composition; crown closure; stand age; stand height; and the biogeoclimatic zone, subzone, and variant.

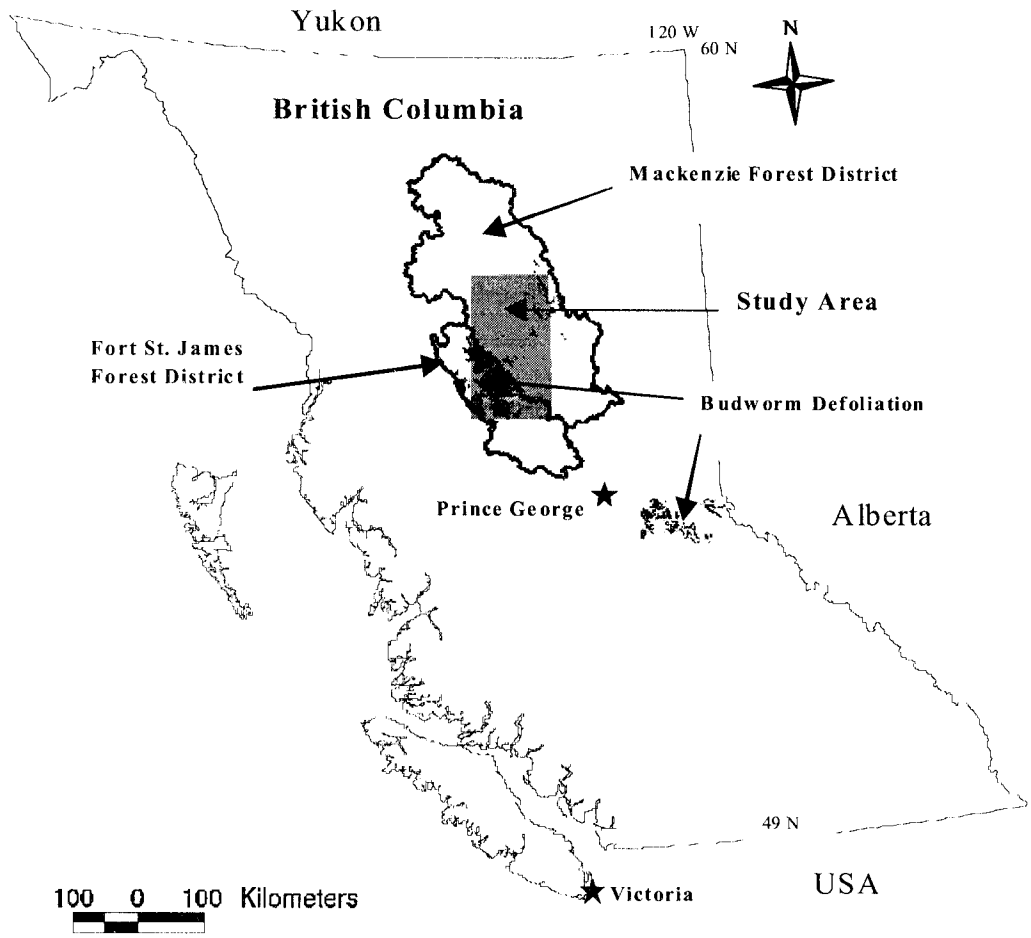


**Figure 1. Location of the study area and two-year cycle budworm defoliation in British Columbia.**

The latest outbreak was first recorded in the Mackenzie Forest District in 1989 and in the Fort St. James Forest District in 1991. Defoliation information was not recorded for the Mackenzie Forest District in 1997. Defoliation in the study area, based on the aerial overview survey data, was observed to be more intense and widespread during odd-numbered years when second-year larvae feed. This observation was consistent with the two-year life cycle of *C. biennis* (Mathers 1932, Freeman 1967, Harvey 1967, Shepherd et al. 1995). Only the defoliation information observed for these odd-numbered feeding years was used to classify the stands. Stand classifications included: (1) all forest stands, (2) forest stands for which defoliation was observed in at least one odd-numbered year from 1985 to 1997, and (3) forest stands for which defoliation was observed for three or more years.

**Analysis of Forest Cover**. Forest cover polygons that did not represent forested stands, such as swamps, rock outcrops, and recent harvesting areas, were removed for the purposes of analysis. The remaining 111,846 polygons covered an area of 20,632 square kilometers, with 2,829 square kilometers (14%) having experienced defoliation. The forest cover polygons were assigned to a defoliation class if the spatial extent of the polygon was entirely within the spatial extent of a defoliation class.

The sum of the areas of the polygons in each defoliation class was determined for each biogeoclimatic zone. The two most prevalently defoliated biogeoclimatic zones were selected, and the area of each variant of these two zones was then determined for each polygon class. The sum of the areas of the polygons with *A. lasiocarpa* and host *Picea* species as the primary and secondary tree species was determined for each defoliation class. Stand age was determined for each defoliation class using an area-weighted average. Site index is a commonly used measure of site quality and was determined for selected biogeoclimatic classifications and each defoliation class using area-weighted averages. Site index is the stand height (in metres) when the stand is 50 years old, with age measured at 1.3 metres above the base of the tree.

## Results

The forested study area included five biogeoclimatic zones (Table 1). The Sub-Boreal Spruce (SBS) biogeoclimatic zone covered 25% of the forested study area and occurs at lower elevations from the valley bottoms up to 1300 metres. It has short, warm, moist summers and cold, snowy winters (Meidinger and Pojar 1991). The Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone covered 41% of the forested study area and occurs at mid elevations (above the SBS zone) between 900 and 1700 metres. It has cool, short summers and long, cold winters (Meidinger and Pojar 1991). Precipitation in this zone is highly variable. The Alpine Tundra (AT) biogeoclimatic zone occurs at the highest elevations, above the ESSF biogeoclimatic zone. It covered 11% of the forested study area. The two other biogeoclimatic zones in the study area were the Boreal White and Black Spruce (BWBS) biogeoclimatic zone, which covered 15% of the area, and the Spruce-Willow-Birch (SWB) biogeoclimatic zone, which covered 8%.

**Table 1. Percentage of all forest polygons, all defoliated polygons, and polygons defoliated three years in each biogeoclimatic zone**

| Polygon Class | SBS[a] | ESSF[b] | BWBS[c] | AT[d] | SWB[e] | Total |
|---|---|---|---|---|---|---|
| All Forest Polygons | 25 | 41 | 15 | 11 | 8 | 100 |
| All Defoliated Polygons | 33 | 50 | 12 | 4 | 1 | 100 |
| Polygons Defoliated Three Years | 66 | 27 | 6 | 1 | 0 | 100 |

[a] Sub-boreal spruce biogeoclimatic zone
[b] Engelmann spruce-subalpine fir biogeoclimatic zone
[c] Boreal white and black spruce biogeoclimatic zone
[d] Alpine tundra biogeoclimatic zone
[e] Spruce-willow-birch biogeoclimatic zone

The defoliated stands showed a different breakdown by biogeoclimatic zone. The SBS zone accounted for 33% of the defoliated polygon area and the ESSF zone accounted for 50%. The remaining defoliated polygon area was in the BWBS zone (12%), the AT zone (4%), and the SWB zone (1%). Polygons that had the most prolonged defoliation (at least 3 odd-numbered years between 1985 and 1997) were more prevalent in the SBS zone (66% of the most defoliated polygon area) than in the ESSF zone (27% of the most defoliated

polygon area). The BWBS biogeoclimatic zone accounted for 6% of the area and the AT zone accounted for the remaining 1%.

Within the ESSF stands, ESSFmv3, a variant of the moist, very cold subzone, was the most extensive (Table 2). The ESSFmc stands, a variant of the moist, cold subzone, were the most prone to defoliation, representing 9% of the forested ESSF polygon area and 32% of the most defoliated ESSF polygon area. Of the SBS stands, the most extensive subzone variant in all forested stands was the SBSmk1, a variant of the moist, cool subzone, at 42% of the forested polygon area in the SBS zone (Table 3). Of the most defoliated stands, SBSwk3, a variant of the wet, cool subzone, was the most extensively defoliated at 68% of the most defoliated polygon area.

**Table 2. Engelmann spruce-subalpine fir variants as a percentage of biogeoclimatic zone area within each polygon class**

| Polygon Class | ESSFmv3[a] | ESSFmc[b] | ESSFmv4[c] | Total |
|---|---|---|---|---|
| All Forest Polygons | 80 | 9 | 11 | 100 |
| All Defoliated Polygons | 84 | 11 | 5 | 100 |
| Polygons Defoliated Three Years | 66 | 32 | 2 | 100 |

[a] Moist very cold subzone variant 3
[b] Moist cold subzone
[c] Moist very cold subzone variant 4

**Table 3. Sub-boreal spruce variants as a percentage of biogeoclimatic zone area within each polygon class**

| Polygon Class | SBSwk3[a] | SBSmk1[b] | SBSmk2[c] | SBSwk2[d] | Total |
|---|---|---|---|---|---|
| All Forest Polygons | 27 | 42 | 21 | 10 | 100 |
| All Defoliated Polygons | 56 | 37 | 3 | 3 | 100 |
| Polygons Defoliated Three Years | 68 | 32 | 0 | 0 | 100 |

[a] Wet cool subzone variant 3
[b] Moist cool subzone variant 1
[c] Moist cool subzone variant 2
[d] Wet cool subzone variant 2

**Leading Species.** Spruce and subalpine fir were the leading species (by volume) on 56% of the forested polygon area (Table 4). These host species were secondary to non-host species on 26% of the forested polygon area. The remaining 18% of the area had non-host species as both primary and secondary cover. Among all defoliated stands, host species were leading on 69% of the defoliated polygon area and secondary on 21% of the area; non-host species were both the primary and secondary species on 10% of the defoliated polygon area. Stands classified as defoliated without host trees as either primary or secondary species either have a minor component of spruce or subalpine fir that experienced defoliation or are surrounded by stands leading in host trees and were therefore included in the defoliation mapped by the aerial overview survey. Stands with three years or more of recorded defoliation had 82% of the most defoliated polygon area leading in host species, 12% of the

area with hosts as secondary species, and 6% of the area with non-host species as both primary and secondary forest cover.

**Table 4. Percent of the forested study area with host and non-host species as primary and secondary forest cover within each polygon class**

| Polygon Class | *A. lasiocarpa* leading | *Picea* sp. leading | *A. lasiocarpa* secondary[a] | *Picea* sp. secondary[b] | Non-host[c] |
|---|---|---|---|---|---|
| All Forest Polygons | 31 | 25 | 5 | 21 | 18 |
| All Defoliated Polygons | 43 | 26 | 6 | 15 | 10 |
| Polygons Defoliated Three Years | 43 | 39 | 3 | 9 | 6 |

[a] Alpine fir secondary to a non-host leading species, usually lodgepole pine
[b] Spruce secondary to a non-host leading species, usually lodgepole pine
[c] Non-host trees make up both primary and secondary species in the stand; the host species is a minor component

**Stand Age.** There was little difference in the area-weighted, average stand age between defoliation classes and between biogeoclimatic classifications, considering the wide range of stand ages observed (Table 5). The mean age for all forested polygons was 141 years, and the mean age for defoliated stands was 154 years. The mean age for the most defoliated stands was 157 years. The younger stand ages represent stands with more frequent stand-replacement disturbances.

**Table 5. Area-weighted stand age for selected biogeoclimatic classifications**

| Polygon Class | ESSFmv3[a] | ESSFmc[b] | SBSwk3[c] | SBSmk1[d] | All Zones |
|---|---|---|---|---|---|
| All Forest Polygons | 160 | 158 | 138 | 116 | 141 |
| All Defoliated Polygons | 160 | 176 | 154 | 119 | 154 |
| Polygons Defoliated Three Years | 170 | 167 | 153 | 133 | 157 |

[a] Engelmann spruce-subalpine fir biogeoclimatic zone moist very cold subzone variant 3
[b] Engelmann spruce-subalpine fir biogeoclimatic zone moist cold subzone
[c] Sub-boreal spruce biogeoclimatic zone wet cool subzone variant 3
[d] Sub-boreal spruce biogeoclimatic zone moist cool subzone variant 1

**Site Index.** There was little difference in the area-weighted, average site indices between defoliation classes for selected biogeoclimatic classifications (Table 6).

**Table 6. Area-weighted, average site index for selected biogeoclimatic classifications**

| Polygon Class | ESSFmv3[a] | ESSFmc[b] | SBSwk3[c] | SBSmk1[d] | All Zones |
|---|---|---|---|---|---|
| All Forest Polygons | 10.8 | 10.4 | 15.9 | 15.0 | 12.1 |
| All Defoliated Polygons | 10.5 | 10.5 | 15.0 | 14.3 | 12.1 |
| Polygons Defoliated Three Years | 10.1 | 11.2 | 13.0 | 13.0 | 12.3 |

[a] Engelmann spruce-subalpine fir biogeoclimatic zone moist very cold subzone variant 3
[b] Engelmann spruce-subalpine fir biogeoclimatic zone moist cold subzone
[c] Sub-boreal spruce biogeoclimatic zone wet cool subzone variant 3
[d] Sub-boreal spruce biogeoclimatic zone moist cool subzone variant 1

## Discussion

The biogeoclimatic zone, subzone, and variant designation of the stand was an important indicator of susceptibility to two-year cycle budworm defoliation. The most susceptible ecosystems were the SBSwk3 and ESSFmc biogeoclimatic classifications. Within these susceptible biogeoclimatic designations, those forest stands with a higher proportion of host species were more likely to experience repeated budworm defoliation. Stand age and site index were found to be less indicative of budworm defoliation risk. Continued study of forest characteristics and budworm defoliation is required to allow the prediction of defoliation risk and severity. Based on this study, a set of permanent plots was established to monitor the long-term impacts of this defoliator on the timber resources of British Columbia. Information from these plots will aid in planning, timber supply analysis, and possible silvic intervention to reduce risk, such as favoring pine or other non-host trees in high risk areas.

## Acknowledgments

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# The Role of Biotic Factors in Gypsy Moth Population Dynamics in Slovakia: Present Knowledge

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**ABSTRACT** This paper presents the current knowledge about the bioregulation complex that affects gypsy moth population dynamics in Slovakia. The study involved the presence and efficacy of pathogens, parasitoids, and predators in naturally occurring oak forest stands in southwestern Slovakia from 1990 to 1999. Mortality caused by pathogens was 33.7% in the progression phase, 62.3% in the culmination phase, 33.3% in the regression phase, and 59% in latency. Mortality due to parasitoids was 47.3% in the progression phase, 51.1% in the culmination phase, 64.0% in the regression phase, and 60.3% in latency. Preliminary results on the predation of gypsy moth egg masses and pupae are also discussed.

THE GYPSY MOTH is the most serious pest of broadleaved stands (mainly oak stands) in Slovakia. Outbreaks occur in 6- to 12-year cycles (Patocka et al. 1999). During the last gypsy moth outbreak from 1992 to 1994, more than 18,000 ha of forest stands were heavily damaged. As a result of long-term decline in oak stand health, defoliation can cause increased tree mortality in subsequent years; therefore, infested stands are treated with biopesticides, mainly *Bacillus thuringiensis*. However, we are trying to find another possible approach for controlling this pest that involves taking management actions prior to the development of outbreaks (Novotný and Turcáni 1997, 1999). One option is to improve the efficiency of the natural bioregulation complex of the gypsy moth that consists of pathogens, parasitoids, and predators. This requires that we have knowledge about the natural bioregulation complex and what organisms in this complex affect gypsy moth abundance at different host densities. The basic goal is to manage pest population density by manipulating aspects of the bioregulation complex with minimal costs and without impact on the environment. For this reason, it is important that we monitor the density of gypsy moth populations and their natural enemies during all gradation cycles. The bioregulation complex of gypsy moths is quite well known in the United States (Doane and McManus 1981). In Central Europe, a few scientists have studied the bioregulation complex, specifically parasitoids (Capek 1971, Novotný and Capek 1989, Zúbrik and Novotný 1997), predators (Turcek 1949, Randik 1967), and during the last 15 years, pathogens (Novotný 1989). More detailed studies were initiated in 1990 when we began monitoring gypsy moth populations in a series of permanent sites in Slovakia (Novotný et al. 1998). The objective of our paper is to

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report on the results of our studies on the population dynamics of the gypsy moth and its bioregulation complex.

## Materials and Methods

**Monitoring Population Density.** In order to monitor the abundance of gypsy moth populations, we established a series of 12 permanent plots throughout the gypsy moth outbreak area in southern Slovakia. We used the Modified Turcek Method (MTM) (Turcáni 1998b) to monitor populations. In order to use this system, it is necessary to determine the average number of egg masses at four points (every point consists of 30 trees). All egg masses that occur on tree boles to a height of 5 to 8 m are counted. If the average number of egg masses per tree exceeds 1.00, the counting is completed. If the count is below 1.00 egg masses per tree, it is necessary to count egg masses further at an additional four points (for a total of 240 trees). If the average number of egg masses per tree is below 0.3, it is necessary to count egg masses at an additional 8 points (for a total of 480 trees). Pheromone monitoring was conducted in the same plots in order to supplement the egg mass monitoring (Turcáni 1998a).

**Monitoring the Presence and Efficacy of Pathogens.** Screening for the presence of entomopathogens in gypsy moth populations was conducted from 1993 to 1998 on six permanent research plots: Kurinec, Trebisov, Pata, Businces, Parovske Haje, and Kovacova. All research plots were situated in gypsy moth primary outbreak areas; however, populations were frequently in the latency phase during these years. Turkey oak (*Quercus cerris*) was the dominant tree species at these locations. The larvae were collected in stages L1-L2, L3-L4, and L5-L6 and reared on oak foliage under laboratory conditions. Larvae were collected (1) from oak leaves either directly or by using the "beating" method and (2) using burlap bands that were placed around 100 trees. Over 1,415 larvae were collected and 835 dead larvae were examined in order to determine the presence or absence of pathogens. Tissue smears of dead larvae were fixed by alcohol, stained with Giemsa, and then examined under light microscopy. Using this procedure, we were able to assign the cause of mortality into the following categories: virus, bacteria, microsporidia, fungus, mixed infection, and undetermined.

**Monitoring the Presence and Efficacy of Parasitoids.**

Egg Parasitism. Field studies involving parasitoids were conducted on 10 study plots in southwestern Slovakia from 1991 to 1993 and again in 1995. The dominant tree species in these plots were *Q. cerris* and *Q. petraea* and the following species occurred in the understory: *Prunus spinosa*, *Ligustrum vulgare*, *Acer compestre*, *Carpinus betulus*, and *Crataegus* sp. Observations were made at eight sites in 1991, six sites in 1992 and 1993, and at two sites in 1995, for a total of 22 site-years.

To estimate egg parasitism, 10 egg masses were collected randomly from each locality in March. In some years, when gypsy moth populations were low and egg masses were difficult to find, samples of fewer than 10 egg masses were collected. Egg masses were enclosed separately in Petri dishes and stored at 5°C. At the end of April, they were incubated in the laboratory at 20°C and 60% RH until parasitoid emergence was completed (September). In addition to parasitized eggs, we counted the number of hatched larve and the number of sterile eggs in each mass.

Larval and Pupal Parasitism. Studies of larval and pupal parasitism were conducted at four sites (average age 40 to 60 years) in southwestern Slovakia from 1992 to 1996. Observations were made at three sites in 1992 and in 1994, at four sites in 1993, and at two sites in 1995 and 1996. A total of 14 data sets was obtained. From each site, we attempted to collect individuals from the following life stages: L3-L4, L5-L6, and pupae. We used the "beating" method to collect early larval stages and collected late-stage larvae and pupae from branches and other refugia. When populations were in latency and regression phases and we anticipated that the abundance of the pest would be low, we introduced egg masses from other areas where the populations were higher. In these circumstances, we placed 25 to 50 egg masses on a cluster of 4 to 6 trees.

Larvae were reared in the laboratory in groups of 25 to 30 individuals in open top glass containers at a temperature of ca. 20°C and relative humidity of ca. 60%. The caterpillars were fed oak leaves and mortality was recorded daily. After pupation, 3 to 5 pupae were placed in Petri dishes and mortality and parasitism were recorded after emergence. The same procedure was used for pupae that had been collected in the field. Parasitized larvae and pupae were maintained until parasitoids emerged, at which time they were pinned and identified.

For every gradation phase, the percent mortality (U%) for all life stages combined and percent survival (P% = 100 - U%) were calculated to provide an estimate of the percent of the population that survived to the adult stage (Novotný 1989).

$$U\% = \sum_{x=1}^{ps} r_x$$

$x$ = pest development stage (egg = 1; L1-L2 = 2; L3-L4 = 3; L5-L6 = 4; pupae = 5)
$ps$ = number of pest development stages
$r_x$ = reduced number of specimens in stage $x$ ($r_x = y_x * 0.01) * z_x$
$y_x$ = percent mortality in stage $x$ of the pest
$z_x$ = the initial number of specimens in stage $x$ of the pest reduced by mortality from the previous phase ($z_1 = 100$, $z_x = z_{x-1} - r_{x-1}$).

**Monitoring the Presence and Efficacy of Predators.**

Egg Predation. Predation of naturally deposited egg masses was studied during the winter of 1997-1998 on five study sites (V. Zaluzie, Kovacova, Pata, Tehla, and Parovske Haje) and during the winter of 1998-1999 on 12 sites (Casta, Parovske Haje, Velke Zaluzie, Tesarske Mlynany, Zvolenak, Kovacova, Pata, Tehla, Vojnice, Businces, Kurinec, and Trebisov). Four hundred and eighty trees were examined at each site. Eighteen egg masses were located and checked from 1997 to 1998 and 79 egg masses were examined from 1998 to 1999. We rated egg mass damage using the following scale: no damage, damage below 10%, damage between 11 and 30%, damage between 31 and 60%, and damage above 60%.

Pupal Predation. The pupal predation studies were established during the summers of 1998 and 1999. In 1998, we exposed 100 artificially reared pupae on each of three study plots (Zvolenak, Pata, and Kovacova). The pupae were attached to pieces of burlap that were placed on the ground on transects. Evaluation of damage (mortality) was recorded on the first, second, sixth, and seventh day after their placement. In 1999, the same methodology

was used; however, five study plots were established (Tesarske Mlynany, Zvolenak, Pata, Tehla, and Businces). In 1999, damage (mortality) was evaluated on the first, third, and seventh day using the following scale: (1) the pupa was undamaged, (2) the pupa was damaged, and (3) the pupa was missing.

## Results

**Monitoring Population Density.** The gypsy moth population density declined overall but varied among study plots from 1990 to 1998 (Figures 1 to 4). Abundance on the Kovacova plot was influenced by "control in advance" (Novotný and Turcáni 1997).

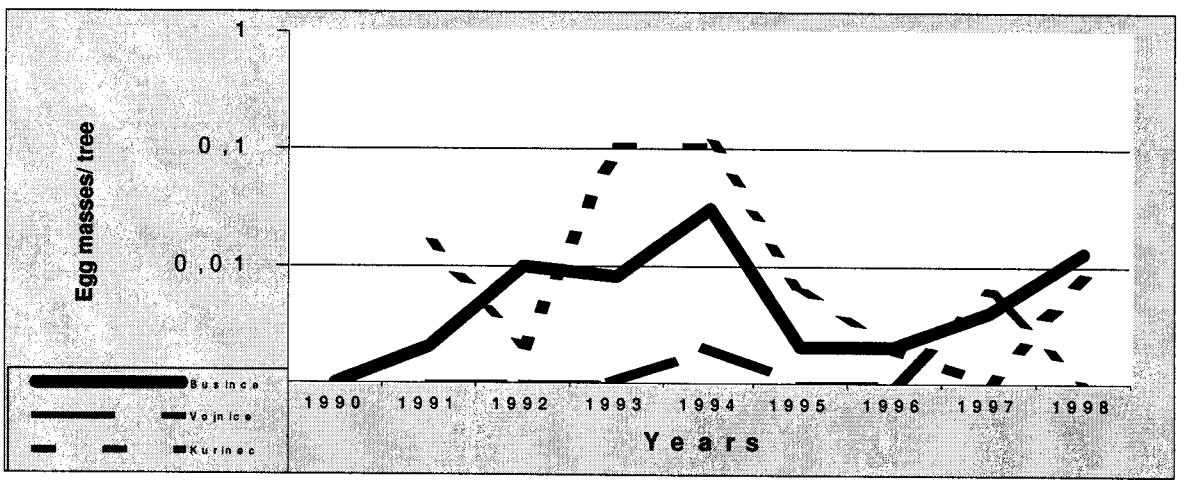


**Figure 1. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Businces, Vojnice, and Kurinec plots.**

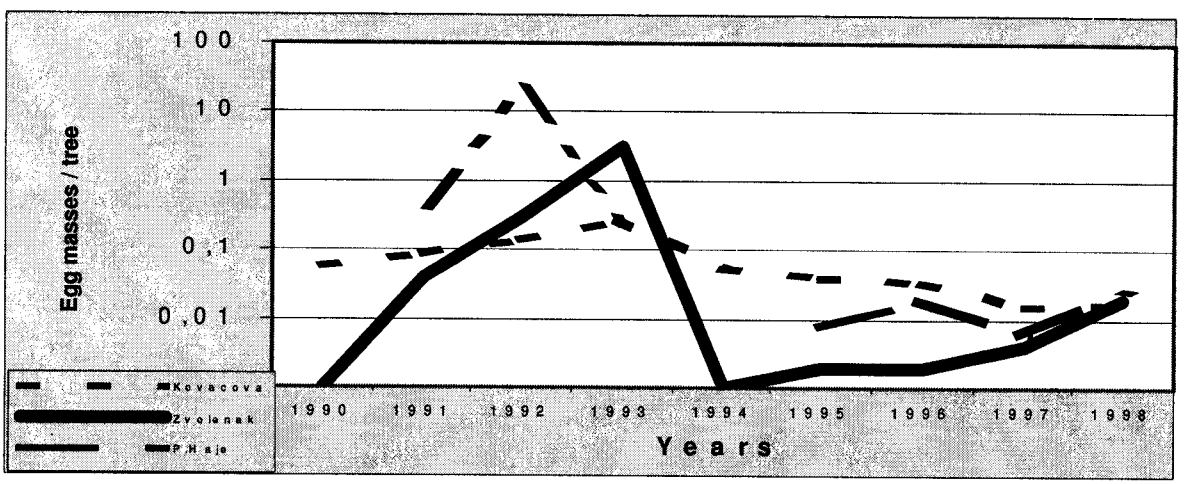


**Figure 2. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Kovacova, Zvolenak, and Parovske Haje plots.**

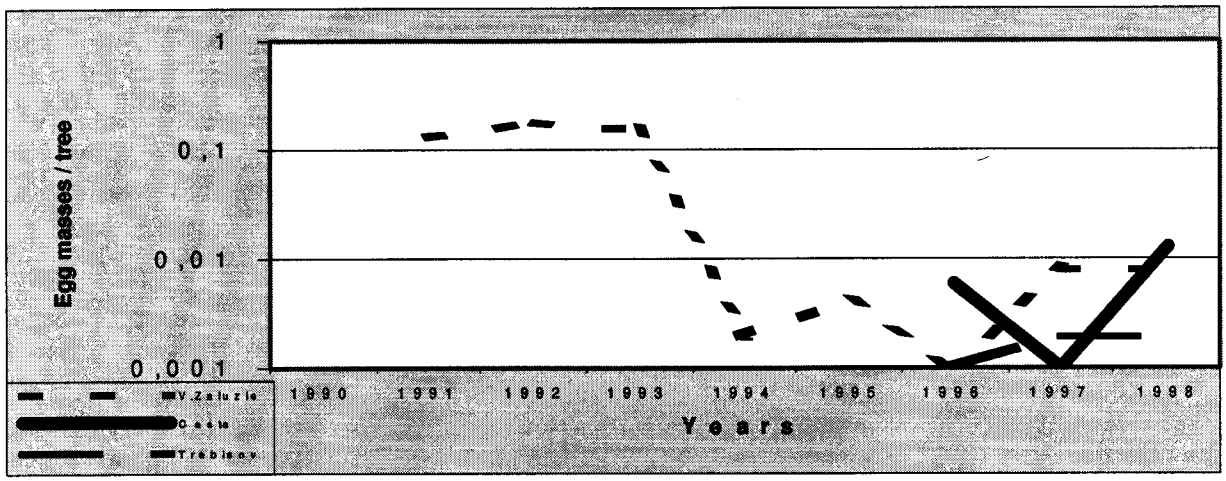


**Figure 3. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Velke Zaluzie, Casta, and Trebisov plots.**

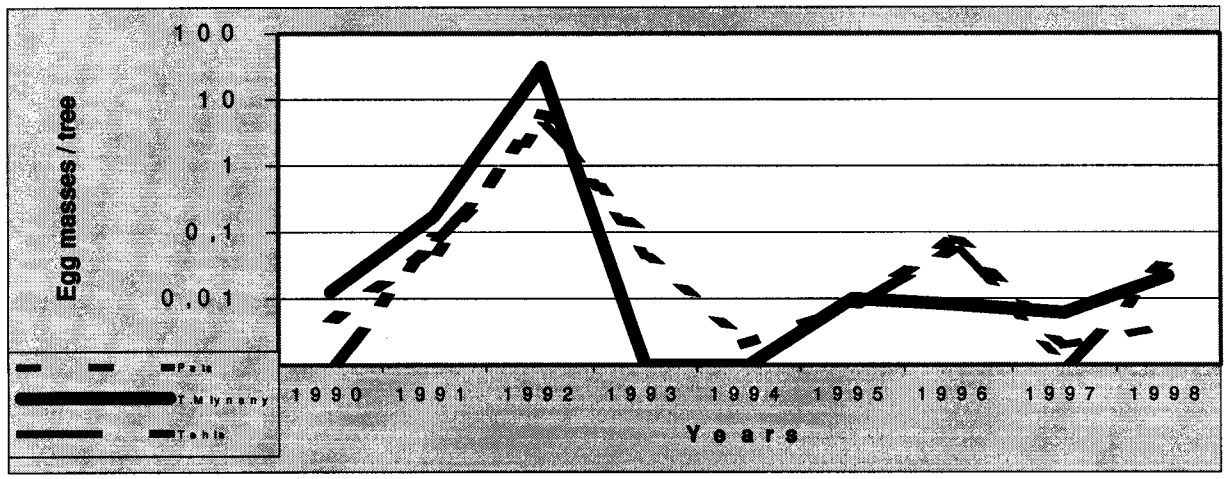


**Figure 4. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Pata, Tesarske Mlynany, and Tehla plots.**

**Monitoring the Presence and Efficacy of Pathogens.** From 1993 to 1998, average larval mortality was 59.0% (Table 1). Larval mortality (reared under lab conditions) varied from 24.4% (1998) to 69.7% (1995). In 1994, all reared larvae were dissected in the L6 stage to determine the presence or absence of pathogens. Therefore, the 100% mortality in 1994 was due not to natural causes but to the dissection of all surviving larvae.

The highest levels of mortality in any one year were caused by viruses (37.1% in 1993) and undetermined causes (36.7% in 1996). However, during the 6-year period, the major causes of mortality on average were as follows: undetermined reasons of mortality (23.9%), bacteria (22.4%), mixed infection (22.3%), and virus (20.2%). Mixed infection of two or three entomopathogens was very common and caused annual mortality that varied from 0 to 47% (Table 2). The highest average mortality (25.6%) was attributed to the combined presence of bacteria and fungi (B+F).

**Table 1. Entomopathogenic microorganisms present in dead gypsy moth larvae**

| Year | Virus | Microsp. | Bacteria | Fungi | MIX[a] | URM[b] | 1[c]/2[d] | Mortality |
|---|---|---|---|---|---|---|---|---|
| | | | | % | | | | % |
| 1993 | 37.1 | 2.4 | 18.1 | 9.5 | 10.0 | 22.9 | 412/210 | 50.9 |
| 1994 | 36.4 | 3.2 | 13.6 | 11.6 | 26.0 | 9.2 | 250/250 | 100.0 |
| 1995 | 7.2 | 0.9 | 35.7 | 10.2 | 12.8 | 33.2 | 337/235 | 69.7 |
| 1996 | 13.4 | 3.3 | 23.3 | 0.0 | 23.3 | 36.7 | 84/30 | 35.7 |
| 1997 | 14.5 | 6.4 | 21.0 | 4.8 | 30.7 | 22.6 | 135/62 | 45.9 |
| 1998 | 12.5 | 4.2 | 22.9 | 10.4 | 31.3 | 18.7 | 197/48 | 24.4 |
| Average | 20.2 | 3.4 | 22.4 | 7.8 | 22.3 | 23.9 | 1,415/835 | 59.0 |

MIX[a] = mixed infections
URM[b] = undetermined reasons of mortality
1[c] = total number of larvae examined
2[d] = number of dead larvae

**Table 2. Mixed infections of entomopathogens present in dead gypsy moth larvae[a]**

| Year | V+M | V+B | V+F | M+B | M+F | B+F | V+M+B | V+M+F | V+B+F | M+B+F |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | % | | | | |
| 1993 | 14 | 29 | 32 | 10 | 0 | 10 | 5 | 0 | 0 | 0 |
| 1994 | 21 | 28 | 12 | 3 | 5 | 8 | 9 | 6 | 3 | 5 |
| 1995 | 13 | 37 | 0 | 7 | 0 | 30 | 3 | 0 | 3 | 7 |
| 1996 | 29 | 0 | 0 | 0 | 0 | 43 | 14 | 0 | 14 | 0 |
| 1997 | 21 | 26 | 0 | 0 | 0 | 16 | 32 | 0 | 5 | 0 |
| 1998 | 20 | 0 | 13 | 7 | 0 | 47 | 0 | 13 | 0 | 0 |
| Average | 19.7 | 20.0 | 9.5 | 4.5 | 0.8 | 25.6 | 10.5 | 3.2 | 4.2 | 2.0 |

[a] V = virus; M = microsporidia; B = bacteria; F = fungi

From 1993 to 1994, the highest percent mortality was caused by viruses even though most gypsy moth populations were at relatively low densities. In 1995, population densities were still low (<.05 egg masses/tree) in almost all plots. That year, bacteria were the most common pathogens recovered. In the late latency phase (1996 to 1998), most mortality was attributed to mixed infections and undetermined reasons of mortality.

**Monitoring the Presence and Efficacy of Parasitoids.**

Egg Parasitism. From 1991 to 1993 and in 1995, 61,052 eggs were examined. Only 751 (1.23%) of the eggs were parasitized and total egg mortality was 4.84%. The highest parasitism rate was observed at the Parovske Haje plot in 1995 (10.08%).

We have identified two egg parasitoids: *Anastatus disparis* and *Ooencyrtus kuvanae.* Their distribution was uneven and their effect on host egg mortality in individual years and at particular locations was varied, although the parasitoids were more efficient in the regression phase of the population. Earlier studies in Slovakia also determined low rates of egg parasitism. Capek (1971) estimated egg parasitism to be between 0.9 and 1.0% and Novotný and Capek (1989) estimated egg parasitism to be 3.45%.

We have not found any significant relationship between the average number of egg masses per tree (gypsy moth population density) and parasitism rate ($r = 0.168$, $n = 21$, $F = 0.55$, $P = 0.05$). There is a slight decline in the rate of parasitism with a decline in host population density (Zúbrik and Novotný 1997).

Larval and Pupal Parasitism. We examined 4,170 larvae and pupae in our experiments and of this total, 664 specimens (15.92%) were parasitized. Of this total, 55.7% were parasitized by Tachinidae, 23.8% by Braconidae, 14.5% by Ichneumonidae, and 6.0% by Chalcididae (Table 3). In total, 23 species of parasitoids and hyperparasitoids were identified.

**Table 3. The most abundant parasitoids attacking gypsy moth larvae and pupae**

| Family / Species | Number of Caterpillars Parasitized | Proportion (%) of Each Individual Species of the Total Number Parasitized (n = 664) | Order |
|---|---|---|---|
| | Average (min/max)[a] | Average (min/max)[a] | |
| Braconidae | | | |
| *Cotesia melanoscelus* | 82 (0/25) | 12.3 (0/39.5) | 3 |
| *Glyptapanteles liparidis* | 53 (0/14) | 8.0 (0/25.8) | 4 |
| *Glyptapanteles porthetriae* | 22 (0/12) | 3.3 (0/9.8) | 7 |
| Tachinidae | | | |
| *Parasetigena silvestris* | 195 (4/36) | 29.4 (14.7/54.2) | 1 |
| *Blepharipa pratensis* | 132 (0/26) | 19.9 (0/41.2) | 2 |
| *Zenillia libatrix* | 13 (0/4) | 1.9 (0/7.9) | 10 |
| *Compsilura concinnata* | 14 (0/8) | 2.1 (0/5.1) | 9 |
| Ichneumonidae | | | |
| *Phobocampe lymantriae* | 32 (0/28) | 4.9 (0/22.9) | 6 |
| *Phobocampe unicincta* | 18 (0/5) | 2.7 (0/10.5) | 8 |
| *Hyposoter tricoloripes* | 22 (0/11) | 3.3 (0/45.8) | 7 |
| Chalcididae | | | |
| *Monodontomerus sp.* | 38 (0/38) | 5.7 (0/36.5) | 5 |
| TOTAL | 664 | | |

[a] The average was calculated from all study plots; minimum and maximum values were recorded on a single plot.

**Mortality during Population Gradation Phases.** By definition, gypsy moth populations are in latency when egg mass densities are estimated to be between 0.005 and 0.02 egg masses per tree (Figures 1 to 4). During this time, egg parasitism was slightly higher than in other phases (4.23%, Table 4) though still insignificant. High levels of parasitism occurred during the early instars and were attributed mainly to the Braconids *C. melanoscelus* and *G. liparidis*. Entomopathogens are not usually important at these low densities.

During the initial phase of progradation, pest population abundance may increase 150 fold; this was associated with a slight decrease in generation mortality, especially during the egg and L1-L2 stages. However, parasitism of the L3-L6 stages was still significant (Table 4). The most abundant parasitoids were the oligophagous tachinids *P. silvestris* and *B. pratensis* along with the more polyphagous species *C. concinnata* and *Z. libatrix*. Collectively, the tachinids accounted for 69.8% mortality.

**Table 4. Percent mortality for each gypsy moth life stage and all life stages combined (U%) caused by parasitoids and percent surviving population (P%) for each gradation phase**

| Gradation Phase[a] | Egg | Caterpillar | | | Pupae | U% | P% |
|---|---|---|---|---|---|---|---|
| | | L1-L2 | L3-L4 | L5-L6 | | | |
| LATENCY | 4.23 | 13.97 | 17.57 | 14.88 | 9.57 | 60.27 | 39.73 |
| I. ACCR. | 1.20 | 2.96 | 27.79 | 15.65 | 9.95 | 57.55 | 42.45 |
| C. ACCR. | 0.0 | 2.00 | 9.80 | 11.46 | 13.81 | 37.07 | 62.93 |
| CULMIN. | 0.1 | 0.99 | 16.52 | 17.55 | 15.89 | 51.05 | 48.95 |
| REGR. | 0.3 | 13.90 | 13.72 | 36.01 | - | 63.98 | 36.02 |

[a] Latency = latency phase; I. ACCR. = initial progradation phase; C. ACCR. = continued progradation phase; CULMIN. = culmination phase; REGR. = regression phase

Population survival increased significantly during the continued progradation phase (62.9%) and was reflected in significant declines in parasitism in all larval stages (Table 4), but especially in the L3-L4 stages.

Maximum pest population density occurs during the culmination phase when oak forests are heavily or completely defoliated. Mortality of all gypsy moth life stages caused by parasitoids, pathogens, and undetermined causes was estimated at 91%, which contributed to the collapse of the outbreak population. By the end of summer, very few egg masses were found on some of the plots.

In the regression phase, generation survival was lowest (36.02%, Table 4) and total parasitism was highest, especially in the L5-L6 stages. The most important parasitoids were the oligophagous tachinids *P. silvestris* and *B. pratensi*. Total egg mortality was 11.65% mainly due to pathogens and undetermined causes of mortality and possibly poor embryonation. The overall influence of pathogens declined during regression. No estimate of pupal mortality is provided because we were unable to locate any native pupae in these populations.

**Preliminary Study of the Presence and Efficacy of Predators.** During the winter of 1997-1998, 100% of 18 egg masses were damaged (Table 5). However, the damage was characterized as light ($\leq$30% of the eggs damaged) in 77% of the egg masses and as heavy (>30% of the eggs damaged) in 23% of the egg masses. Damage was primarily caused by birds, although in some cases, we observed beetles from the family Dermestidae. Based on the character of the damage (on the upper portion of the egg mass), we predict that the egg masses were damaged mainly by *Sitta europea*. In the subsequent year, we estimated damage on all 12 monitoring plots (79 egg masses) and damage frequency reached 77% (Table 5). Of the total, 51% of the egg masses were lightly damaged and 26% were heavily damaged. We estimated that the population density in the winter of 1997-1998 varied from 0.002 to 0.016 egg masses per tree, whereas in the winter of 1998-1999, the density varied from 0.004 to 0.033 egg masses per tree.

**Table 5. Frequency and severity of damage to gypsy moth egg masses in Slovakia during latency**

| Year | Winter 1997 – 1998 | | | | Winter 1998 – 1999 | | | |
|---|---|---|---|---|---|---|---|---|
| Place | Undamaged Egg Masses | Damaged Egg Masses | Frequency of Damage | Quantity of Damage | Undamaged Egg Masses | Damaged Egg Masses | Frequency of Damage | Quantity of Damage |
| V. Zaluzie | 0 | 3 | 100% | 23.3% | 0 | 4 | 100% | 47.5% |
| Kovacova | 0 | 7 | 100% | 12.9% | 2 | 6 | 75% | 9.4% |
| Pata | 0 | 1 | 100% | 20.0% | 0 | 2 | 100% | 25.0% |
| T.Mlynany | 0 | 4 | 100% | 31.3% | 2 | 8 | 80% | 24.0% |
| P. Haje | 0 | 3 | 100% | 23.3% | 1 | 12 | 92% | 19.6% |
| Vojnice | x[a] | x | x | x | 0 | 0 | 0% | 0.0% |
| Zvolenak | x | x | x | x | 6 | 3 | 33% | 10.0% |
| Tehla | x | x | x | x | 3 | 13 | 81% | 25.9% |
| Businee | x | x | x | x | 3 | 3 | 50% | 10.0% |
| Kurinec | x | x | x | X | 0 | 4 | 100% | 27.5% |
| Casta | x | x | x | X | 1 | 5 | 83% | 35.0% |
| Trebisov | x | x | x | X | 0 | 1 | 100% | 80.0% |
| TOTAL | 0 | 18 | 100% | 20.8% | 18 | 61 | 77% | 22.5% |

[a] x = Plots were not examined in this period

Predation of pupae in the summer of 1998 reached a maximum on the 7th day after their exposure. Seventy-eight to one hundred percent of the pupae were either damaged or had disappeared. Those pupae that disappeared are assumed to have been removed by vertebrate predators. Losses in this category varied from 57 to 96% (Table 6).

**Table 6. Predation (%) of gypsy moth pupae in Slovakia during latency (summers of 1998 and 1999)**

| Plot[a] | 2 | 3 | 6 | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|---|---|
| Year | 1998 | 1998 | 1998 | 1999 | 1999 | 1999 | 1999 | 1999 |
| Nondamaged 1 | 18 | 0 | 22 | 23 | 20 | 5 | 5 | 1 |
| Damaged 2 | 25 | 4 | 13 | 21 | 17 | 25 | 0 | 0 |
| Dissapeared 3 | 57 | 96 | 65 | 56 | 63 | 70 | 39 | 99 |
| Mortality % | 82 | 100 | 78 | 77 | 80 | 95 | 89 | 99 |

[a] 1 = Tesarske Mlynany; 2 = Zvolenak; 3 = Pata; 4 = Tehla; 5 = Businee; 6 = Kovacova

In the following year, pupae were exposed on four plots within the primary gypsy moth outbreak area in Slovakia and on one plot in a secondary outbreak area. Predation in the primary outbreak area varied from 77 to 95% and was 99% in the secondary outbreak area (Table 6).

Among the Invertebrata that damaged pupae, we observed ants, wasps, earwigs (Japygidae), beetles from the Dermestidae family (*Dermestes murinus* L., 1758), and Staphylinidae.

## Discussion

The results of this study and an earier study by Novotný (1989) indicate that the significance of individual entomopathogens varies depending on the different gradation phases of gypsy moth populations. Bacteria and viruses were the most frequent entomopathogens in the progression, culmination, and regression phases of gypsy moth populations. Viruses were recognized as the dominant factor in larval mortality during gypsy moth outbreaks. Bacteria spores were very common in dead gypsy moth larvae but not as the primary infection. Bacterial infections developed when gypsy moth larvae died due to other causes (physical stress, temperature or moisture changes, etc.). However, during the latency period, most mortality was caused by undetermined reasons (URM). The importance of URM in bioregulation during latency was also mentioned in Skinner et al. (1993).

In latency, parasitoids were very effective (58.54% of mortality) because their specialized searching capacity enabled them to find gypsy moth larvae even at low densities. Mills et al. (1986) observed that after exposing gypsy moth larvae on sites where gypsy moth population density was very low, only *Compsilura concinnata* and *Ceranthia samarensis* were able to readily locate and parasitize larvae. Oligophagous species of tachinids were found in later years. In our studies, where we supplemented populations by adding egg masses, *Cotesia melanoscelus* was the most common parasitoid recovered. Similar results were published by Liebhold and Elkinton (1989).

Barbosa et al. (1975) compared gypsy moth parasitism rates in areas of high and low host density. In almost all cases, the parasitism was higher in latency than in culmination. High rates of parasitism in latency were also reported by Eichorn (1996). We found that undetermined reasons of mortality, together with bacteria, were also important factors during latency. Similar results were mentioned in Skinner et al. (1993).

Our experiments also confirmed the results of Campbell and Sloan (1977) concerning the importance of parasitoids in historical outbreak areas. In only one case in the initial phase of progression was the coefficient of parasitoid bioregulation higher than that of pathogens. The most abundant parasitoids were oligophagous tachinids.

When the population density of *L. dispar* is the highest, conditions are optimal for the development of entomopathogens. Larvae that are stressed by lack of preferred foliage or that are forced to feed on non-preferred hosts are susceptible to infection by pathogens, especially viruses. Extremely high densities of larvae also enhance the horizontal transmission of entomopathogens among the population. A similar mechanism occurs in North American gypsy moth populations (Doane and McManus 1981). The broad spectrum of pathogens recovered during our experiments is typical for gypsy moth populations in Europe (Novotný 1989).

During the regression phase, the activity of pathogens declined. The results of some other authors are a little different (Doane and McManus 1981, Novotný 1989). Normally, we would expect the importance of pathogens to be the highest during the regression phase, as with parasitoids. Our results are not typical possibly because of the methodology that we employed. Due to a lack of native insects within the sites in the regression phase, we introduced egg masses from sites where the population density was higher; therefore, only a small proportion of larvae originated from the previous generation. Our actions might have affected the pathogen load and modified the incidence of disease attributed to latent infections.

Bathon (1993) reported that some common species of Tachinidae contributed to the decline of outbreaks in Siberia in 1957 and caused up to 90% mortality of larvae and pupae. According to Maier and Bogenschutz (1990), the tachinid parasitoids *P. silvestris* and *B. schineri* caused the termination of a gypsy moth outbreak in Oberrheintal in 1986.

Novotný (1989) suggested that the bioregulation efficiency of parasitoids decreases during the regression phase while bioregulation by pathogens increases. Many other authors report that diseases caused by entomopathogens are the main reason for the termination of gypsy moth outbreaks, resulting in regression (Campbell 1963, Capek 1971, Novotný 1989). The main agents of disease are virosis and bacteriosis in the United States (Doane 1970), virosis and microsporidia in Europe (Weiser 1987), and virosis and bacteriosis in Slovakia (Novotný 1989).

The role of birds in the predation of gypsy moth egg masses during latency in Slovakia seems to be quite important. We measured egg mass predation during the winters of 1997-1998 and 1998-1999 and determined that 77 to 100% of the egg masses were damaged to some degree, although the extent of damage overall was light to moderate. We have not evaluated the importance of other biotic (invertebrates) or abiotic factors that might contribute to overwintering mortality. According to Capek et al. (1999), when the population density reached 4 egg masses per tree, 80% of the masses were undamaged, 10% were partially damaged, and 10% were totally damaged. When the population density reached 15.7 egg masses per tree, 71% of the masses were undamaged, 22% were partially damaged, and 7% were totally damaged. These data do not agree exactly with our results in that we rarely observed egg masses that were totally damaged; damage was usually below 30%. In another study (Randik 1967), 7.0 to 15.5% of the egg masses were damaged when egg mass densities were between 0.01 and 0.07 per tree, 45 to 46% were damaged when egg mass densities were between 1.2 and 2.1 per tree, and 14.5 to 19.7% were damaged when egg mass densities were between 8.1 and 8.2 per tree. These data represent low values of predation; however, the population densities in these experiments were much higher than during our observations. The author mentioned the need to acquire data on the effects of predation during the latency phase of gradations; however, until now these studies have not been conducted.

Turcek (1949) listed the following species as egg mass predators: *Certhia familiaris*, *Sitta europaea*, *Parus major*, *Parus caeruleus*, *Parus atricapitalis*, and *Aegithalos caudatus.* Although we did not make direct observations of bird activity in our studies, we did notice that species of tits (*Parus* spp.) and *S. europaea* were common in the study area. *S. europaea* is known to damage the upper portion of egg masses. Higashiura (1989) conducted more intensive studies on the effect of bird predation on gypsy moth egg masses in Japan. He found that at egg mass densities varying from 6 to 231 per ha (0.01 to 0.5 egg masses per tree), the average predation by birds varied widely. He found that from 1978 to 1983, the predation rate increased with increasing prey density. However, the trend was most noticeable only in very low-density plots; there was no increase in the predation rate in high-density plots. In a later article (Higashiura 1989), the mean predation rate during a 9-year period was 38.8% (maximum = 84%). He concluded that in certain plots, bird predation on egg masses is as important as are parasitoids on egg and larval stages. Most species of birds are generalist feeders who have many alternative hosts and therefore are not dependent ecologically on gypsy moth egg masses as their major source of food. Therefore, predation of egg masses by birds might depend on several factors, such as the availability of alternative foods, host and prey densities, and the severity of the winter. Higashiura (1989) suggested

that gypsy moth egg masses are unpalatable to birds and that species such as nut hatches (*Sitta*) feed on egg masses simply to avoid starvation during stressful periods. It is quite probable that bird predation is an important part of the bioregulation complex in Slovakia, mainly in the regression and latency phases and probably in the initial phase of progression. Additional studies are being planned to evaluate the effects of bird predation on egg masses.

Estimates of larval predation have not been obtained in Slovakia; however, Turcek (1949) listed the following species of birds as predators of gypsy moths during the culmination phase: *Coloeus monedula*, *Garrulus glandarius*, *Sturnus vulgaris*, *Oriolus oriolus*, *Coccothraustes coccothraustes*, *Fringilla coelebs*, *Passer domesticus*, *Passer montanus*, *Emberiza citrinella*, *Motacilla alba*, *S. europea*, *P. major*, *P. caerulens*, *Parus palustris*, *P. atricapitalis*, *Lanius senator*, *Lanius collurio*, *Dendrocopos major*, *Dendrocopos minor*, *Upupa epops*, and *Cuculus canorus*.

Pupal predation was studied only in 1998 and 1999 during latency; however, we found high mortality in all cases (fom 78 to 100% in 1998 and from 77 to 99% in 1999). Elkinton and Liebhold (1990) found that in low-density populations (below 50 egg masses/ha-0.1 egg masses/tree), pupae predation rates were positively correlated with gypsy moth population density. These findings support the hypothesis that predation by small mammals is responsible for the regulation of low-density gypsy moth populations. At higher population densities, predation by small mammals was much lower. As in the case of bird predation of egg masses, no evidence exists suggesting that gypsy moth populations significantly affect the reproductive successes of small mammal species. These results confirm the findings of Elkinton et al. (1996) who found significant dependence between the acorn crop and small mammal population density, suggesting that the acorn crop in some cases can thoroughly influence the occurrence or size of gypsy moth outbreaks. Most of the small mammals and birds that feed on gypsy moth are generalists for which gypsy moth is a minor component in their diet. The authors also found that during lower population densities, parasitoids and pathogens are responsible for less than 50% of the total mortality. Losses during the larval stages appear to be caused mainly by predation. During our experiments, we confirmed the results of Campbell and Sloan (1977) that vertebrate predation on pupae (mainly small mammals) was much greater than that caused by invertebrates. We don't have information about the species composition of this group; however, we can predict that as in the United States (Elkinton and Liebhold 1990), they play an important role, mainly in the progradation phase. Among Invertebrata on study sites, we found low numbers of ants, wasps, earwigs, and beetles from the family Dermestidae. Turcek (1949) observed the following species feeding on pupae: *O. oriolus*, *S. europaea*, *P. major*, *L. collurio*, *D. major*, and *D. minor*.

Elkinton and Liebhold (1990) consider *Calosoma sycophanta* to be an important predator and Weseloh et al. (1995) showed that *C. sycophanta* consumed approximately 75% of the pupae on tree stems but a much lower percentage of the pupae on leaves and small branches. Little, if any, data exists about predation by *C. sycophanta* during low population levels in Slovakia. Recently, Gschwanter et al. (1999) conducted studies at two sites in Burgenland, Austria, to estimate predation of gypsy moth pupae that had been exposed on tree boles over a period of several weeks. At Klingenbach, total mortality over the entire exposure period was 92.2% while at Siegendorf, total mortality was 67.0%. Most of the mortality was caused by mice, especially *Apodemus flavicollis*, and to a lesser extent, *A. sylvaticus*. The authors concluded that the higher mortality caused by small mammal

predators as well as the higher captures of mice at Klingenbach (38 vs. 13 at Siegendorf) are related to the higher density of ground cover at this site. A similar idea about the importance of habitat was presented by Liebhold et al. (1998) who found that the level of small mammal abundance and predation by small animals was higher in oak forests, lower in birch forests, and lowest in larch forests. They suggested as well that the role of predation in gypsy moth population dynamics has been underestimated and should be studied further.

Very little is known about the predation of gypsy moth adults; however, Turcek (1949) analyzed the stomach contents of birds during the culmination phase of a gypsy moth gradation and listed the following bird species as predators of adult gypsy moths: *S. europea*, *P. major*, *P. caerulens*, *P. atricapitalis*, *L. collurio*, *Muscicapa striata*, *Phylloscopus collybita*, *Sylvia atricapila*, *Hirundo rustica*, and *Caprimulgus europaeus*. Since male moths exhibit diurnal activity and females do not actively fly but are conspicuous on tree boles and branches, we suggest that predation of this life stage by birds could be very significant.

Based on our data and discussions, we conclude that biotic factors play an important role in the dynamics of gypsy moth populations in Slovakia. These results are summarized in Table 7.

**Table 7. The mortality of gypsy moth life stages caused by different biotic factors during different phases of gradation**

| Factor | Pathogens – Mortality % | | | | Parasitoids – Mortality % | | | | Predators – Mortality % | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GP[a] | Egg | Cater. | Pupae | Adult | Egg | Cater. | Pupae | Adult | Egg | Cater. | Pupae | Adult |
| PP | NI[b] | 31.7 | 2.0 | NI | 0.6 | 34.8 | 11.9 | NI | 4.9 | NK[c] | NK | NK |
| CU | NI | 60.3 | 2.0 | NI | 0.1 | 35.1 | 15.9 | NI | 11.4 | NK | NK | NK |
| RE | NI | 33.3 | 0.0 | NI | 0.3 | 63.7 | NK | NI | NK | NK | NK | NK |
| LA | NI | 59.0 | NK | NI | 4.2 | 46.5 | 9.6 | NI | 21.5 | NK | 86.3 | NK |

[a] GP = gradation phase; PP = progradation phase; CU = culmination phase; RE = regression phase; LA = latency phase

[b] NI = not important

[c] NK = not known

## Conclusions

- Mortality caused by pathogens reached 59% in the latency phase but varied greatly in different years (24.4% to 69.7%). The highest share of mortality was caused by viruses. At the beginning of latency, viruses caused the most mortality; however, mixed infections and undetermined reasons of mortality were more important during the continuous latency phase.
- Parasitoids caused 47.3% mortality during the progradation phase; however, their importance increased during the culmination (51.1%) and regression (64%) phases and during latency (60.3%).
- Predators are the least studied group; however, our preliminary studies suggest that they are important. We recorded egg mass predation rates of 4.9% during the progradation phase, 11.4% during the culmination phase, and 21.5% during latency. We also recorded 86.3% mortality of pupae during exposure studies conducted during latency.

The most important research needed is to determine the role of predators in all developmental stages of the gypsy moth and during all phases of gradation and to ascertain the role of competition among groups of biotic agents (pathogens, parasitoids, and predators) and determine the importance of this competition for gypsy moth population dynamics.

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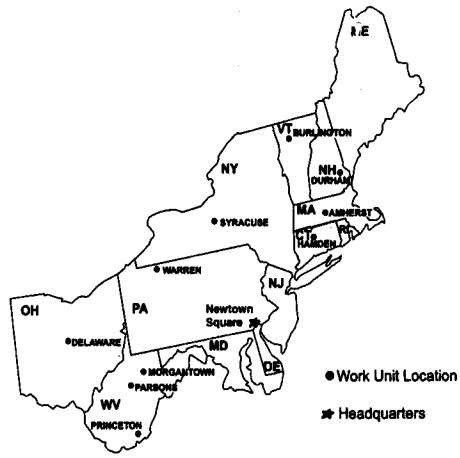
**Keywords:** Forest insect, defoliator, integrated management, population dynamics, ecology.

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