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Integrated Management and Dynamics of Forest Defoliating Insects

Edited by:

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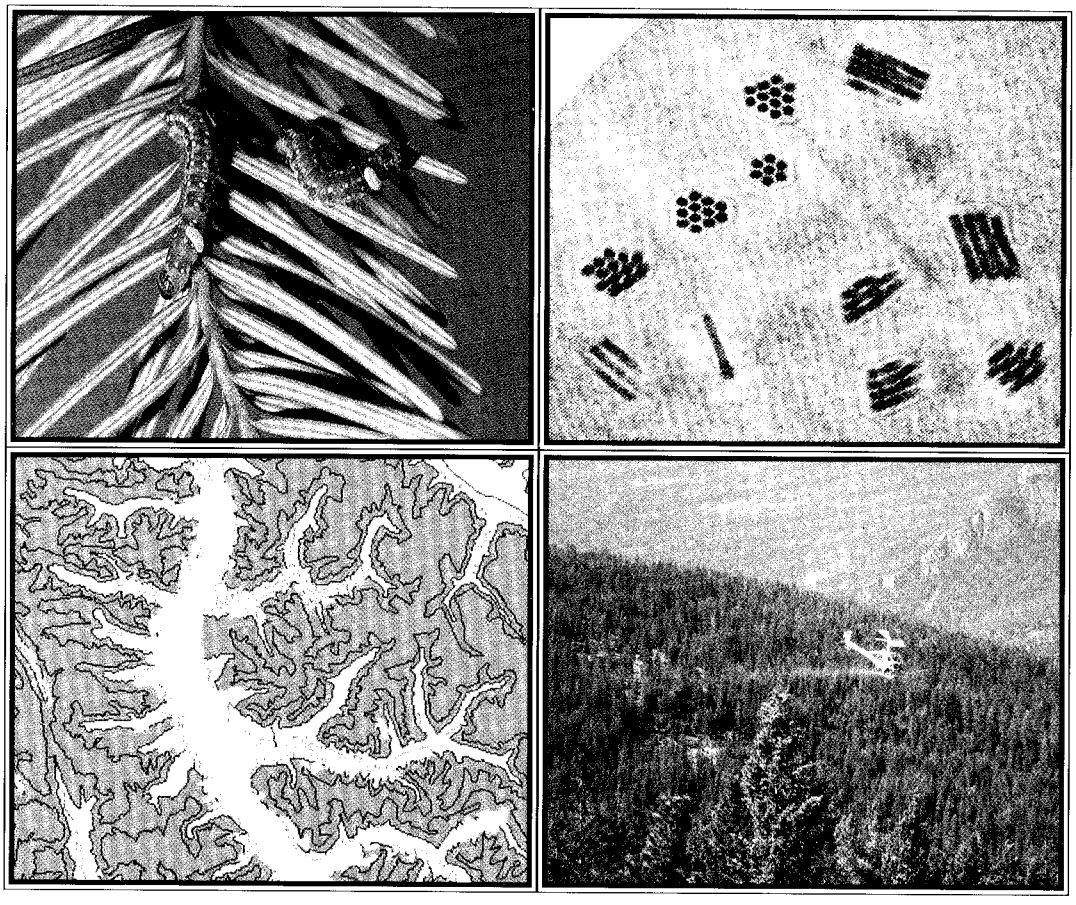
Victoria, British Columbia, Canada
August 15-19, 1999



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The photographs on the cover (from the upper left corner going clockwise) were taken by the following individuals: western spruce budworm larvae with ectoparasites (Imre S. Otvos), Douglas-fir tussock moth nucleopolyhedrosis virus (John C. Cunningham), helicopter spraying of a Douglas-fir tussock moth infestation with OpNPV (Imre S. Otvos), and a map comparing western hemlock looper defoliation to biogeoclimatic zones (Neil Borecky).

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[1] A meeting sponsored by the International Union of Forestry Research Organizations (IUFRO) Working Party S7.03-06, "Integrated Management of Forest Defoliating Insects," and Working Party S7.03.07, "Population Dynamics of Forest Insects."

PREFACE

These proceedings result from a conference, "Integrated Management and Dynamics of Forest Defoliating Insects," held at the University of Victoria, British Columbia, Canada, on August 15-19, 1999. The meeting was a joint meeting of International Union of Forestry Research Organization (IUFRO) working parties 7.03.06, "Integrated Management of Forest Defoliators," and 7.03.07, "Population Dynamics of Forest Insects."

This meeting was the second joint meeting between these two IUFRO working parties and further demonstrated the value of combined meetings between these two groups. The first joint meeting of IUFRO working groups 7.03.06 and 7.03.07 was held in the Slovak Republic in August of 1996. The proceedings of that meeting were published as U.S. Department of Agriculture Forest Service Northeastern Forest Experiment Station General Technical Report NE-247.

The meeting in Victoria was attended by 65 scientists representing 19 countries. A total of 39 oral presentations were given and 11 poster presentations were displayed. The papers presented at the meeting covered a wide spectrum of topics ranging from applied to theoretical areas of focus, but all of these papers addressed some aspect of either the population biology or management of foliage-feeding forest insects. Submittal of a paper for inclusion in these proceedings was optional, thus explaining the smaller number of papers in this volume compared to the total number of presentations.

Holding an international conference such as this required the assistance of numerous individuals and we would like to thank all volunteers from the Pacific Forestry Centre, Natural Resources Canada Canadian Forest Service for their help. Their work on organizing the meeting, registration, and facilitating the field trip was outstanding and made the entire meeting much more valuable for all participants. We also thank the University of Victoria for the use of their meeting facilities. Abbott Laboratories and Phero Tech Inc. both contributed funds for this meeting and we gratefully acknowledge their assistance. The USDA Forest Service Northeastern Research Station and the USDA Forest Service Forest Health Technology Enterprise Team sponsored publication of these proceedings and we thank them for making this volume possible.

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Control of the Most Dangerous Insects of Greek Forests and Plantations

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ABSTRACT Among the considerably large number of insects living in forest ecosystems and plantations of fast growing tree species in Greece, only a few normally constitute a serious danger, and even fewer need to be controlled occasionally. Their control, which can either be carried out from the ground or from the air, includes the use of (1) insecticides that act as inhibitors of cuticle development; (2) preparations based on *B. thurigiensis* used mainly for the control of *Thaumetopoea pityocampa* Schiff, *Stilpnotia salicis* L., *Lymantria dispar* L., and *Laspeyresia splendana* Hbn.; and (3) Diazinon for control of the following wood boring insects in poplar plantations: *Sciapteron tabaniformis* Rott., *Cossus cossus* L., and *Melanophila picta* Pall.. The Greek Forest Service is rather cautious about using insecticides in forest ecosystems and plantations of fast growing trees, especially when these are located near water (e.g., rivers and lakes). In the case of high, productive forests, protection and conservation of ecological stability are the highest priority, even at the expense of maximizing forest production. To the contrary, in recreational forests and parks or areas that attract tourists and in various other plantations, aerial applications are used only when insects tend to cause serious problems, e.g., in order to protect goods received from the forest or in order to preserve forest product quality.

THE LISTS IN Tables 1 and 2 include insects that appear most frequently in Greek forest ecosystems as well as in poplar and cypress plantations and chestnut orchards (Avtzis 1989).

Table 1. Insects that appear most frequently with softwood species of Greek forest ecosystems

Softwoods		
Pine Forests	**Cypress Plantations**	**Fir Forests**
Criocephalus rusticus L.	*Buprestis cupressi* Germ.	*Argyresthia fundella* F. Rösl.
Dioryctria splendidela H.S.	*Phloesinus armatus* Reitt.	*Cryphalus piceae* Ratz.
Evetria buoliana Schiff.	*Phloesinus aubei* Perr.	*Dioryctria abietella* Schiff.
Ips erosus Woll.		*Epinotia subsequana* Haw.
Ips sexdentatus Boern.		*Ernobius kailidisi* Johnson
Monophlebus hellenicus Gen.		*Pityokteines curvidens* Germ.
Myelophilus piniperda L.		*Pityokteines spinidens* Reitt.
Neodiprion sertifer Geoffr.		*Pityokteines vorontzowi* Jacobson
Pissodes notatus F.		*Platypus oxyurus* Duf.
Thaumetopoea pityocampa Schiff.		*Sirex cyaneus* F.
		Trypodendron lineatum Oliv.
		Urocerus gigas L.

Pages 1-5 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.

Table 2. Insects that appear most frequently with hardwood species of Greek forest ecosystems

Hardwoods	
Poplar Plantations	**Oak and Evergreen Forests**
Agrilus ater L.	*Cerambyx cerdo* L.
Cossus cossus L.	*Coraebus bifasciatus* Ol.
Diaspis pentagona Targ.	*Euproctis chrysorrhoea* L.
Dicranura vinula L.	*Lymantria dispar* L.
Melanophila picta Pall.	*Malacosoma neustria* L.
Melasoma populi L.	*Tortrix viridana* L.
Phloeomyzus passerini Sign.	
Phloeomyzus redelei H.R.S.	
Sciapteron tabaniformis Rott.	
Stilpnotia salicis L.	
Chestnut Orchards	**Elm Trees (along roads)**
Balaninus elephas Gyll.	*Scolytus scotytus* F.
Laspeyresia splendana Hbn.	*Scolytus multistriatus* Marsh.

At this point, it is worth mentioning that these are not the only insects that appear in the forests and plantations of Greece (Kailidis 1986). In addition, the intensity and appearance rate are not the same for all species, and the control of certain harmful insects is not always possible depending on ecological, technical, and funding issues.

All insects listed above can be divided into three groups. The first group consists of only two species: the needle-eating *Thaumetopoea pityocampa* Schiff. (pine processionary caterpillar) and the leaf defoliator *Lymantria dispar* L. (gypsy moth). Rather restricted control measures are applied yearly for both species. The extent of control measures depends mainly on the intensity of the defoliation, on the damage that the defoliation could potentially cause, and on the ability of the Forest Service to cover the financial cost of control.

A second, smaller group includes some insects of poplar plantations and chestnut orchards that are rarely controlled. A third group includes all the remaining insects cited in the lists that are hardly ever controlled.

Materials and Methods

Group A (Yearly Applications)

***Thaumetopoea pityocampa* Schiff. (Pine Processionary Caterpillar).** This needle-eating insect is found throughout Greece and is the most common defoliator of pine forests. These forests cover a total area of 870,486 ha (Ministry of Agriculture 1991); Table 3 lists these forested areas by overstory tree species.

Table 3. Forested area by overstory tree species in Greece

Species	Area
Pinus halepensis and *Pinus brutia*	567,731 ha (65.11%)
Pinus nigra	281,692 ha (32.40%)
Pinus silvestris	20,955 ha (2.40%)
Pinus pinea	108 ha (0.01%)

T. pityocampa attacks all pine species at varying intensities (Avtzis 1983a, 1986; Schopf and Avtzis 1987). It is found nearly everywhere in Greece from sea level to altitudes of 1800 m on Mount Olympus. It does not exist in some areas of Central Greece because of unsuitable weather conditions, nor is it found on some islands of the Aegean Sea, possibly because of geographical isolation (Avtzis 1983b).

The pine processionary moth has one generation per year, but a small percentage of its pupae exhibits extended diapause. The problems this insect causes can be grouped into three categories: (1) health problems to humans (e.g. eczema, etc.), (2) aesthetic problems (nests in trees, defoliation, etc.), and (3) economic problems due to growth loss resulting from defoliation (Bouchon and Toth 1971).

The control of *T. pityocampa* can be conducted mechanically from the ground by removing and burning overwintering nests. This can be done only in young pine plantations and under particular circumstances. Control of *T. pityocampa* can also be conducted from the ground or from the air using insecticides that (1) act by interfering with chitin deposition (contain inhibitors of cuticle development) and (2) are based on the so called bioinsecticides, such as the preparation that contains *B. thuringiensis* (Avtzis1998).

Mechanical control is conducted during winter before the beginning of the process of pupation into the soil in spring. Control using preparations that influence chitin synthesis or that contain bioinsecticides is conducted primarily during the second and third larval instar stages (October to November).

***Lymantria dispar* L. (Gypsy Moth).** The gypsy moth is a notorious pest in Greece. This extremely polyphagous leaf-eating insect has over 300 different tree species as its host (Coulson and Witter 1984) and causes great damage to poplar plantations, oak forests (1,471,839 ha), and evergreen ecosystems (3,153,882 ha) (Ministry of Agriculture 1991).

In poplar plantations and oak forests, the damage caused by gypsy moth is primarily tree growth loss (Schwenke 1978), and in a few cases, there are problems concerning landscape aesthetics and human health. In evergreen ecosystems, growth loss caused by defoliation is less important. Because these ecosystems occur along the coast and are generally in areas with great touristic interest, the most serious concerns involve aesthetic damage to the landscape and human health.

However, the appearance of *L. dispar* in evergreen ecosystems that consist mainly of *Quercus coccifera* and partly of *Quercus ilex, Phillyrea media, Ceratonia siliqua, Laurus nobilis, Arbutus* sp., and *Pistacia* sp. has both direct and indirect impacts on animal breeding and production. The direct effect involves competition for food between grazing animals (sheep and goats) and *L. dispar*, particularly during heavy defoliation periods. The foliage of those species, especially *Q. coccifera,* is food for both *L. dispar* and grazing animals.

The indirect effect on animals, especially on diary production, involves problems caused by the hairs of gypsy moth caterpillars. During feeding activity and general insect

development, part of their hair sticks on the host plant. These hairs can cause stress, uneasiness, and enervation when they pass to the external breathing system of grazing animals, which smell their food before consuming it. As a result there is a reduction in diary production.

The control of gypsy moth is being conducted from the ground or from the air using preparations that (1) act by interfering with chitin deposition (contain inhibitors of cuticle development) and (2) are based on the so called bioinsecticides, such as the preparation that contains *B. thuringiensis* (Avtzis1998). Gypsy moth control is being carried out in the early spring, right after young leaves emerge and during egg hatch.

Group B (Rarely Controlled)

***Stilpnotia salicis* L. (Silk Moth).** This leaf-eating insect has two generations per year and causes serious growth loss, especially following heavy defoliation in poplar plantations (Schwenke 1978). Its control is carried out in early spring, right after young larvae crawl into the crown. Control is conducted either from the ground or by aerial application using the same preparations as described in treating insects in Goup A.

Wood Boring Insects on Polpar Trees. The following wood boring insects mainly affect tree physiology and secondarily devalue the technical features of wood: (1) *Sciapteron tabaniformis* Rott., (2) *Cossus cossus* L., and (3) *Melanophila picta* Pall.. Control of these secondary harmful insects of poplar is conducted in spring during the adult flight and oviposition period. It is accomplished from the ground by totally covering the lower part of the stem with Diazinon 60wp.

***Laspeyresia splendana* Hb.** This insect attacks chestnut seeds and is controlled wherever and whenever it causes serious problems (Dimoulas 1986). Control is conducted in the summer during the adult flight and oviposition period using aerial applications of preparations that block chitin synthesis (contain inhibitors of cuticle development).

As has been pointed out, the Greek Forest Service has been using preparations that block chitin synthesis, Bt productions (Foray 48B), and Diazinon for the control of harmful insects. During the past few years, the following preparations were primarily used: (1) Dimilin 25wp or Alsystin (cuticle development inhibitor group) at a dosage of 250 gr/25 L water/ha, (2) Foray 48B (bioinsecticides group) at a dosage of 1.5L formulation/ha, and (3) Diazinon 60wp (chemical insecticides group) for ground applications at a dosage of 100 gr/100 L water. Aerial spraying was applied mostly with the Polish aircraft PZL-M18 (Dromader), Grumman-GR 164 airplanes, and Augusta Bell helicopters.

Discussion

Greece is located in Southern Europe in the temperate zone. Its Mediterranean climate is favorable for insect population development. Because chemical insecticides are widely used in agriculture, the Greek Forest Service, which manages nearly 60% of Greece's total land area, is particularly cautious about using aerial applications of insecticides in forest ecosystems and plantations.

This cautiousness increased after 1995 when, according to the decision of certain Research Institutes, the Highest Council of the State decided that aerial applications used for the control of *Dacus olaea* and other harmful insects must be restricted for the protection of

public health as well as for the preservation of ecological stability. After that decision, Forest Service aerial applications were used only when insect epidemics tended to cause serious problems in recreational forests and parks or in vacation areas and various plantations.

The contrary is true in the case of high, productive forests, where the use of aerial applications with chemical preparations must be the final means when all other applied measures within the framework of integrated pest management (Dent 1991) have failed. In such cases, the protection and conservation of ecological stability are of highest priority, even at the expense of maximizing forest products.

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Coarse-Scale Hazard Rating of Western Hemlock Looper in British Columbia

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ABSTRACT The western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst.)) is a serious defoliating pest in western North America. During the 1990-1995 outbreak, this pest was responsible for approximately 63 000 ha of stand mortality in British Columbia. There have been 14 distinct outbreaks, increasing in duration and severity over the past 87 years. Outbreaks tend to occur in Coastal and Interior Western Hemlock biogeoclimatic zones and generally last 2 to 5 years.

A Western Hemlock Looper Hazard Rating System (WHLHRS) is being developed to aid forest managers in dealing with western hemlock looper outbreaks. Province-wide hazard rating has been accomplished at a 2-kilometre grid scale. The hazard-rating values for this grid are based upon the locations of past outbreaks, presence of host forest stands, biogeoclimatic zones, climatic variables, and elevation.

This hazard rating mapping will be useful for future pheromone trap placement, in addition to aiding forest mangers in identifying susceptible forests. The forecasting of defoliation events and the identification of larger scale risk areas are the goals of the WHLHRS. The WHLHRS, as a whole, is anticipated to aid forest managers in dealing with outbreaks of western hemlock looper in an effective fashion through either direct control measures or modified silviculture practices.

OVER THE PAST 87 years, there have been 14 outbreaks of western hemlock looper (WHL) (*Lambdina fiscellaria lugubrosa* (Hulst)) (Lepidoptera: Geometridae) in British Columbia (B.C.), Canada. These outbreaks have increased in size, distribution, and intensity. This insect has been responsible for large areas of severe defoliation and tree mortality in recent years, particularly in the Nelson, Cariboo, and Prince George Forest regions of eastern and central British Columbia. During the last outbreak alone (1990-1995), over 63,000 ha of trees were killed and another 272,000 ha defoliated to varying degrees by the WHL. Outbreaks characteristically begin in old growth western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and remain within the Coastal Western Hemlock and Interior Western Hemlock biogeoclimatic zones (Krajina 1965, Pojar et al. 1987). Outbreaks have occasionally spilled into non-preferred tree species such as western red cedar (*Thuja plicata* Donn), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western white pine (*Pinus monticola* Dougl.), among others, and their characteristic biogeoclimatic zones (Harris et al. 1982, Parfett et al. 1995).

Logging industry representatives from interior British Columbia indicated their desire for some form of hazard rating system to be developed so that high-risk areas can be identified and monitored. This report outlines some of the major steps in developing a hazard rating system for the western hemlock looper, with the intention of delivering such a system to aid forest managers in their decision-making process.

Pages 6-15 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.

The creation of the Western Hemlock Looper Hazard Rating System (WHLHRS) is designed to be a multi-stage process. This initial stage involves risk rating the entire Province at a coarse 2-km grid scale. This grid was developed to identify similar traits among regions that have experienced a looper outbreak and to exclude areas that possess no risk for the development of WHL outbreaks. The next stages will involve prediction of the timing and stand-level location of western hemlock looper attacks.

It is hoped that the identification of areas at risk to WHL outbreaks will aid several components of the forestry sector. Forest managers, although they most likely have already identified problem areas prior to this, will now have an accurate definition of areas at risk for looper outbreak. It may also allow for the implementation of preventative silviculture. Following harvesting, areas that are known to harbor looper outbreaks may be re-planted with non-host or less suitable tree species for the looper. The identification of risk areas will also aid in population monitoring of the WHL. Pheromone trapping of adult male looper moths has been conducted in B.C. since 1992. At present, 23 locations selected by Forest Insect Disease Survey (FIDS) rangers based upon their professional and empirical experience are being sampled. In conjunction with the hazard rating mapping, placement of additional traps in the future and continued monitoring of these "sentinel traps" will provide a thorough coverage of at-risk areas. It is expected that a permanent pheromone trap network, supported by other sampling methods, will provide the final basis for outbreak forecasting.

Materials and Methods

Hardware and Software. An extensive Geographic Information System (GIS) is already in place at the Pacific Forestry Centre. Most analysis has occurred using the Environmental System Research Institute's (E.S.R.I.) software program ARC/INFO (version 6.0). Display and map production was performed using ESRI's Arcview (version 3.0a). This software sits on a UNIX network operating on a SUN Sparcstation platform. Data are stored on a RAID system disk

Digital Data. The most extensive portion of this project has been to research and collect digital data. Because the objective of hazard rating has been to define areas with similar physical and climatic parameters where looper outbreaks have occurred (i.e. elevation, temperature, etc.), the acquisition of accurate digital data is essential. Digital data have the potential to contain many sources of error; the details are lengthy and can be best explained by a good GIS textbook. Sources of error include: sampling error, equipment calibration, transformation error, classification error, machine precision, digitizing error, errors of scale, compounding, etc. Two of the main problems in obtaining data for this project were: (1) data availability was limited due to differing scales and / or prescision and (2) lack of existing data. The latter will be discussed at the end of this section.

Data Summary.

(1) Western Hemlock Looper Defoliation data (1911 to 1995)
(2) Grid Location of Mature Hemlock Stands in B.C. based upon Forest Inventory Planning Files (1996)
(3) Biogeoclimatic Zones (Ministry of Environment Lands and Parks)
(4) Digital Elevation Model (DEM) of British Columbia (USGS)
(5) Ecodistricts of Canada (CanSIS 1995)

(6) Precipitation by Ecodistrict (CanSIS 1995, Environment Canada 1961 to 1990 Climate Normals, Polestar Geomatics)
(7) Temperature by Ecodistrict (CanSIS 1995, Environment Canada 1961 to 1990 Climate Normals, Polestar Geomatics)

The WHL defoliation data were previously produced by a number of sources and based upon annual FIDS reports. WHL defoliation data were recorded during aerial surveys in late summer after insect feeding was completed. Defoliation surveys from fixed-wing aircraft were accomplished by sketching defoliated areas onto 1:100,000 or 1:250,000 scale maps, with an estimated 200- to 300-m positional accuracy for the defoliated polygons (Bob Erickson NRCAN-CFS-Pacific, personal communication). The former FIDS rangers digitized and classified defoliation areas from annual aerial survey maps since 1985 by defoliation severity. In addition, we digitized previous years' sketch maps and interpreted descriptive reports of early outbreaks into a digital representation (Parfett et al. 1985). The construction of this database was part of a prior project.

Point locations of mature hemlock stands were taken from the database component of Forest Inventory Planning (FIP) files that contain information on forest cover in ASCII text format. Mature hemlock is defined as any stand that has an age class of six and above (i.e. all stands older than 120 years). This age class was chosen based on the FIDS rangers' experience and empirical observations of WHL outbreaks. These points, representing the centroid of forest-stand polygons, are referenced in UTM coordinates to the lower left hand corner of a 2-km by 2-km grid coverage of British Columbia. Attribute information includes: stand area, composition, age class, road access, UTM zone, and percent hemlock in each stand. This point information was in a comma-delimited format. It was imported, projected, and joined in ARC/INFO as an Arc coverage. Multiple stands within the same grid were combined and stand area, age class, and percent hemlock were averaged using an area-weighted function. In addition, 1,000 m was added to the easting and the northing to place the point in the middle of the grid. This data is intended for use at a scale of 1:20,000.

Biogeoclimatic data have been made available for electronic use by the British Columbia Ministry of Forests. These data have been referenced to varying scales at different locations; specific details are available at:

ftp.env.gov.bc.ca/dist/arcwhse/wildlife/qbec_bc_meta.txt

The DEM data have a 1,000-m precision and are based upon the USGS DEM of North America. Because we were limited to our coarsest data scale, we declined to use a more detailed DEM.

Obtaining accurate and precise climate models for B.C. was the single most constraining task during the course of this project. Several groups are in the midst of creating Canadian climate models. Two of the more promising models are being constructed by D.W. McKenney of the Canadian Forestry Service in Sault Ste. Marie, Canada, and Christopher Daly of Oregon State University, U.S.A.. The decision was made to use Ecodistrict normals in the analysis. The production of these data was commissioned by Agriculture and Agrifood Canada and is readily available over the Internet via: http://res.agr.ca/CANSIS/NSDB/ECOSTRAT/DISTRICT/climate.html (Note: This website address is case sensitive). These data are an average of the 1961 to 1990 climate data in each ecodististrict. The downside of these data is that these normals are aggregated into large areas. The positive aspect is that ecodistrict data does have the advantage of its unique classifications. In either case, the availability of decent climate data has been a major limiting

factor. As a result of this, climate data were weighted considerably less than was originally planned.

Process. The rationale and theory behind the WHLHRS is that it's necessary to find areas bearing common characteristics to regions that have experienced past WHL outbreaks. This entails comparing each areas's parameters to WHL outbreak area parameters and determining the specific characteristics (if any) that exist during outbreaks (i.e., if the majority of outbreaks occurs between 500 and 600 m in elevation, then all areas between 500 and 600 m in elevation share this common characteristic with outbreaks). These common characteristics are mapped and added together to determine locations across the Province that share the same specific charcteristics as regions where WHL outbreaks have occurred. This process involves six steps:

(1) Data research and gathering. In this initial stage we examined what data might pertain to outbreaks, as well as determined the availability.

(2) Overlaying each separate parameter (DEM, Climate Data, Biogeoclimatic Zones) with WHL outbreaks.

(3) Analysis and identification of parameters common to outbreak areas. Each parameter was examined by range (e.g., elevation of 0 to 200 m, 200 to 400 m, etc.) for the WHL outbreak area. This was then compared to the WHL total outbreak area.

(4) Rasterization of the parameters is a fairly simple process. The transformation from polygons to raster data format in ArcInfo was performed using the percentages as grid values. For example, if 60% of the area where outbreaks have occurred lay within 500 to 1,000 m of elevation, the resulting grid value for those areas was 6. Areas below 1% were given a value of 0.

(5) Weighting of the parameters was performed using two methods. First, the FIDS rangers were given a survey that requested they rank the parameters in order of importance based upon their experience when considering areas at risk for WHL outbreak. The results of this survey largely ended up being a collaborative consensus among the rangers, giving a fairly uniform ranking system.

The final global weighting, based upon the rangers' ranking of importance of the eight factors, is tempered by the accuracy of the data. Parameters are also weighted locally by the distribution of past defoliation through the range of the data. Parameter suitability for hazard assessment is evaluated by whether or not there was a difference in the distribution between defoliated and undefoliated hemlock stands for each parameter. Distributions that are identical between defoliated and undefoliated stands are excluded from this analysis. The following figures were derived by overlaying defoliated and undefoliated hemlock stands with the individual parameters and comparing their distributions. Ideally, defoliated stands will possess a different distribution than undefoliated stands if a particular parameter is to be of any use in the analysis.

It is apparent that the distribution of defoliated stands when considering elevation is much more clustered than the undefoliated stands, although it tends to follow a similar trend (Fig. 1).

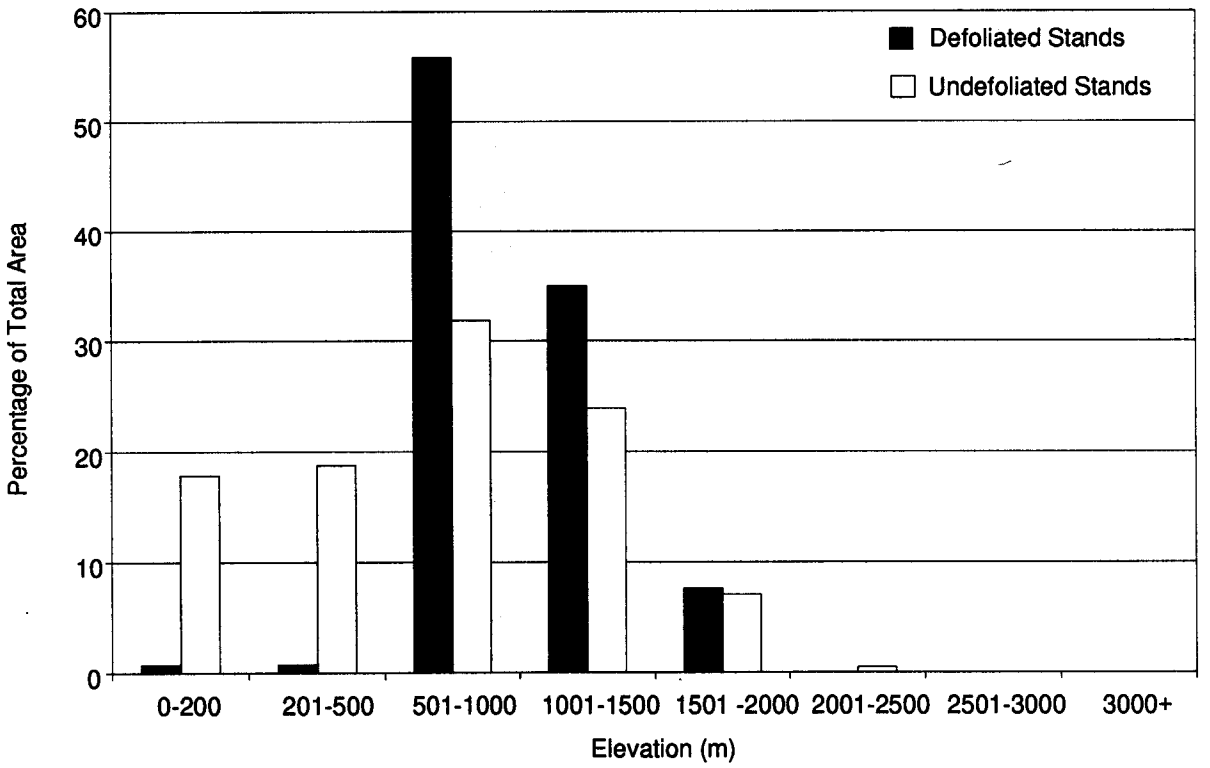

Figure 1. The distribution of undefoliated and WHL-defoliated mature hemlock stands by elevation in British Columbia.

In general, the majority of the defoliated stands were within the 500 to 1,500 m elevation range, whereas the undefoliated stands tended to be more normally distributed. The main drawback of using coarse-scale DEM data is that it does not account for detailed topography. This can be misleading, for example, where an area of high relief along the coast of B.C. has the same elevation as the valley floors of the interior. The fact that the low relief of the valley floors has harbored the majority of the attacks (Erickson 1984) is ignored in this situation. The DEM data is given the least amount of weight with regard to the final hazard model. The primary use of this data was to remove unreasonable areas from the analysis, such as high altitude regions.

Most of the defoliation occurred within ecodisticts receiving, on average, between 36 and 46 cm of precipitation in June (Fig. 2). Once again, this differed greatly from the distribution of the undefoliated hemlock stands, making this a potentially useful parameter in identifying areas prone to outbreaks.

Significant differences in the distribution of defoliated versus undefoliated stands also occurred for the biogeoclimatic zones and the rest of the climate data (minimum, maximum, and average temperatures for June and July as well as precipitation for those months).

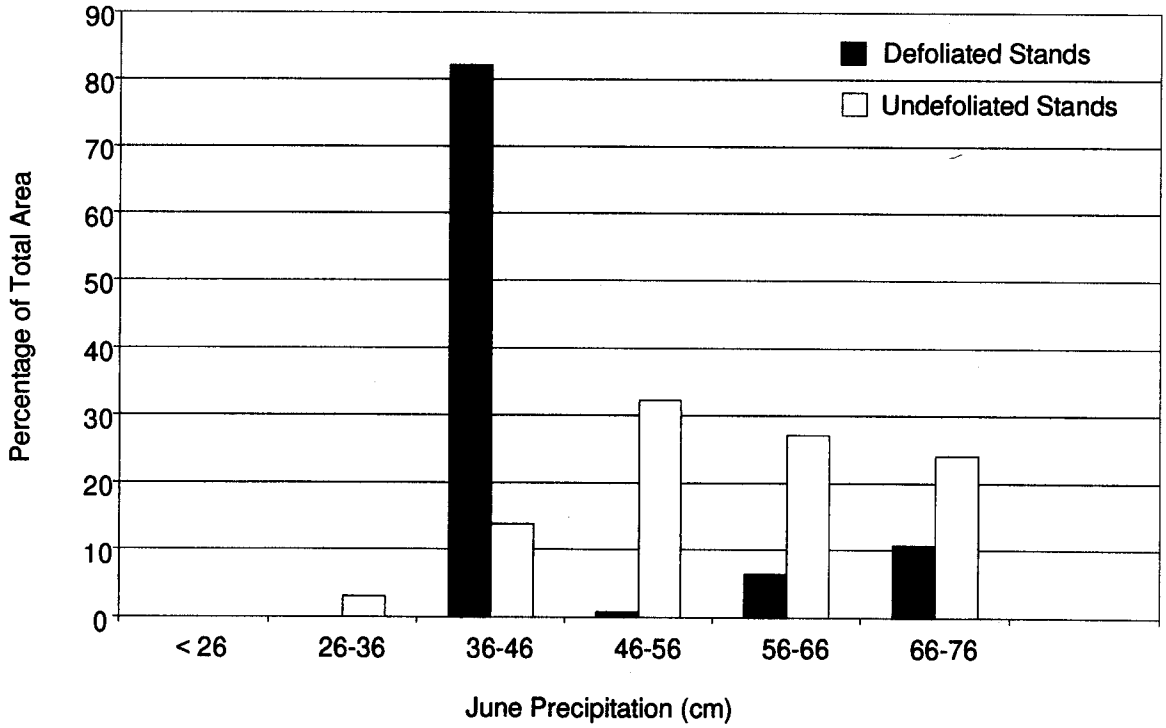

Figure 2. The distribution of undefoliated and WHL-defoliated mature hemlock stands by average June precipitation in British Columbia.

In addition to the DEM, biogeoclimatic data, and climate data, various stand characteristics were explored and were found to have differing distributions between defoliated and undefoliated stands. Given the looper's preference for mature growth hemlock, stands that were younger than 120 years were excluded from the analysis, but other characteristics, such as percent hemlock and stand size, were examined. Looper attacks are not limited to mature hemlock; however, because we are using point-source forest cover data for the entire Province, it is impossible to include all forest stands in the analysis. Actual stand preference will be examined in the next phase of analysis, utilizing more detailed forest cover data within smaller test regions.

We can see that stand areas of defoliated and undefoliated hemlocks did not differ in distribution (Fig. 3). It is evident that this lack of distinction renders stand size ineffective as a characteristic for defining areas at risk from defoliation at this scale. Overall stand hemlock content presented similar results, indicating that stand characteristics are not a factor in determining outbreaks, and that the presence of host trees is the only stand requirement.

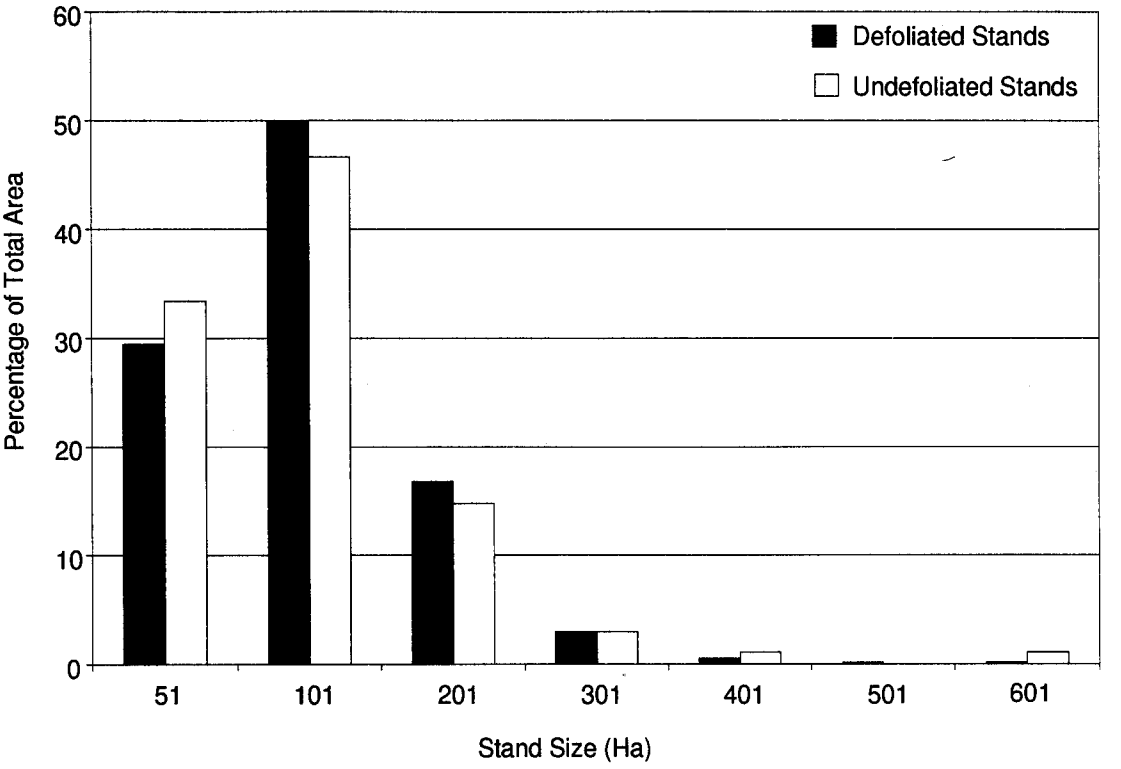

Figure 3. The distribution of undefoliated and WHL-defoliated mature hemlock stands by stand size in British Columbia.

Once the final parameters were chosen, the weighting scheme was applied to the individual parameters. Grid values were multiplied by the weight given to each parameter (Table 1). The proximity to past outbreaks was considered the most important factor at this scale, as outbreaks tend to occur within the same areas, provided the stands are not killed during the course of defoliation or through some other form of disturbance. Past hazard rating models only considered this factor in a vector-based hazard rating system. We feel that the addition of other variables improves the scope and coverage of this system.

Table 1. Weighting scheme for final parameters

Parameter	Weighting
Proximity to past outbreak	20
Location of Mature Hemlock	10
Biogeoclimatic Zones	3[a]
Climate factors	0.25[a,b]
DEM	1

[a] These weightings were multiplied by the existing grid value to give a higher number, whereas the first two parameters were binary, either receiving the weighted amount or zero

[b] The climate factors (Average June and July Precipitation, Average June and July Temperature, and Minimum and Maximum Temperature for June and July) were all added

(6) For the final hazard grid production, several weighting schemes were considered. Many models consider a multiplicative function, whereby all parameters are multiplied by one another. This type of model tends to emphasise interactions among parameters; the obvious result is that the whole is greater than the sum of the parts. The data available to the WHLHRS is somewhat non specific. Climate data is aggregated to an average of values over each ecodistrict. We felt that an additive model would be less misleading, particularly given the spatial area where specific interactions are unknown given the present data coverage. As a result, the parameters were added to one another to arrive at a summed grid. The areas that are most in common with the outbreak areas have increasingly higher numbers. The areas most at risk have experienced past outbreaks.

Once this final hazard-rating grid had been calculated, it was multiplied by a binary grid to exclude regions that are unlikely to harbor looper outbreaks. As previously mentioned, such regions include high elevations such as mountain tops, non-host biogeoclimatic zones, etc. It was hoped that one could exclude regions that have been logged of mature trees, but this data was unavailable for inclusion on a province-wide level. A negative impact of its inclusion would be that the hazard rating would exclude areas that may benefit from silviculture planning. The final raster layer has a resolution of 2,000 m. The majority of the data was able to be converted to raster with a 1,000-m resolution; however, the mature hemlock data had been located to the aforementioned 2-km grid, hence the resolution limitation.

Results and Discussion

The final raster grid gives hazard scale values from 0 to 72. Cell locations were rated as minimal, low, medium or high with regard to WHL outbreak hazard. This was an arbitrary classification, although there was some rationale used in determining bin values. There are numerous ways of devising classification schemes; however, it may be preferable for forest managers to use their own judgement when aggregating values into bins, based upon their own objectives. For the purposes of this report, a minimum was established for low risk areas; cells had to have experienced defoliation in the past, or they must possess many of the same qualities as areas that have been defoliated. Due to the spatial aggregation of the climate data, histogram analysis identified several natural breaks in the distribution of the cell values. For the purposes of display, these breaks were used to classify cell values. The data was classified as follows: < 20 = minimal risk, 20-27 = low risk, 28-36 = medium risk, and 36+ = high risk. The final hazard rating analysis was then plotted using an HP DesignJet 755CM plotter.

Figure 4 gives an overview of the areas at risk in British Columbia, projected in Lambert conformal conic, using a NAD27 datum and a Clarke1866 spheroid. The inset area detailed is the Nelson Forest Region. The highest risk areas conform to locations where defoliation has occurred in the past, as one would expect based upon the weighting system. Medium and lower risk regions are located near the high risk regions and typically include areas that have mature hemlock and/or a susceptible biogeoclimatic zone in combination with climate variables similar to previously defoliated regions. Limitations with the present hazard-rating mapping include being constrained by the lack of specific data for the entire province as well as its limited operational use. A more accurate climate model is imperative

to refining the hazard rating. Climate data have been given relatively low weighting and it is also prohibitive when considering a multiplicative model. A more refined DEM and contours would also improve the accuracy of the mapping. The present mapping provides decision support when considering the placement of pheromone trapping. It also provides a good reference for generalized risk regions.

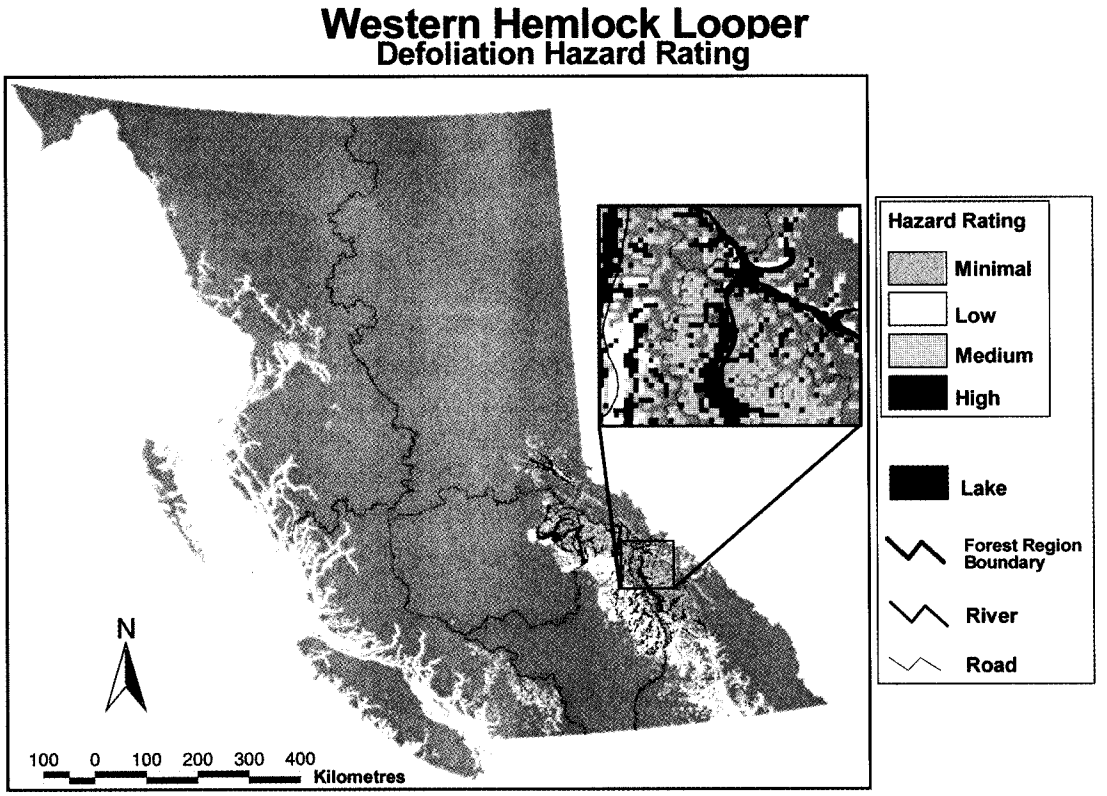

Figure 4. Coarse-scale hazard rating for the Province of British Columbia, Canada.

Although stand-level mapping was not within the scope of the initial province-wide hazard assessment, this will become the focus of the next stage of hazard and risk rating. Future refinement will focus upon specific stand attributes, drawing upon nearby climate station data, and site-specific information and data (pheromone trap counts, defoliation history, etc.) to use risk rating at the stand level.

Conclusion

Efforts in the coming months will be concentrated on the creation of a more detailed stand-level risk assessment rating. Many components are required to realize such a system and research into these components is continuing. Various models that incorporate local weather conditions, three-tree beating data on looper larval density (used as a proxy measure of population until pheromone trapping follows one cycle), biogeoclimatic zones, and tree stand characteristics will be evaluated. Current pheromone trap locations will be examined and moved if necessary after the stands most likely to suffer looper attacks have been clearly identified. The aim of creating a forecasting system to predict western hemlock looper outbreaks is an attainable goal.

The WHLHRS hinges on accurate data for its operation; however, the acquisition of accurate data requires time. Data availability is often limited by technology, storage space, and fiscal constraints. Essential to this process is a need to know how the data are being used. By identifying the end product, pheromone trapping can proceed in areas identified as having a high risk of future defoliation, and the present pheromone trap system can be expanded as trap catches rise. Climate data from these trapping sites can be used in conjunction with defoliation history and stand health to forecast the probability of future outbreaks and subsequent stand mortality. In addition to this, more accurate climate models and DEMs may be employed in the near future and used to refine existing hazard rating maps. It is anticipated that such a system will aid forest managers in dealing with western hemlock looper outbreaks in an effective fashion, both through direct and indirect pest management methods, depending on the value of the threatened stands.

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Effects of Gypsy Moth Defoliation on Tree Growth – Preliminary Models for Effects of Cumulative Defoliation on Individual Host Tree Radial Increment

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ABSTRACT Two hundred and one stands in the Ridge and Valley physiographic province of central Pennsylvania (USA) were followed from 1978 to 1985 and approximately one third of these stands were followed until 1995. Individual trees on three 0.10-acre (0.040 ha) plots per stand were visited each year. These stands experienced two major defoliation episodes by the gypsy moth (*Lymantria dispar* L.), first from 1981 to 1982 and again from 1986 to 1987; some trees and stands also experienced significant defoliation in the early 1990s. In 1995, increment core samples were collected from plot trees based on a matrix of species, stand defoliation history, and crown class (dominance). In this paper, we consider only core samples from the red oak and white oak species groups. We first examine the relationship between the sample population and the earlier classification of the forested area where the research sites are located. Results indicated that using these data, models can be developed across the site classification scheme. We then consider the appropriateness of developing a single model for both species groups. Finally, we consider a cumulative effects model with the data organized by severity of defoliation to individual trees over three years (current and the past two years' defoliation). Results provide reasonable individual tree growth effects for the species under consideration. In a forest model that uses individual tree lists to simulate forest stands, these growth effects models can be linked to population dynamics models for the gypsy moth to obtain a dynamic model for an individual stand or larger forested areas.

GYPSY MOTH (*LYMANTRIA dispar* L.) is a non-native pest in North America. After it was introduced through an accidental release in the Boston area in 1869 (Liebhold et al. 1989), it has been slowly spreading, generally moving west and south. Because the adult female does not fly more than a few feet, if at all, the population spread has been quite slow and central Pennsylvania was not generally infested until the 1980s. The data used in this study are all taken from the study area originally set up by David Gansner and Owen Herrick in 1978 (USDA Forest Service Cooperative Study 4820-FS-NE-4201-35). The objectives of the original study were to monitor gypsy moth impacts in forest stands and evaluate and refine stand hazard rating procedures that predict tree mortality and value loss following a gypsy moth outbreak (Gansner and Herrick 1984, Herrick and Gansner 1986, Gansner 1987, Herrick and Gansner 1987a). As gypsy moth first invades a new area, populations can reach outbreak proportions in just two or three years, as happened in central Pennsylvania. Gypsy moth populations were first seen in 1979, and by 1980, considerable defoliation was recorded on many of the study plots. The cooperative study ended in 1984, but by then the USDA Forest Service State and Private Forestry – Forest Pest Management staff had agreed to continue the monitoring project for several years (Gypsy moth hazard rating pilot project field guide – 1983, Jesus A. Cota and Frank J. Kenny, unpublished). In 1986, the new Forest

Pages 16-30 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.

Service gypsy moth research project RWU-NE-4507, Silvicultural Options for the Gypsy Moth, in Morgantown, WV, agreed to continue following approximately one third of the study plots. Due to limitations in available support, 75 of the original 201 stands (225 plots) were selected to be maintained.

Data collection continued following the previous standards, but tree vigor (health) ratings were added to the data set. These plots were visited annually from their establishment in 1978 until 1992 and again in 1995; although field data was collected in 1985, we do not have these data to include in our analyses. Gypsy moth defoliation continued through the 1980s and to a lesser degree in the early 1990s; however, heavy mortality in the early 1980s reduced vulnerability of many of the residual stands. The influx of natural enemies may have also reduced the severity of defoliation impacts from subsequent outbreaks in many of the stands that were severely affected by the initial outbreaks. While considerable attention has been given to defoliation effects on tree mortality (Gottschalk et al. 1998) and stand composition (Feicht et al. 1993), to date these data have not been used to investigate the effects on tree growth.

Location and Description of the Study Site

Originally, three plots were established in each of 201 stands in the Ridge and Valley physiographic province of central Pennsylvania. The stands are all located from Nittany Mountain, just northeast of State College, PA south and east to just northwest of Harrisburg, PA; all are located west of the Susquehanna River. Stands were located on ridge tops or generally dry, upper slopes that were dominated by oak species. Plots were permanently marked and described for future relocation. The 0.1-acre circular plots were laid out 300 feet apart in an equilateral triangle. Physiographic features were recorded for each plot and all trees 3 inches in diameter at breast height (dbh) were permanently marked with paint.

Due to limitations in available support, 75 stands (225 plots) of the original 201 stands were selected to be maintained beyond 1985. The original stands were classified using methods for rating stand susceptibility to defoliation and vulnerability to mortality following defoliation that were developed by Gansner and Herrick (Gansner and Herrick 1985, Herrick and Gansner 1987b). The original distribution of stands was 24, 40, and 35 percent in the high, moderate, and low defoliation classes, respectively. Approximately one third of the 75-stand subset was drawn from each of the three defoliation classes. Since the subset was selected in 1986, some stands were protected from imminent defoliation in the early 1990s by spraying and a few were sufficiently affected that they were incorporated into salvage sales. These stands have been dropped from the data set for this study. At present, there are 22, 19, and 22 stands, respectively, in the high, moderate, and low defoliation classes.

The Data

For this study, we used the final defoliation classification of stands to stratify data collection. Approximately one third of the sample trees were to come from each of three defoliation classes (high, moderate, and low), three tree dominance classes (dominant/codominant, intermediate, and suppressed), and three species groups (red oak group, white oak group, and other species). A total of 477 trees was sampled by extracting two increment cores per tree at breast height and coring as close as possible to pith. Table 1 displays the tree counts by species and species group for the 303 oaks sampled using this

stratification. In addition, 174 non-oak trees were sampled for dendrochronological growth analysis, but the majority of these were red maple (71 trees); it has been discovered that the diameter growth pattern of this species is not conducive to analysis using increment cores.

Table 1. The number of oak trees sampled by species and species group in each defoliation and dominance class

Species Alpa Code	Species Numeric Code	Species Common Name	Defoliation Class (No. Trees Sampled)		
			High	Moderate	Low
WO	802	White Oak	4-0-0[a]	1-1-1	6-5-5
CO	832	Chestnut Oak	17-19-16	18-16-16	11-22-13
White Oak Group			21-19-16	19-17-17	17-27-18
RO	833	Red Oak	13-7-5	18-16-8	16-20-8
BO	837	Black Oak	6-7-2	1-2-1	3-3-1
SO	806	Scarlet Oak	6-2-1	1-3-1	1-0-0
Red Oak Group			25-16-8	20-21-10	20-3-9

[a] The sequence a-b-c gives the counts for the three dominance classes: a = dominant/codominant, b = intermediate, c = suppressed.

Atlhough a well-distributed sampling plan was carried out, for this study we used only those oak samples that had two cores per tree and were found to be consistently dated using the Cofecha program from the International Tree Ring Society's (ITRDB) Program Library (Grissino-Mayer et al. 1997). Those samples are summarized in Table 2. We are in the process of re-dating, re-measuring, and analyzing the remaining data to increase the strength of the analysis that we present here. The increment cores were mounted, dried, and sanded. After manual dating of each sample, ring width was measured using a digital micrometer equipped with a microscope. The ring-width series measured from two cores per tree constitutes the basic raw data. For this preliminary analysis, we considered the data for five species of interest: northern red oak (*Quercus rubra*), white oak (*Q. alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and black oak (*Q. velutina*).

Table 2. The number of trees used in this study by species in each defoliation and dominance class (the comments on the sample size are based on the ITRDB standard of 10 trees to construct a species chronology)

Species Alpa Code	Species Numeric Code	Species Common Name	Defoliation Class (No. Trees Sampled[a])		
			High	Moderate	Low
WO	802	White Oak	5 (I)	0	14 (MS)
CO	832	Chestnut Oak	34 (S)	39 (S)	33 (S)
RO	833	Northern Red Oak	17 (MS)	23 (S)	29 (S)
BO	837	Black Oak	3 (I)	1 (I)	3 (I)
SO	806	Scarlet Oak	6 (I)	3 (I)	3 (I)

[a] I = Insufficient sample size
S = Sufficient sample size
MS = Moderately sufficient sample size

The available data (number of sampled trees) for each species is given in Table 2. Based on the rule of thumb set forth by the International Tree Ring Data Bank, a minimum of 10 trees was required to build a species chronology. Therefore, the comment regarding the sample size (number of trees per species) is based on this standard. Except for chestnut oak

and northern red oak, the other tree species did not have sufficient samples to carry out a more elaborate statistical analysis. We plan to complete those analyses following reprocessing of the field samples.

Tree-Ring Data Quality Control

Before tree ring chronologies were developed, the quality of the measured tree-ring series was tested using the Cofecha program of Holmes (Holmes et al. 1986) from the ITRDB Program Library (Grissino-Mayer et al. 1997). The program checked for cross-dating errors, measurement errors, and other ring width irregularities that might limit the usability of the ring-width time series for tree ring analysis. Based on the output from the Cofecha program, cores with no measurement or dating errors were used in further analysis. Cores with dating or measurement problems were removed from the data set. This resulted in a reduction of the sample size (number of trees/species). In light of the common characteristics of the species, two species groups were created:

(1) Red oak group (Species Group I): contains all data for northern red oak, scarlet oak, and black oak.
(2) White oak group (Species Group II): contains all data for white oak and chestnut oak.

Three chronologies (standard, residual, and arstan) were developed using the ARSTAN program (Holmes et al. 1986); due to negligible differences in these chronologies, we chose to use the standard chronology as a response variable in the analysis of growth in relation to defoliation. All subsequent statistical analyses showed nearly identical results for all chronologies. A standard chronology is most commonly used in tree ring research.

Methods

A ring width produced in a particular year is a function (product) of several interrelated biological, physical, stand, and climatic factors. Since our main objective was to understand or evaluate the effect of defoliation on growth, it was necessary to use a growth response variable that reflected the effect of defoliation; hence, factors that affected the width of an annual ring produced in a given year that were not related to defoliation (e.g., dbh and biological persistence) were removed from the ring-width series.

After the quality check, the ring-width series of each remaining core (for both species groups) was standardized (Fritts 1976, Cook 1985) to remove long-term trends in growth associated with tree age, size, and stand dynamics. The need for standardization prior to creating a stand-average ring chronology is discussed in detail in Fritts (1976) and Cook (1987). Because the ring-width series were rarely more than 100 years long, negative exponential or linear regression curves were used to detrend the series.

After the growth curve was estimated for each series, each value of the series was then divided by the corresponding value of the growth curve. The resulting ratio was a series without trend or long waves. This process transformed the ring-width values to tree-ring indices that exhibited a mean of 1 and a variance that was independent of tree age, position within the trunk, and mean growth of the tree. This kind of transformation is called detrending, or standardization, and its purpose is to remove long-term trend or low frequency variance from the tree-ring series.

Mathematically, let R_t be the ring width (mm) for year t and G_t be the fitted ring width (mm) from the detrending model for year t. Then

$$I_t = \frac{R_t}{G_t}$$

is a unitless tree-ring index for year t. In this step, R_t for each core is transformed into I_t. The resulting index series (I_t), also called the "filtered" or "smoothed" series for each core, is a series "free" of long-term trend or low frequency variance. If $I_t > 1$, then growth in year t is above average, and if $I_t < 1$, then growth in year t is below average.

An additional source of variation in ring-width series arises from the persistence of various effects into subsequent years through variation in food reserves and preconditioning of growth. That is, tree ring series invariably possess some degree of serial persistence or autocorrelation that is principally due to physiological preconditioning within the tree. Therefore, the information contained in a given ring width is somewhat determined by past tree growth and vigor. The autocorrelation structure of tree ring indices can be adequately modeled as an autoregressive process. The magnitude of autocorrelation can be assessed by calculating autocorrelation and partial correlation functions. The general autoregressive (AR) process of order P has the form:

$$I_t = \left(\sum_{i=1}^{P} \phi_i I_{t-i} \right) + e_t$$

where:

I_t is the observed process for year t, e.g., ring index for year t

ϕ_i is the autoregressive coefficient of the AR (P) process, i years past

e_t is an unobserved error that does not contain any autocorrelation

Programs like ARSTAN use such time series techniques to model and transform each filtered series to a residual series statistically equivalent to white noise. That is, due to the existence of autocorrelation in the indices, the ring-width index of each year for each core is autoregressed by the index of the previous year. The residuals of the autoregression model are used as response variables for further statistical analysis. However, the analyses performed using these pre-whitened chronologies provided similar results as those using the standard chronologies in this study.

Results

Chronology Comparison. After the species groupings were performed, the data were analyzed in ARSTAN to create standard chronologies for each defoliation rating: high, moderate, and low. Figure 1 compares the standard chronology for high, low, and moderately rated stands in Species Group I. Figure 2 depicts the same information as in Figure 1 but for Species Group II. In both figures, there was no apparent difference in chronologies due to defoliation rating (high, moderate, and low). To confirm this visual comparison of chronologies, a two-way analysis of variance was performed to detect any statistical significance. The analysis was conducted using year and the ratings (high, moderate, and low) as treatment groups and standard chronology as the response variable.

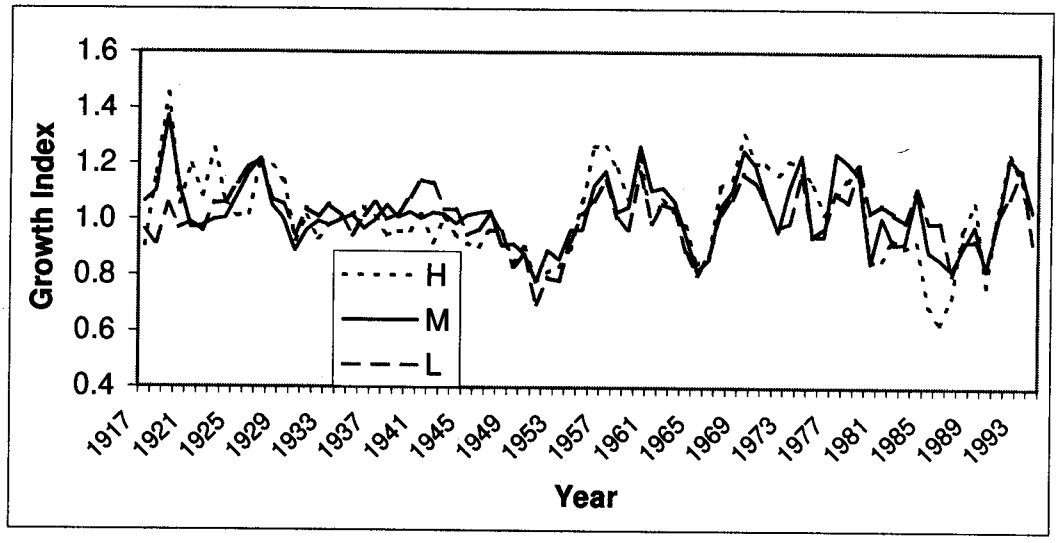

Figure 1. Standard chronologies for Species Group I (red oak group) in the high (H), moderate (M), and low (L) defoliation classes.

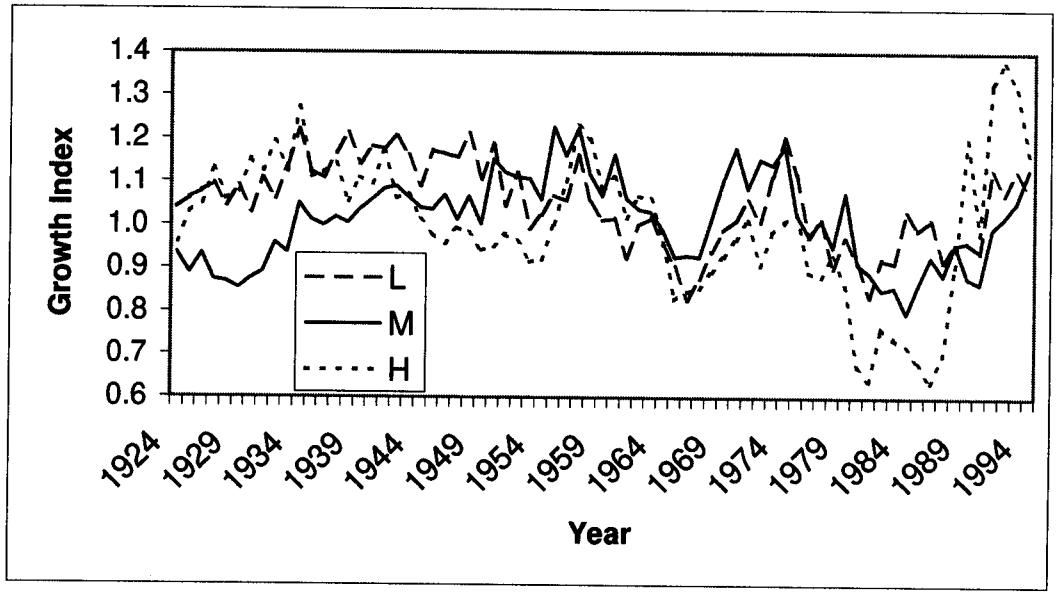

Figure 2. Standard chronologies for Species Group II (white oak group) in the high (H), moderate (M), and low (L) defoliation classes.

Analysis of variance was used to investigate the differences among standard chronologies within the original defoliation classification. Tables 3 and 4 show the results of the ANOVA. The response variable in this analysis was the standard chronology index and the independent variables were year and defoliation class.

Table 3. Summary statistics and a two-factor analysis of variance comparing standard chronologies in the high, moderate, and low defoliation classes for Species Group I (red oak group)

SUMMARY						
Defoliation Class	*Sample Size*	Sum	Average	Variance		
High	78	79.827	1.023423	0.02347		
Moderate	78	79.745	1.022372	0.014467		
Low	78	78.673	1.008628	0.010654		
ANOVA						
Source of Variation	***SS***	df	***MS***	***F***	P-value	F crit
Year	2.921063	77	0.037936	7.120945	4.3E-25	1.371692
Class	0.010631	2	0.005315	0.99776	0.371075	3.054765
Error	0.820414	154	0.005327			

Table 4. Summary statistics and a two-factor analysis of variance comparing standard chronologies in the high, moderate, and low defoliation classes for Species Group II (white oak group)

SUMMARY						
Defoliation Class	Sample Size	Sum	Average	Variance		
Low	71	74.656	1.051493	0.009523		
Moderate	71	71.848	1.011944	0.010379		
High	71	71.173	1.002437	0.025733		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Year	1.940603	70	0.027723	3.095365	6.79E-09	1.392513
Class	0.096112	2	0.048056	5.365612	0.005685	3.060762
Error	1.253876	140	0.008956			

These results indicated that for both species groups, there were no significant differences among the standard chronologies due to differences in defoliation classification of the stands. Because the P value for the white oak group was low, we re-analyzed just the data where defoliation data existed to confirm the fact that the between-class differences were not significant. The result was not significant over the shortened range ($F_{2,32} = 1.01896$, $P = 0.37238$). Thus, it was reasonable to combine tree ring series from these classes in further analysis.

Growth In Relation To Defoliation. Individual tree defoliation data was only available from 1978 to 1992. The pattern of average defoliation over time is depicted in Figures 3 and 4 for Species Group I and II, respectively. The figures indicate that defoliation varied in a haphazard manner with no clear and detectable cyclic trend. A meaningful statistical comparison of the defoliation data among the different classes could not be made due to (1) small sample size (14 observations) and (2) the fact that the assumption of homogeneity of variance was violated (see Table 5).

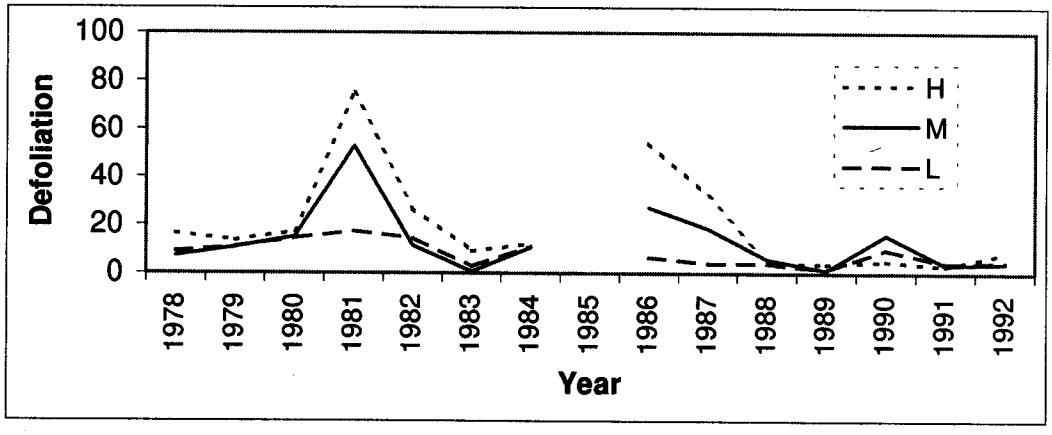

Figure 3. Pattern of average defoliation over time for Species Group I (red oak group) at high (H), moderate (M), and low (L) defoliation sites.

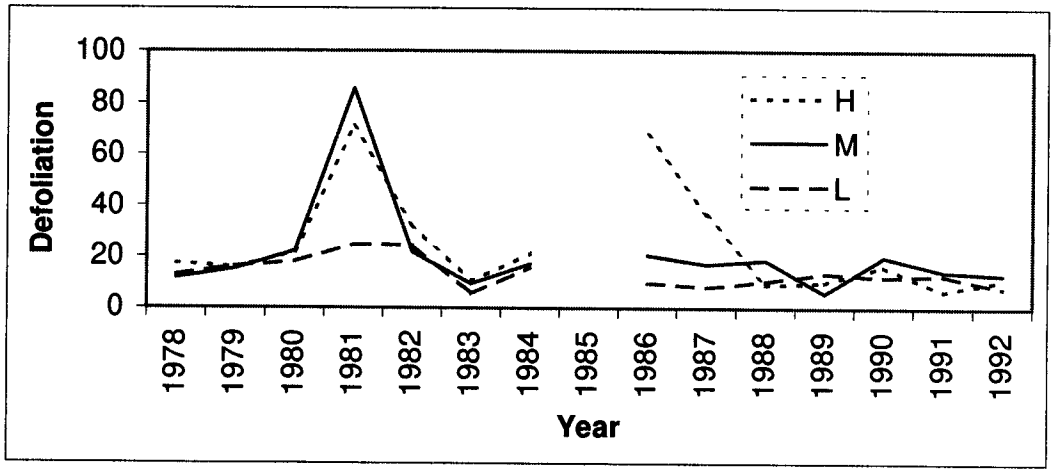

Figure 4. Pattern of average defoliation over time for Species Group II (white oak group) at high (H), moderate (M), and low (L) defoliation sites.

Table 5. Summary statistics (sample size, total, average, and sample variance) of defoliation data by defoliation class for both species groups (red oak and white oak) showing a clear trend in average defoliation and considerable differences in variance

SUMMARY: Red Oak Group				
Defoliation Class	Sample Size	Sum	Average	Variance
High	14	271.6667	19.40476	660.3022
Moderate	14	185.1429	13.22449	182.941
Low	14	110.4348	7.888199	27.62417
SUMMARY: White Oak Group				
Defoliation Class	Sample Size	Sum	Average	Variance
High	14	357.1429	25.5102	333.3931
Moderate	14	268.5714	19.18367	341.1976
Low	14	208	14.85714	37.20879

There was a considerable difference in variability of the defoliation data in stands rated high, moderate, and low, as was expected from the original classification scheme. The summary in Table 5 indicates that variability appeared to increase with the defoliation rating of the stand. It also shows a clear pattern in average defoliation (Fig. 5) where stands rated high had the highest average defoliation, followed by stands rated moderate and low.

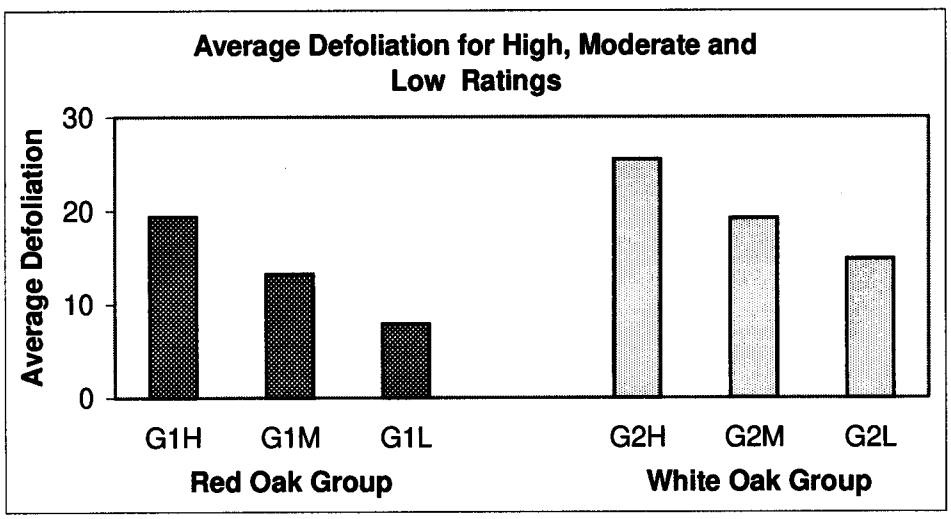

Figure 5. Trend of average defoliation with respect to defoliation classifications for both species groups, indicating a decreasing trend in average defoliation across these classes. (G1 = Species Group I, G2 = Species Group II, H=high, M=moderate, and L=low).

A comparison of chronologies for the period where defoliation data was available (1978 to 1992) showed that the standard chronology for stands classified as high tended to be lower than those of the other stands (Fig. 6 and 7).

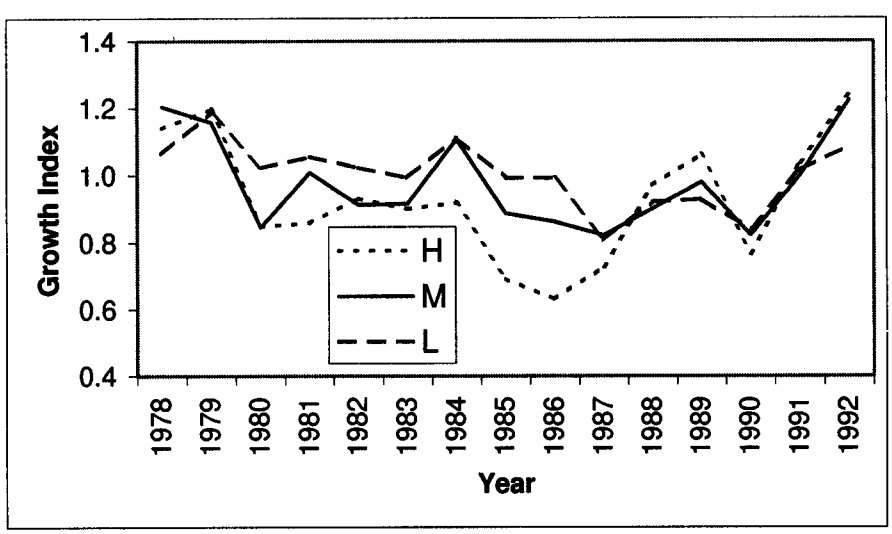

Figure 6. Pattern of the standard chronology for those years when defoliation data were available for Species Group I (red oak group) at high (H), moderate (M), and low (L) defoliation ratings; this shows that the chronology for stands rated high is well below the chronologies for stands rated moderate and low for most of the period.

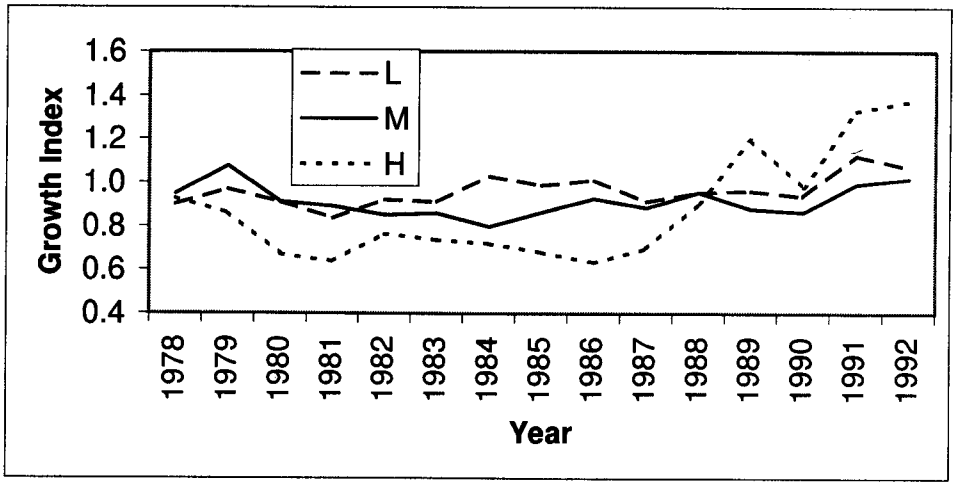

Figure 7. Pattern of the standard chronology for those years when defoliation data were available for Species Group II (white oak group) at high (H), moderate (M), and low (L) defoliation ratings; this shows that the chronology for stands rated high is well below the chronologies for stands rated moderate and low for most of the period.

After recognizing that the effects of defoliation on growth (standard chronologies) between the species groups were similar, we combined the samples and restructured our analysis to investigate the differences among the defoliation histories of these data. We reorganized the sample data into five defoliation severity groups:

(1) At least 2 years of 90+% defoliation (Group 1 or G1)
(2) At least 2 years of 80+% defoliation (Group 2 or G2)
(3) At least 2 years of 70+% defoliation (Group 3 or G3)
(4) At least 2 years of 50+% defoliation (Group 4 or G4)
(5) All remaining samples

The defoliation pattern among these groups and the effects on growth can be seen in Figures 8 and 9, respectively.

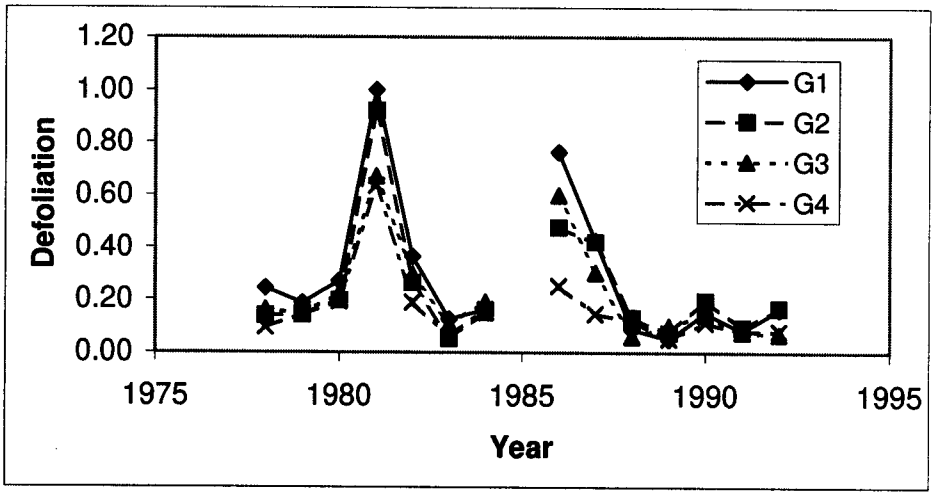

Figure 8. Defoliation data (proportion of crown defoliated) by defoliation severity group.

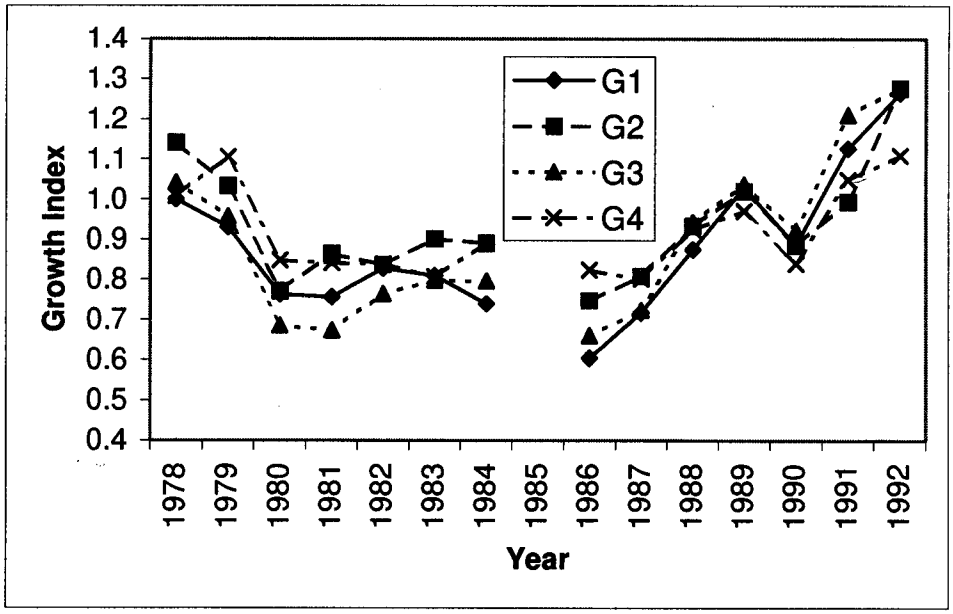

Figure 9. Growth index data by defoliation severity group.

A review of these data revealed the expected differences in defoliation among groups while the differences among series growth indices showed a consistency that suggested that there was not a significant difference among these groups. Analysis of variance supported this fact (Table 6).

Table 6. Analysis of variance for grouped series differences

SUMMARY						
Defolation Severity Group	Sample Size		Sum	Average		Variance
Group 1	14		12.33	0.880714		0.031293
Group 2	14		13.104	0.936		0.021365
Group 3	14		12.487	0.891929		0.039022
Group 4	14		12.86	0.918571		0.012165
ANOVA						
Source of Variation	SS	Df	MS	F	P-value	F crit
Between Groups	0.0265	3	0.008833	0.340245	0.796298	2.782599
Within Groups	1.349987	52	0.025961			
Total	1.376487	55				

The results in Table 6 suggested that we could combine and analyze the data in a single defoliation effects model. We then constructed cumulative defoliation effects models of the form $G_t = F(defol_t + defol_{t-1} + defol_{t-2})$, where G_t is the growth index for year t as a function of the current and past two years of defoliation. Defoliation was expressed as a proportion of the crown defoliated (between 0.0 and 1.0) for each year so the cumulative defoliation value can be between 0.0 and 3.0. This can be seen in Figure 10.

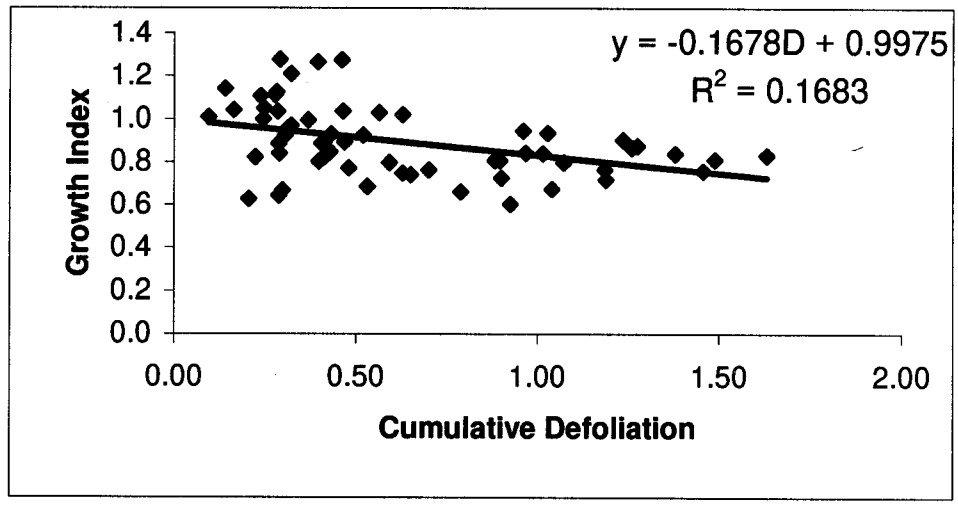

Figure 10. Growth index as a function of cumulative defoliation over the current and past two years. Cumulative defoliation values range between 0.0 and 3.0 as the sum of three proportions.

This showed a clear decrease from the norm ($G_t = 1$) for the standard chronology. Testing this model using linear regression produced a very reasonable, as well as highly significant, trend and intercept, as can be seen in Table 7.

Table 7. Regression results for current growth index as a function of the current and the past two years' defoliation

Regression Statistics					
Multiple R	0.410244				
R^2	0.1683				
Adjusted R^2	0.15396				
Standard Error	0.15034				
Observations	60				
ANOVA					
	df	SS	MS	F	Significance F
Regression	1	0.265274	0.265274	11.73669	0.001132
Residual	58	1.310922	0.022602		
Total	59	1.576195			
	Coefficients	Standard Error	t Stat	P-value	
Intercept	0.997489	0.036316	27.46695	6.16E-35	
D	-0.16779	0.048977	-3.42589	0.001132	

First note that the intercept was quite near 1.0, which implies that the model predicts a neutral effect (no growth impact) for either very light defoliation or as defoliation decreases. Following the development of this cumulative effects model, we considered the possible effects of having no defoliation data for these trees in 1985. After reviewing Figure 8, we considered using an estimated value of 20 percent for the average in each defoliation class. Using these data proved to change the model only slightly. The regression results are presented in Table 8 and Figure 11 provides the fitted curve.

Table 8. Regression results for current growth index as a function of the current and the past two years' defoliation after assuming defoliation in 1985 averaged 20 percent

Regression Statistics					
Multiple R	0.510936				
R^2	0.261056				
Adjusted R^2	0.248315				
Standard Error	0.141709				
Observations	60				
ANOVA					
	df	SS	MS	F	Significance F
Regression	1	0.411475	0.411475	20.49036	3.03E-05
Residual	58	1.16472	0.020081		
Total	59	1.576195			
	Coefficients	Standard Error	t Stat	P-value	
Intercept	1.029956	0.035483	29.02697	3.1E-36	
D	-0.20642	0.045601	-4.52663	3.03E-05	

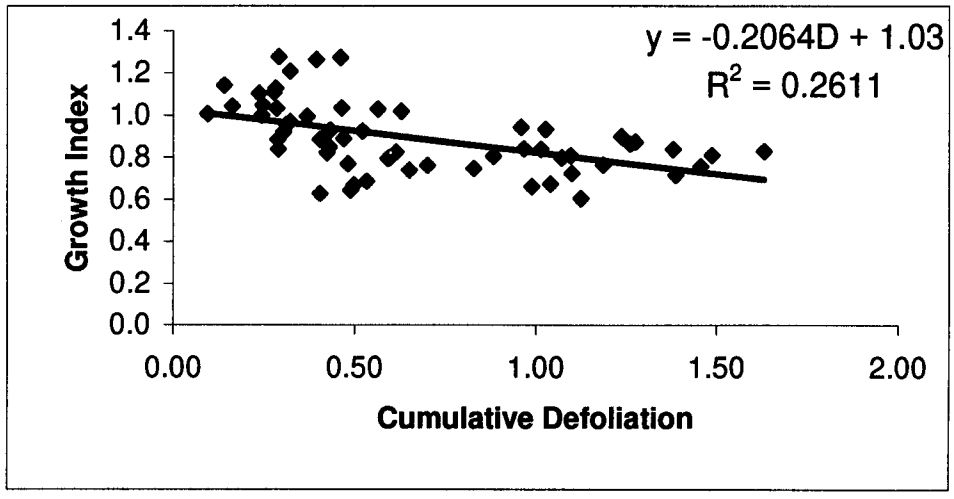

Figure 11. Growth index as a function of cumulative defoliation after substituting 20 percent for missing defoliation data in 1985. Cumulative defoliation values range between 0.0 and 3.0 as the sum of three proportions.

Discussion and Conclusions

The models that were derived from these data are quite reasonable considering the range of data. We would expect that either of these models would provide an acceptable means to predict the effects of defoliation outbreaks on oak species. Because we are able to remeasure and verify the quality from the remaining samples, we expect to strengthen these models as well as investigate the possible interactions of growth effects associated with site conditions and tree vigor or health that may adversely affect growth more strongly during outbreaks. The current models available for predicting individual tree loss from defoliation (Colbert and Sheehan 1995) within the gypsy moth life system model (GMLSM) were

developed by fitting data published earlier by Campbell and Garlo (1982) and Baker (1941). The models developed for the GMLSM indicate a maximum decrease in growth of approximately 40 percent, whereas these models predict slightly less for the range of data averages in the aggregate chronologies. However, at the extreme of individual tree defoliation, these models would predict more growth loss.

These models are the first that we are aware of that were derived directly from field data where both defoliation and growth data were available for individual trees. Muzika and Liebhold (1999) provided estimates for individual host species, including those in the red oak and white oak groups considered here. Their analyses indicated that both current and the previous year's defoliation affected growth. They did not consider lag beyond one year nor did they construct a cumulative effects model. Their approach did provide different weights (separate coefficients) for the current and previous year's defoliation.

Acknowledgments

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Recent Invasions of Five Species of Leafmining Lepidoptera in Hungary

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ABSTRACT Five species of leafmining Lepidoptera have expanded their range into Hungary during the last two decades. One of them (*Phyllonorycter leucographella*) is native to Southern Europe, while three species (*Argyresthia thuiella*, *Parectopa robiniella*, and *Phyllonorycter robiniella*) were accidentally introduced to Europe from North America. The origin of *Cameraria ohridella* is still not certain, although it was probably introduced from Asia. Three of the five species (*A. thuiella*, *Ph. Leucographella*, and *C. ohridella*) attack popular ornamental trees (*Aesculus*, *Pyracantha*, and *Thuja*) and the other two feed exclusively on black locust (*Robinia pseudoacacia*), an introduced, but widely planted, tree. The history of introduction, range expansion, and present and potential economic importance of these five insects in Hungary are discussed.

THE SPREAD OF organisms is always followed with great interest, particularly if they are exotic and have the ability to cause significant economic and ecological damage. In the last two decades, a number of insect species have expanded their ranges into Hungary. A number of exotic insects were accidentally introduced from North Africa, while others expanded their distribution from Southern Europe northward into Hungary. Many of these species have become established. These newly established insects include Lepidoptera, scale insects, gall wasps, and gall midges, and even dragonflies. Five species of leafmining microlepidoptera have invaded Hungary during the last 15 years. Three of them attack popular ornamental trees and shrubs (*Aesculus* sp., *Pyracantha coccinea* M.J. Roemer, and *Thuja* sp.), and the other two feed on black locust (*Robinia pseudoacacia* L.). Black locust was purposefully introduced into Hungary in the early 18th century and now comprises 20% of Hungarian forests.

The Invading Species

***Argyresthia thuiella* Packard 1871 (Argyresthiidae).** The wingspan of the adult of this leafmining moth is ca. 8 mm. The moths fly in early summer, and females lay their eggs on young leafelets. It has only one generation a year, unlike the other four leafmining species that have multiple generations. Larvae hatch within 1 to 2 weeks and the caterpillars mine the terminal shoots of the hosts, *Thuja occidentalis* (L.) (particularly the column-like form) and *Chamaecyparis lawsoniana* (A. Murr.) Parl. The larvae overwinter and later pupate in the mine. Symptoms of damage are browning and abscission of the attacked terminal shoots.

The species was accidentally introduced from Canada and the USA to Europe with *Thuja occidentalis* on three separate occasions: in 1971 to the Netherlands, in 1975 to Germany and in 1976 to Austria (Kurir 1983). From these introductions, it spread and was

Pages 31-36 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.

later recorded in several other European countries, including Switzerland (1989), Croatia (1991), and the Czech and Slovak Republic (1989) (Povolny 1990, Opalicki 1991).

The species probably spread into Hungary from neighboring Croatia. It was first recorded in the summer of 1997 near Zalaegerszeg in southwestern Hungary. It is possible that this insect was already present in Hungary prior to this, but population densities were below detectable levels. The distribution of this insect is currently restricted to southwestern Hungary, but will probably gradually spread and infest its hosts throughout the whole country. Because this species is univoltine and the host plants have an island-like distribution, a relatively slow rate of spread can be predicted. However, transporting infested ornamental plants within the country may help create newer foci of colonization and accelerate its spread within Hungary. The species has become part of the European fauna since its introduction in the 1970s and appears to have the ability to cause significant aesthetic and physiological damage to its hosts, two very popular ornamental plants.

***Phyllonorycter leucographella* (Zeller, 1850) (Gracillariidae).** The adult wingspan of this small leafmining moth is about 6 to 8 mm. The species usually has 2 to 3 generations per year in Hungary. Caterpillars feed in a long mine close to the upper leaf surface and overwinter in the mines. Its principle host is firethorn, *Pyracantha coccinea* M.J. Roemer, although occasionally it also feeds on *Crataegus* spp.

This insect is native to Southern Europe and was probably introduced accidentally into several countries in Western Europe on transported plant material. Firethorn is one of the most popular ornamental shrubs in many European countries. It keeps its leaves in the winter, and larvae overwintering in the mines are hard to detect. Because of this cryptic habit, it is very easy to unknowingly transport infected plant material.

In the 1970s, *Ph. leucographella* was found in France, Switzerland, and Austria. Since *Pyracantha* is native to the Mediterranean regions of France, it is possible it was always present there without being reported because of its cryptic habit. Even though this insect has not been reported from countries in Europe other than those mentioned above, it can be assumed that *Ph. leucographella* is likely to occur in Spain, Greece, Albania, Russia (Crimea), Turkey, and the southern part of the former Yugoslavia where its principle host plant is native.

This insect was later recorded in Germany (1980) and the Netherlands (1984), etc. (Stigter and Frankenhuyzen 1991, Sefrova 1999). By the mid 1990s, it had spread in continental Europe as far north as Denmark (Buhl et al. 1994). Considering the "jump-like" or multiple foci of spread within Europe, one may conclude that several separate introductions have occurred.

The first record of this insect in the United Kingdom was in 1989 (Emmet 1989). It is almost certain that the species was transported across the Channel on infected plants. Nash et al. (1995) studied the spread of this species in Great Britain. Besides the "natural" spread of the insect, they found several foci of colonization outside the main distribution range that were undoubtedly due to human activities.

This insect has spread eastward into Hungary and was first recorded in Sopron, near the Austrian border, in the fall of 1991 (Csóka 1992). The rate of spread within Hungary is slow compared to the spread of *Parectopa robiniella, Cameraria ohridella,* and *Phyllonorycter robiniella.* In nearly 10 years, it only advanced ca. 200 to 220 km eastward. The difference in the distribution of the hosts of these species may explain the difference in the rate of spread. *Aesculus* and *Robinia* can be found outside cities and villages as

continuous rows of shade trees alongside roads, and *Robinia* is also grown in shelter belts. On the other hand, *Pyracantha* is restricted to cities and villages and is planted as an ornamental shrub, providing rather small and sporadic islands of the host plant, making colonization by this insect much more difficult.

***Cameraria ohridella* Deschka and Dimic, 1986 (Gracillariidae).** Adults of this species have a wingspan of ca. 6 to 8 mm. In Hungary it has 2 to 3 generations per year. The moths of the first generation fly in April and May. The first generation larvae mine leaves in the lower part of the crown. The 2nd and 3rd generations mine leaves higher in the crown, with the result that the leaves turn brown progressively from the bottom up through the crown. In heavy infestations, up to 100 to 150 mines can be found in a single leaf. The pupa overwinters in the leaf litter. Heavy infestations cause browning and early leaf fall in July, and repeated defoliation over several years can cause tree mortality.

Members of this family are genus monophagous on *Aesculus,* but can occasionally complete their development on *Acer platanoides* L. and *A. pseudoplatanus* L. (Gregor et al. 1998). The introduced North American species of *Aesculus (pavia, parviflora,* and *glabra*) appear to be more resistant than *A. hippocastanum,* a native of Europe.

The native distribution range of this species is not clear. The genus *Cameraria* was not represented by any other species earlier in Europe, but several species belonging to this genus can be found both in Asia and North America. This supports the idea that *C. ohridella* was introduced into Europe. The most likely hypothesis for its introduction into Europe is that the species was accidentally introduced from China into Albania in the last 30 years by immigrants and later spread on its own until it was first found at Lake Ohrid in Macedonia in 1985 and described as a new species a year later. Lake Ohrid is located very close to the Albanian border. It was not possible to check this hypothesis because until recently Albania was closed to outsiders and it is still closed to scientists from Europe. In the late 1980s the species expanded its range throughout the countries of the former Yugoslavia. In 1989 it was found in Zagreb, Croatia (Maceljski and Bertic 1995).

In 1989, *Cameraria ohridella* was discovered near Linz, Austria, approximately 1,000 km northwest of Lake Ohrid, Macedonia. It was introduced on purpose by an entomologist to study the species, unfortunately without considering the possible consequences of its escape. This Austrian location served as a starting point for invasion to many Central European countries. *Cameraria* spread from Linz in several directions, reaching Germany in 1992 (Heitland et al. 1999, Skuhravy 1999), the Czech Republic in 1993 (Skuhravy 1999), France in 1992 (Skuhravy 1999), Switzerland in 1998 (Kenis and Forster 1998), Slovakia in 1994 (Zúbrik 1998), and Poland in 1998 (Skuhravy 1999). Skuhravy (1999) summarized the expansion of the European distribution of this species. It is probable that the introduction of this insect into Hungary was from two different directions. Damage by this insect was first reported in 1993 in southwestern Hungary, very close to the Croatian and Slovenian border (Szabóky 1994), suggesting that this insect spread from the south into Hungary. In the following year (1994), very high population levels were reported near Sopron in northwestern Hungary, close to the Austrian border. It is highly likely the invasion near Sopron was from Austria, where the species was already common and abundant by that time. By 1997, the species had shown rapid expansion and was distributed throughout the whole country. The flying adults of the first generation probably crossed the Danube in 1994 where it flows from north to south in the middle of the country. The first reported signs of damage on trees east of the Danube were found in midsummer of 1994. At present, the insect can be

found practically everywhere in Hungary where its hosts are present, and this insect is extremely abundant in many places. The host, *Aesculus* spp. (particularly *A. hippocastaneum*), is the most common and popular ornamental tree both in Hungary and Central Europe and can be found in nearly every town and village. Hickory is also one of the preferred shade trees along roads between towns and villages. These roadside trees probably accelerated the expansion of its range significantly. In addition, *A. hippocastaneum* is also planted in some forested areas in Hungary to increase the food supply for game animals, such as red deer and wild boars.

***Parectopa robiniella* Clemens 1859 (Gracillariidae).** This tiny leafmining moth has a wingspan of 5 mm and has 2 to 3 generations per year in Hungary. It is monophagous, feeding only on black locust, and its caterpillars make irregular, forking mines near the upper leaf surface. The caterpillars overwinter in cocoons spun on leaves and pupate in the spring. *P. robiniella* is native to North America and was accidentally introduced into Italy, where it was first found near Milan, northern Italy, in 1970 (Vidano 1970). From there it gradually spread in several directions. People probably facilitated this spread to several additional locations in Europe.

This insect was first reported in southern Hungary in 1983 (Maceljski and Igrc 1984). It spread relatively quickly within the country and within ca. 6 to 8 years became common everywhere in Hungary and very abundant in many places. It is interesting to note that in the first years of its invasion into Hungary, it was found mainly on small trees and sprouts of its host trees; it now also attacks mature host trees. Severe infestations cause early leaf fall as early as late June. Damaged trees often refoliate if weather conditions are favorable. The area damaged by this species has increased significantly during the last decade (Csóka 1998).

***Phyllonorycter robiniella* Clemens 1859 (Gracillariidae).** The adults of this small moth have a wingspan of 5.5 to 6.5 mm. Like *P. robiniellia*, this species is also monophagous on *Robinia pseudoacacia* and has 2 to 3 generations per year. The caterpillars make irregular, oval-shaped blotch mines on the underside of the leaves. Like the former species, it is also native to North America and is found there throughout the natural range of *Robinia pseudoacacia*. *Ph. robiniella* was accidentally introduced to Europe and first reported near Basel, Switzerland, in 1983 (Whitebread 1990). Later, it was also reported in France, Germany, northern Italy (1988), Austria (1989), and Slovakia (1992). It spread gradually through Austria, reaching Hungary in the mid 1990s. Damage (leaf mines) caused by this insect was first observed in the autumn of 1996 in northwestern Hungary (Szabóky and Csóka 1997). However, according to Sefrova (pers. comm.), it was already present in Hungary in 1993. It causes the same type of damage as *Parectopa robiniella* – leaf fall in early or mid summer. These two species often occur together. The long-term impact of repeated defoliation by this insect is as yet unkown.

The rate of spread of this species increased significantly after reaching the Hungarian border. In 2 years it had practically invaded the whole country, a distance of ca. 500km from west to east. The extremely fast spread of these two species (*Ph. robiniella* and *Parectopa robiniella*) on black locust, particularly *Ph. robiniella*, is a phenomenon unique to Hungary because black locust, the most abundant tree species, is found throughout the whole country. Black locust stands comprise more than 340,000 hectares, or 20% of the forested area in Hungary. This tree was introduced in the early 18th century and later was widely planted throughout the country. Hungary currently has more black locust stands than all other European countries combined. Widespread planting programs were justified by the desirable

characteristics of this species: it grows fast (even on relatively poor sites), the timber is hard and quite resistant to woodrot, and its wood is also excellent for firewood. The tree is also good for honey production and does not have any serious pests. The last reason may no longer be accurate and justified. Because of the importance of this host plant in Hungary, the last two species of leafminer have the potential to cause negative economic impacts in general and have very serious effects on the Hungarian forest industry in particular, probably greater than anywhere else in Europe.

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Implementation of a Program to Optimize the Use of *Bacillus thuringiensis* Against the Browntail Moth (*Euproctis chrysorrhoea*)

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ABSTRACT Laboratory and field studies were conducted over a period of 3 years to develop formulations of *Bacillus thuringiensis* (*Bt*) that would be efficacious against the browntail moth (*Euproctis chrysorrhoea*), a serious pest of forest and shade trees and shrub vegetation in coastal areas of Maine and Massachusetts. Standard feeding bioassays and a novel electrophysiological procedure were used to determine the susceptibility of browntail moth larvae to the insecticidal crystal protein toxins that are incorporated into commercial formulations of *Bt*. The electrophysiological method, voltage/current clamp analysis, is discussed in detail.

THE BROWNTAIL MOTH (*Euproctis chrysorrhoea*) (BTM), is found throughout Europe, northern Africa, and Asia, where it defoliates orchard, forest, and shade trees (Lipa 1996). In the United Kingdom it is found most frequently on woody Rosaceae and on fruit trees in urban and suburban areas (Kelly et al. 1989). In Croatia, *E. chrysorrhoea* is a serious pest in English oak (*Quercus robur*) forests, 6,000 to 10,000 ha of which were sprayed annually with a pyrethroid insecticide during a recent outbreak (B. Hrasovec, pers. comm.). Each year, BTM larvae damage cork oak (*Q. suber*) plantations in southern Europe and stands of deciduous trees in central and eastern Europe. Outbreaks occur at intervals of 7 to 8 years and last 3 to 4 years (Lipa 1996). In addition, both larvae and pupae are covered with urticating hairs that can cause a severe and persistent skin rash on humans and trigger an asthmatic reaction in sensitive individuals (Blair 1979).

E. chrysorrhoea was accidentally introduced into the United States in 1897 near Somerville, Massachusetts (Schaefer 1989). By 1914, the BTM was found throughout most of New England and southern Canada. Populations declined thereafter and by 1960 there were residual populations only on the outer dunes of the Cape Cod National Seashore and on the islands in and around Casco Bay, Maine.

However, there was a subsequent resurgence of *E. chrysorrhoea* populations that began in 1989. By 1995, species of *Quercus,* serviceberry (*Amelanchier canadensis*), beach plum (*Prunus maritima*), and bayberry (*Myrica pensylvania*) were severely defoliated on 28 islands in Casco Bay, while the infestation on the mainland encompassed 176,000 ha. On the National Seashore, the Park Service is concerned about the impact of *E. chrysorrhoea* on the shrub vegetation (Rosaceae) that stabilizes the outer dunes, the effect of urticating hairs on the high-density visitor population, and the displacement of native species. In the Casco Bay area, concern is focused on defoliation, unsightly webs, and public health on the inhabited islands and heavily populated coastal areas. Beginning in the mid 1980s, attempts were made to control the BTM on shrub vegetation on National Park Service lands by mechanically

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clipping overwintering webs and destroying them. However, this approach is not practical where webs are on terminal branches of oak trees that are inaccessible from the ground. Although a chemical pesticide, diflubenzuron, is effective against the BTM, it has a long residual and is toxic to certain aquatic arthropods. Residents in and around Casco Bay expressed concern about the proximity of spray blocks to the ocean and possible adverse effects of diflubenzuron on the shellfish industry and the commercially important American lobster (*Homaris americanus*).

Early attempts to control BTM populations with commercial formulations of *Bacillus thuringiensis* (*Bt*), a microbial pesticide that is used successfully against the closely related gypsy moth (*Lymantria dispar* L.) and other Lepidoptera pests, were not effective (Bradbury 1995). A series of studies was initiated in 1995 to determine the reason for the poor performance of *Bt* against the BTM and to develop and evaluate novel formulations of *Bt* that could be used to control BTM populations in environmentally sensitive habitats.

Materials and Methods

Rearing Methodology. Laboratory bioassay studies on BTM larvae were initiated in June 1995. Late-stage larvae were collected from an infestation in Maine and returned to the Northeastern Research Station laboratory at Hamden, Connecticut. Repeated attempts to obtain data using standard larval bioassay procedures with both oak foliage and artificial diet (Bell et al. 1981) were unsuccessful because larvae would not feed on the diet and consumed little of the oak foliage.

In March 1996, we began working with second-stage larvae that emerged from overwintering nests to establish a lab rearing protocol. Larvae that were offered potted oak (*Q. rubra)* seedlings initially skeletonized the leaves but did not survive to the third stage. Attempts to transfer larvae to fresh foliage resulted in cessation of feeding by the entire colony. It became apparent that any disruption in the integrity of the larval colony and associated webbing, e.g., to thin the number of larvae to a manageable number (10 to 20) for bioassay purposes, caused the larvae to discontinue feeding.

We then attempted to establish colonies in the laboratory from third and fourth instar larvae that had been collected in the field along with their communal webs that were interwoven with leaves and twigs. Larvae would not feed when transferred to potted oak seedlings but fed on freshly cut oak foliage if the entire colony was placed near the foliage bouquet. Using this technique, we were able to initiate bioassays by treating foliage bouquets with a predetermined dose of *Bt* using a spray tower (Hubbard and Lewis 1973) and then placing the treated bouquets in a small plastic cage along with the entire colony. This procedure was not wholly satisfactory because we could not control the number of larvae per replicate (colony) before treatment, nor determine the actual number of larvae/replicate until the end of the bioassay period when we opened the nests and separated the larvae. Although the response of the larvae to *Bt* using this procedure was extremely variable, we were able to obtain important initial information.

Efforts were then directed at establishing BTM larvae on an artificial diet (Bell et al. 1981). We collected egg masses from the field in 1996, placed the entire egg mass directly on the artificial diet, and incubated egg masses under several temperatures and light regimes. We determined that emerging BTM larvae will adapt to artificial diet, forego diapause, and develop to adults under the following conditions: (1) place the egg mass in a 6-oz Dixie Cup

half filled with Bell diet and incubate under continuous light at 22 to 24°C and 30 to 40% RH; (2) after eclosion, allow the larvae to form a heavy web on the surface of the diet for 7 to 10 days; (3) transfer the larvae and webbing gently to fresh diet and incubate for 10 days; and (4) at this point, thin the colony to ca. 50 larvae per cup and use in feeding bioassays.

Electrophysiological Studies. Preliminary feeding bioassays suggested that BTM larvae were not highly susceptible to commercial *Bt* formulations used commonly against the gypsy moth and other forest Lepidoptera. Since there were no data available on the susceptibility of BTM to different insecticidal crystal proteins (ICP) that are present in commercial formulations of *Bt* and because of the difficulty encountered in developing a standardized bioassay procedure such as that which exists for the gypsy moth (Dubois 1986) and other species, we recognized the need for a more efficient procedure.

With assistance from Prof. Donald Dean, Ohio State University, we began electrophysiological (voltage clamp) bioassays of specific purified ICPs against excised midguts of the BTM, using the procedure described by Liegig et al. (1995), to determine their binding characteristics. Previous studies have shown that the site of action of the Cry classes of ICP toxins is the membrane of the midgut cells, and that the binding characteristics of specific ICPs to midgut cell receptors correlate closely with their toxicity to individual species.

Fourth-stage larvae collected from the Casco Bay area were used in the initial studies of purified ICPs. *Bt* formulations containing the same toxins were used to challenge BTM larvae at the equivalent dose of 10 BIU/ha. Four replicates of 20 larvae each were assayed and treatment effects were analyzed by ANOVA; means were compared using an unpaired t test.

Ground Application. Laboratory bioassays conducted in 1996 indicated that the BTM is most sensitive to the CryIAc toxin that is incorporated as one of the complex of toxins found in most commercial formulations of *Bt*. The objective of the 1997 ground application study was to evaluate the efficacy of CrIAc alone and CryIAc added to Condor OF® and Foray 48B® against the BTM when applied at the highest registered dose of 98.8 BIU/ha using a conventional mist blower. CryIAc was provided by Mycogen Corporation as a pure toxin preparation under the name MVPII®.

Three 0.4-ha blocks separated by a 16.7-m buffer zone were established for each treatment and the untreated control. Six sleeve cages were placed at random on northern red oak (*Quercus rubra)* branches in each block immediately after spray application; a minimum of 50 third and fourth instar larvae were placed in each cage. Counts of live and dead larvae were made at 4, 8, 12, and 16 days after spray and dead larvae were removed after being counted. Additionally, six branches containing BTM larvae were placed in plastic bags, chilled, and returned to the lab where they were placed in Melrose boxes. Mortality of larvae was recorded daily for 10 days.

MVPII® was applied at a rate of 954 nanograms of active ingredient (AI) per cm^2 of leaf surface. Condor OF® and Foray 48B® were applied at 98.8 BIU/ha with the same concentration of MVPII® added to the mixture.

Aerial Application. Based on the encouraging results of the ground application conducted in 1997 and additional bioassays that were conducted over the winter months, an aerial spray trial was conducted in May 1998 to determine the efficacy of Foray 48B® and MVPII® applied at 39 oz/ha at a ratio of 0.6 to 1 against BTM larvae. The test was conducted on Peaks Island, located within the City of Portland, Maine. This area was chosen because it

supported a light to moderate (3 to 10 overwintering webs/northern red oak) population of the BTM.

An 81-ha block was established and marked for treatment. Twelve sleeve cages were distributed at random throughout the block and attached to northern red oak branches; 20 larvae were placed within the cages within several hours after the *Bt* formulation was applied. An equal number of cages were established in the same way in unsprayed areas on the island where larval densities based on the number of webs/tree were similar to those in the treated area. Counts of live and dead larvae within the cages were made immediately after treatment and 4, 8, 12, and 16 days after spraying. Dead larvae were removed after each observation.

The *Bt* formulation that was tested consisted of two parts of Foray 48B® to three parts of MVPII® applied undiluted at 7.0 l/ha. In terms of active ingredients, this dose represented 35.3 BIU/ha of Foray 48B® and 117.999 g/ha of MVPII®. A Thrush Commander aircraft equipped with 8-AU 5000 Micronair nozzles was calibrated to deliver droplets within a range of 125 to 135 μ VMD (volume mean density). Treatment commenced on the morning of May 18, 1998.

Results

Laboratory Bioassays. Foliage bioassays with commercial formulations of *Bt* with known ICP composition provided the first clue that the BTM was most susceptible to the CryIAc toxin (Table 1).

Table 1. Simulated aerial application of *Bacillus thuringiensis* formulations at 8 BIU/acre equivalent against fourth and fifth instar browntail moth larvae (mortality after 5 days)

Formulation	ICP Composition (Cry)							Dead	C.V.[a]
	IAa	IAb	IAc	IB	IC	ID	IIA		
Control								6.7	1.71
Foray 48B®[b]	x	x	x					86.2	0.08
Dipel 6AF®	x	x	x					58.3	0.84
Condor OF®	x		x				x	76.9	0.49
Xentari®	x	x						22.1	1.40
CryMax®	x				x		x	38.8	1.06

[a] Four replicates with 50 to 250 larvae per replicate
[b] Dose used was 4 BIU/acre equivalent

Pure toxin feeding bioassays on foliage bouquets confirmed that CryIAc without spores caused significantly higher mortality than CryIAa or CryIAb (Table 2).

Table 2. Pure insecticidal crystal protein (ICP) bioassays with and without HD-73 spores against fourth and fifth instar browntail moth larvae

Preparation	Spores	Percent Mortality at Day 6	
		Actual	Corrected[b]
Foray 48B®[a]	+	46	31
CryIAa	-	46	31
CryIAa	+	41	24
CryIAb	-	41	24
CryIAb	+	17	0
CryIAc	-	82	77
CryIAc	+	88	85
Controls	0	22	

[a] = 8 BIU/acre equivalent CP provided by Mycogen Corp. as MVPII® (pseudomonas encapsulated) formulations and applied on bouquets at 3.6 to 4.0 grams/ml/bouquet. Spore concentration = 25 per application (3 reps, 250 larvae/rep)
[b] Corrected by Abbott formula

Augmentation of Foray 48B® or Condor OF® with MVPII®, a commercial preparation of CryIAc, resulted in significant increase in mortality compared to that with either *Bt* formulation alone. A low mixture ratio of *Bt*:MVPII® (0.6:1) increased the efficacy of the Foray 48B® formulation significantly; a ratio of 5.3:1 increased the efficacy of Condor OF®.

Electrophysiological Studies. Voltage clamp assays conducted on the isolated midguts of fourth and fifth instar larvae confirmed that, based on the inhibition of electrical activity (-μA/minute), the BTM is much more susceptible to the CryIAc ICP (Table 3).

Table 3. Rate of short-circuit current inhibition (-μA/minute) of browntail moth larval midguts by activated insecticidal crystal proteins (ICP) of *Bacillus thuringiensis*

ICP	-μA/minute	Mean	R^2	% μA loss/minute	Mean
CryIAa	-0.182		72	1.82	
	-0.187		96	2.67	
		-0.185			2.25
CryIAb	-0.346		95	2.31	
	-0.121		94	1.34	
		-0.234			1.83
CryIAc	-0.283		98	3.14	
	-0.401		98	3.48	
		-0.342			3.31
CryIIA	-0.065		89	1.63	
	-0.033		72	1.63	
		-0.049			1.63

Ground Application. In the field study, the 5.3:1 mixture of *Bt*: MVPII® resulted in significant larval mortality in the Condor OF® plot 4 days after treatment and 3 days later in the Foray 48B® plot (Table 4).

Table 4. Percent mortality of browntail moth larvae in sleeve cages after treatment with MVPII®, Condor OF® + MVPII® or Foray 48B® + MVPII®, May 29, 1997

	Treatment				ANOVA		
Date	Control	MVPII®	Condor OF® + MVPII®	Foray 48B® + MVPII®	df	F	P
6-03	4.0ac[a]	1.4	13.6B	7.8AB	3,68	9.988	0.000
6-06	4.7a	5.0a	24.7b	17.1b	3,68	15.330	0.000
6-10	5.2a	12.0	41.0b	32.2b	3,68	28.437	0.000
6-13	6.3a	30.7b	71.2b	77.7b	3,68	75.034	0.000
6-19	47.1a	79.6b	98.2b	98.8b	3,68	31.805	0.000

[a] Numbers in rows with the same letter are not significantly different from each other (Tukey HSD Multiple Comparison at $P< 0.05$)

However, there was no difference in the cumulative mortality of larvae between the two *Bt* formulations. MVPII® alone did not differ significantly from the controls until 2 weeks after treatment.

Aerial Application. Mortality of the caged larvae 21 days after treatment was 72% in the treated plot and 16% in the controls (Fig. 1). We attributed the abnormal mortality in two of the control cages to the fact that they had been inadvertently placed near an area that had been sprayed with diflubenzuron. The mean percent mortality in the other 10 sleeve cages was 10.2%.

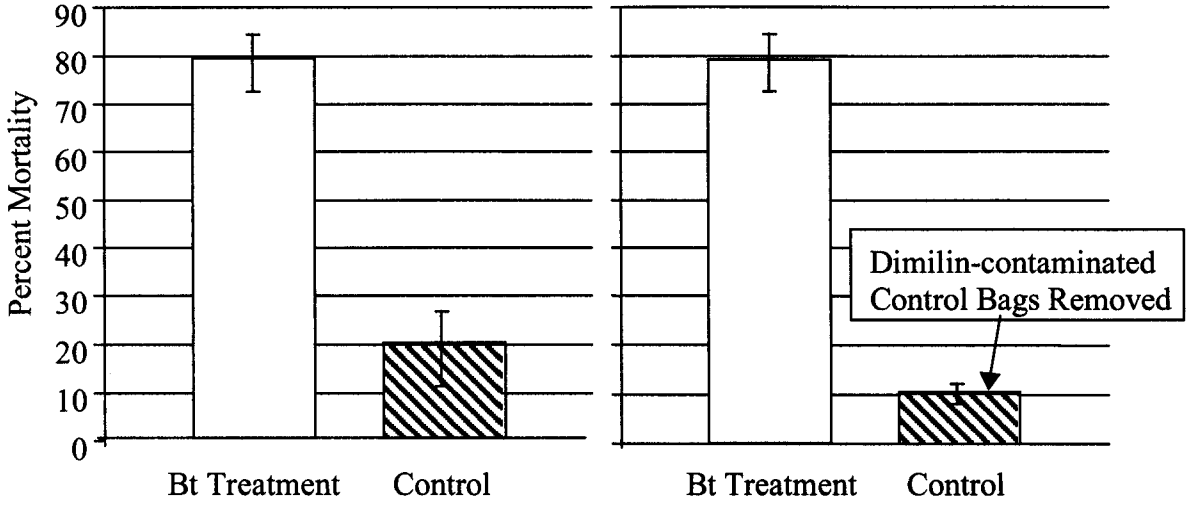

Figure 1. Results of aerial spray trial conducted on Peaks Island, Maine, May 18, 1998. Foray 48B® and MVPII® were applied at 39 oz/ha, a ratio of 0.6 to 1.0.

Discussion

That the BTM is well adapted to survival in rigorous environments makes it difficult to control this species. Communal webs provide a means for all siblings from a single egg mass to overwinter (Schaefer 1989). After completing diapause, larvae feed gregariously in the spring and summer months and produce large communal webs, some of which are more than 30 cm long (Bradbury 1995). The colonial feeding behavior of BTM larvae complicated our attempts to conduct routine bioassays in the laboratory to determine their susceptibility to commercial formations of *Bt* and its ICPs. Although the results of our efforts to overcome this behavior were not entirely satisfactory, we obtained preliminary information suggesting that the response of BTM to commercial *Bt* formulations differed substantially from that of other forest defoliators, e.g., the closely related gypsy moth. These findings provided the stimulus to explore the use of an electrophysiological method as an alternative to standard feeding bioassays that have been used successfully in the past (Dubois 1986). The following section is a brief review of the *Bt* endotoxins (ICPs) and their relationship to voltage/current bioassay procedures

Strains of *Bt* are pathogenic to species within the Lepidoptera, Diptera or Coleoptera depending on the type of delta endotoxins (ICPs) that they produce. The CryIA class is specific to Lepidoptera, the CryII class to Lepidoptera and Diptera, the Cry III class to Coleoptera, and the Cry IV class to Diptera (Dubois et al. 1997). These toxins are selectively toxic to cells in the midgut epithelium of susceptible species.

After they are ingested, the ICPs are solubilized by high ph (>10) in the midgut of larvae to a protease-resistant toxin that binds to specific receptor sites on the brush border membrane of the columnar cells. It has been suggested that this toxin disrupts the transport of potassium (K+), which results in physiological changes in the function of the columnar cells. These cells absorb water, swell, and lyse, resulting in partial destruction of the midgut. This process can be measured by increased short-circuit inhibition across the midgut membrane (Harvey and Wolfersberger 1979). The authors found that 60% of the short-circuit current was inhibited when *Bt* was administered to the isolated midgut of *Manduca sexta*; electrical resistance was reduced by 55% and oxygen uptake was stimulated by ca. 30%. This sequence of events occurs 30 to 40 minutes after ingestion of *Bt* by susceptible larvae and is followed by death from starvation or septicemia 48 to 72 hours later. The voltage/current clamp procedure and the chamber that is used to measure these changes are described in Wood and Moreton (1978).

The voltage/current bioassay procedure was effective in evaluating the susceptibility of BTM larvae to the ICPs used in commercial formulations of *Bt.* This procedure can be used as an alternative to costly and time-consuming feeding bioassays. The results of this procedure, indicating that BTM larvae were more susceptible to the CryIAc insecticidal crystal protein of *Bt*, were confirmed in truck-mounted mistblower applications in 1997 and in aerial applications in 1998. Consequently, a modified commercial formulation of *Bt* that is efficacious against the BTM was developed and evaluated for 3 years. This formulation is a safe alternative to registered chemical contact pesticides and is especially effective in managing BTM populations on environmentally sensitive lands where the use of more efficacious products may adversely affect nontarget species and pose a health risk to humans.

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Implications of Non-Indigenous Insect Introductions in Forest Ecosystems

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ABSTRACT The status of non-indigenous introductions as forest pests in Canada and ongoing research on species associated with solid wood packaging are briefly reviewed. Introductions began soon after the start of European colonization, with many of the early arrivals being of little consequence as pests. Since then, however, a significant number of serious forest insect pests and diseases have reached North America. Some have forever altered forest ecosystems. Through containment rearing of solid wood packaging intercepted in the port of Vancouver, British Columbia, we demonstrate that serious forest pests continue to arrive in association with a variety of commodities. In research studies in urban reserves and forests adjacent to the port, we have found evidence that non-indigenous species of ambrosia beetles and woodborers now predominate in some communities. The potential effects of these species on forest ecosystems are unknown. Adoption and enforcement of regulations to ensure that only pest-free solid wood packaging is used in international trade are required before introductions of invasive bark and woodborers will cease.

THE PURPOSE OF this presentation is to acquaint or reacquaint you with the breadth and magnitude of problems arising from non-indigenous species introductions and establishments, and to inform you of some of the efforts currently underway in Canada to address the issue.

Non-indigenous insects are a threat to forest ecosystems and forest economies. There is ample evidence from around the world of the devastating effects resulting from the intentional or inadvertent movement by humans of plant and animal species outside of their natural range. The majority of the introduced species in North America originated from Europe or Asia as a result of trade with those continents over the past several hundred years. Most of the historical introductions were inadvertent, although on occasion they have been the result of well intentioned but poorly thought out species transfers (e.g., gypsy moth).

Historical Establishments

The first adventive non-indigenous species likely arrived soon after the discovery and colonization of the continent by European explorers and settlers. Some of the first arrivals were ground beetles inadvertently transported with stone and gravel used as ships ballast. Disposal of the ballast into the sea was prohibited by decree to maintain the quality of anchorages in early fishing ports. The ballast, contaminated with the plant and insects of coastal Europe, was deposited on shore (Turnbull 1979). The legacy of this practice is evident today in the disjunct distributions of Carabidae along the east and west coasts of the continent and waterways of the Saint Lawrence River and Great Lakes and in the high proportion of European species present in the fauna of Newfoundland (>13%), the region

Pages 45-55 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.

with the earliest and hence the longest period of settlement in Canada (Scudder 1979, Bousquet 1991).

While many of the earliest arrivals had little impact on forest ecosystems in Canada, further colonization and trade, primarily with Europe, eventually led to the establishment of an increasing number of forest pests in our forests. Some of the more significant non-indigenous insects and diseases established in Canada's forests, the dates of their first discovery, and the tree species attacked are noted in Tables 1 and 2. Liebhold et al. (1995) provide case histories for and review the impacts of a range of non-indigenous forest pests introduced into North America, including the gypsy moth, pine shoot beetle, chestnut blight, and white pine blister rust. These and other introduced taxa have modified forest ecosystems (e.g., virtual elimination of American Chestnut from eastern forests); affected the timber, recreational, and wildlife uses of forest resources; and threatened the viability of endangered species or ecosystems.

Table 1. Significant forest insect pests introduced into Canada (after Anon. 1999)

Insect	Year Introduced	Primary Hosts
*Larch sawfly (*Pristiphora erichsonii*)	1882	larches
Browntail moth *(Euproctis chrysorrhea)*	1902	all deciduous species
Poplar sawfly *(Trichiocampus viminalis)*	1904	trembling aspen, largetooth aspen, balsam poplar
*Larch casebearer (*Coleophora laricella*)	1905	larches
Late birch leaf edgeminer (*Heterarthus nemoratus*)	1905	birches
*Balsam woolly adelgid (*Adelges piceae*)	1908	balsam fir, grand fir, subalpine fir, Pacific silver fir
*Satin moth (*Leucoma salicis*)	1920	poplars
*European spruce sawfly (*Glipinia hercyniae)*	1922	spruces
*Gypsy moth (*Lymantria dispar*)	1924	oaks, birches, larches, willows, basswood, Manitoba maple
*European pine shoot moth (*Rhyacionia buoliana*)	1925	red pine, jack pine, Scots pine
*Winter moth (*Operophtera brumata*)	1920s	oaks, maples, willows
*Mountain-ash sawfly (*Pristiphora geniculata*)	1926	mountain-ash
*Birch leafminer (*Fenusa pusilla*)	1929	birches
Introduced pine sawfly (*Diprion similis*)	1931	pines
Birch casebearer (*Coleophora serratella*)	1933	poplars
*European pine sawfly (*Neodiprion sertifer*)	1939	red pine, Scots pine
Elm leaf beetle (*Pyrrhalta luteola*)	1945	elms
Smaller European elm bark beetle (*Scolytus multistriatus*)	1946	elms
Ambermarked birch leafminer (*Profenusa thomsoni*)	1948	birches
*Apple ermine moth (*Yponomeuta malinella*)	1957	apple
European pine needle midge (*Contarinia baeri*)	1964	red pine, Scots pine
Early birch leaf edgeminer (*Messa nana*)	1967	birches
*Pine false webworm (*Acantholyda erythrocephala*)	1961	pines
Pear thrips (*Taeniothrips inconsequens*)	1989	sugar maple, red maple
Pine shoot beetle (*Tomicus piniperda*)	1993	pines, spruces

* Denotes species for which biological control programs have been implemented

Table 2. Significant forest diseases introduced into Canada (after Anon. 1999)

Disease	Year Introduced	Primary Hosts
Dothichiza canker (*Cryptodiaporthe populea*)	pre 1900	Poplars
Chestnut blight (*Cryphonectria parasitica*)	post 1904	American chestnut
White pine blister rust (*Cronartium ribicola*)	1910	White pine
Willow blight (*Venturia saliciperda*)	ca. 1925	Willows
Dutch elm disease (*Ophistoma ulmi*)	1944	Elms
Scleroderris canker (European race) (*Gremmeniella abietina*)	1978	Pines
European larch canker (*Lachnellula willkommii*)	1980	Larches
Beech bark disease (*Nectria coccinea var. faginata*) and beech scale (*Cryptococcus fagisuga*)	1980	American beech
Butternut canker (*Sirococcus clavigignenti*)	1991	Butternut

While in Victoria, you will have the chance to visit one of the most threatened ecosystems in Canada, the communities dominated by Garry oak (*Quercus garryana* Dougl.) on southeastern Vancouver Island and the adjacent Gulf Islands. This community has been impacted by serious levels of defoliation over the past three decades caused by a sequence of exotic introductions. Much of the original Garry oak woodland has been lost to urbanization. The remaining stands are threatened by urban expansion as well as the effects of defoliation resulting from non-indigenous introductions. More than 800 species of arthropods are associated with Garry oak in this area (Evans 1985). At least 140 of these species are herbivores, feeding on the foliage, acorns, branches, trunk or roots of the tree. One third of the herbivores (48 spp.) are restricted to Garry oak alone. At least 10% of the herbivores (14 spp.) now present on Garry oak are non-indigenous introductions (Table 3). Three of the introduced species (winter moth, the oak leaf phylloxeran, and jumping gall wasp) have adversely affected the health and survival of Garry oak through repeated defoliation or scorching during prolonged outbreaks (Van Sickle 1995; Duncan 1997a,b). The establishment of another exotic oak pest, the gypsy moth, has so far been prevented through ongoing detection and eradication programs (Humble and Stewart 1994). This year, more than 12,000 ha of southern Vancouver Island, including significant areas containing Garry oak, have been treated to eradicate a recently introduced population of gypsy moth.

Current Research

As a consequence of the serious impacts historical non-indigenous introductions have had on agricultural and forest economies, inspection and quarantine systems have been implemented by most nations to prevent introductions of new harmful invasive species or to limit the spread of already established species. In spite of these regulatory efforts, additional non-indigenous species are discovered annually. Factors contributing to the continued introduction of exotic species include the increasing levels of international trade (increasing numbers of introductions), increased speed of transport of imported goods (enhanced survival of adventive organisms), and the difficulties of adequately inspecting containerized cargoes. The movement of people and goods has increased the rate of introductions by orders of magnitude, resulting in a trend towards the globalization of adventive species.

Table 3. Non-indigenous introductions on Garry oak in British Columbia

Species	Common Name
Coleoptera	
Otioryhnchus ovatus (L.)	Strawberry root weevil
Otioryhnchus singularis (L.)	Clay-colored root weevil
Otioryhnchus sulcatus (Fab.)	Black vine weevil
Phyllobius oblongus (L.)	A weevil
Strophosoma melanogrammum Foerster	A weevil
Lepidoptera	
Archips rosana (L.)	European leafroller
Ditula angustoriana Haworth	A leafroller
Choristoneura rosaceana (L.)	Obliquebanded leafroller
***Operophtera brumata* (L.)	Winter moth
†*Lymantria dispar* (L.)	Gypsy moth
Pandemis cerasana Hubner	A leafroller
Spilonota ocellana (Denis & Schiff.)	Eyespotted budmoth
Homoptera	
Moritziella corticallis (Kaltenbach)	An oak bark phylloxeran
***Phylloxera glabra* (Heyden)	Oak leaf phylloxeran
Hymenoptera	
***Neuroterus saltatorius* Edwards	Jumping gall wasp

** Denotes species that has caused serious defoliation

† Species has been recovered from Garry oak but is not established in British Columbia

Most countries have plant quarantine agencies, part of whose job is to monitor the influx of non-indigenous organisms, identify the pathways by which they are entering, and attempt to prevent their entry. The interception records of such quarantine agencies serve as a source of information on what is entering a country; collections made by government agencies and academics provide an indication of what species have established (populations of a species that persist in a new habitat). Unfortunately, neither source provides a complete picture. Interception records only document the species recovered from those imports that are inspected, a small subsample of the total volume of imported goods. Inspection efforts are limited by finite resources. It is often not possible to identify to species due to lack of expertise, financial resources, or facilities to rear to adults. In some cases, stain fungi for example, we lack the diagnostic tools to make positive identifications.

Over the past 5 years our research has focused on non-indigenous species associated with solid wood packaging and dunnage. It has been focused in two areas: the detection of species at ports of entry prior to their establishment and surveys for the detection of non-indigenous introductions in natural forest ecosystems. The primary taxon of concern is the Coleoptera, especially those species living under the bark or in the wood, predominantly the bark and ambrosia beetles (Scolytidae), longhorned woodborers (Cerambycidae), and flat-headed woodborers (Buprestidae).

Interceptions

The recent discovery of established populations of the European pine shoot beetle (*Tomicus piniperda* (L.)) in eastern North America and the Asian longhorned beetle (*Anoplophora glabripennis* Mots.) in New York and Chicago has highlighted the risks of introduction posed by solid wood packaging associated with commodities which themselves cannot harbour exotic species. One aspect of our research has focused on determining the incidence and composition of the arthropod faunas associated with wood packaging. The arthropod fauna associated with containerized shipments of architectural stone from Norway and wire rope spools from Asia are documented below.

Dunnage Associated with Granite Blocks. In July 1998, live beetles were found associated with shipments of granite from Norway. The shipments had entered Canada at the port of Montreal and had been shipped by rail to Vancouver, where the containers were unpacked and the dunnage discarded. Green spruce bolts had been used to brace large granite blocks inside shipping containers. The intercepted dunnage was brought to the CFS quarantine facility in Victoria and held under containment for emergence of the arthropod fauna.

The results of these rearings were alarming. More than 2,500 adult insects representing more than 40 species of bark beetles, woodborers, and their associated parasitoids, predators, and scavengers were recovered from 29 log bolts (Fig. 1). At least three species of Scolytidae of quarantine significance (*Pityogenes chalcographus*, *Polygraphus poligraphus*, and *Ips typographus*) were recovered from these bolts (Table 4).

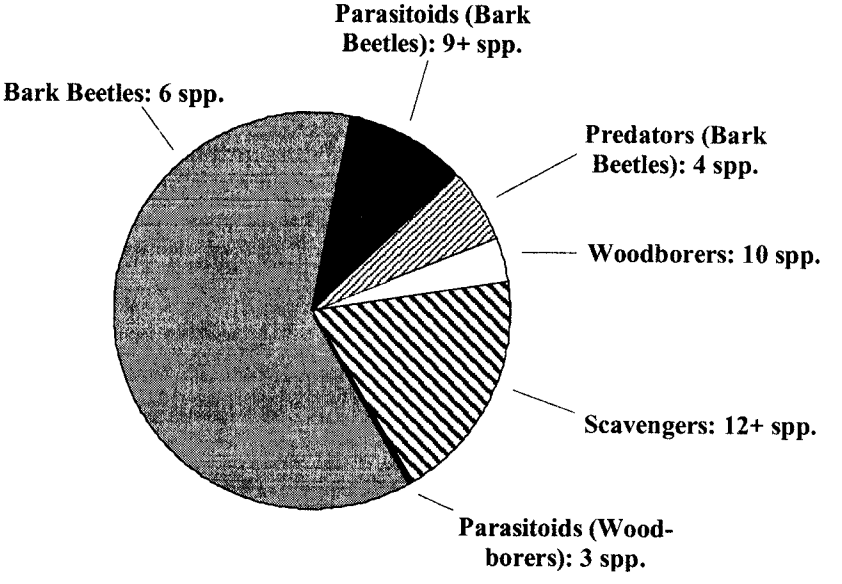

Figure 1. The composition of the arthropod community reared from spruce bolts used as dunnage in large granite block shipments from Norway.

Table 4. Bark and wood-boring beetles and wasps reared from intercepted spruce bolts from Norway used as dunnage; all rearings were done under containment in quarantine

Species and Family	No. of Individuals
Scolytidae	
Pityophthorus micrographus (Linnaeus)	942
Pityogenes chalcographus (Linnaeus)	284
Polygraphus poligraphus Linnaeus	207
Ips typographus (Linnaeus)	27
Crypturgus hispidulus Thoms.	16
Pityophthorus pityographus (Ratzeburg)	1
Cerambycidae	
Tetropium fuscum (Fabricius)	44
Callidium coriaceum Paykull	3
Molorchus minor (Linnaeus)	1
Pogonocherus fasciculatus (Degeer)	1
Semanotus undatus (Linnaeus)	1
Anobiidae	
Anobium sp.	10
Ernobius explanatus (Mannerheim)	4
Curculionidae	
Rhyncholus sp.	1
Melandryidae	
Serropalpus barbatus (Schall.)	7
Siricidae	
Sirex juvencus (Linnaeus)	21

Wire Rope Spools. Interceptions of *A. glabripennis* were first made in British Columbia in 1992. In that year, large numbers of newly emerged adults of *A. glabripennis* along with *A. nobilis* and *A. chinensis* were intercepted emerging from wood packaging in a container of pipe flanges. In 1995, adult *A. glabripennis* were again intercepted in a warehouse in greater Vancouver, this time apparently emerging from wood used to construct spools holding industrial wire rope. This led us to take a closer look at wire rope spools.

In 1997, 50 wire rope spools originating from China were obtained from various importers on Vancouver Island and the lower mainland of British Columbia. Many were empty discarded spools stored at import facilities and may have been in Canada for up to 2 years. The spools were disassembled and examined for evidence of woodborers. Twenty-four percent of the spools examined still contained live woodborers while a total of 31% of the spools had some evidence of past woodborer activity. Six species of longhorned woodborers (Cerambycidae), including *Monochamus alternatus*, *Hesperophanes* [=*Trichoferus*] *campestris*, *Ceresium flavipes*, *Psacothea hilaris*, *Megopis sinica*, and *Rhagium inquisitor*, and one species of Anobiidae, *Ptilineurus* sp., were obtained when wood from these spools was held in containment for adult emergence. The following year, an additional 16 newly arrived spools originating from China were sampled. Live insects were again recovered from 22% of the spools. There was often no visible external evidence of the presence of live

woodborers in these spools: only 63% showed external signs of woodborer activity while all were found to have some evidence of past insect activity when disassembled.

Establishments

Our knowledge of non-indigenous species that have established is very limited; indeed, baseline data on the abundance and distribution of our native species is largely lacking. Our second area of research has focused on detecting non-indigenous species in forest ecosystems and determining their abundance relative to the abundance of our native taxa. These baseline surveys have been conducted using baited funnel traps and through rearing of naturally attacked host material.

Bousquet (1991) recently documented the composition of the Canadian beetle fauna. He recorded 7,436 species of beetles in the Canadian checklist, including 501 non-indigenous species (6% of the Canadian fauna). The highest proportions of non-indigenous species relative to the total provincial faunas occur in Newfoundland and the Maritime provinces (Fig. 2). Considerable variation is evident in the number of non-indigenous beetles found across Canada (Fig. 3), with the highest numbers occurring in Quebec, Ontario, and British Columbia.

When studies were initiated at forested locations around greater Vancouver in 1995, 135 species of Scolytidae and 145 species of Cerambycidae were known to occur in British Columbia (Bousquet 1991, Bright and Skidmore 1997). Five of the species included in the former family were previously established non-indigenous species, while no non-indigenous species of the latter family were known to occur in the province. To date, an additional five species of ambrosia beetles (Scolytidae) and one non-indigenous longhorned woodborer have been discovered in trap surveys. All of the newly discovered Scolytidae are confirmed as established, having been collected from multiple locations over at least three of the years in which sampling was conducted. The single cerambycid discovered was recovered from two locations in only one year.

These newly discovered introductions already comprise a significant proportion of the total bark and ambrosia beetle fauna trapped at some locations (Fig. 4). A similar pattern is evident when the scolytid fauna emerging from naturally attacked host material is examined (Fig. 5). Again, the majority of the emergent adults was non indigenous. Studies are currently being initiated to determine the biology and impacts of these recently introduced species.

The abundance of non-indigenous species relative to our native species of Scolytidae in both trap surveys and rearings from recently dead or dying native tree species indicate that these invasive taxa have successfully adapted to their new environments. At least two of the species of Scolytidae discovered to date are attacking hosts not utilized in their native ranges. One has established more than 1000 km north of its native range where representatives of our native genera do not occur, while the second breeds in conifers as well as species of deciduous trees in genera known as hosts in its native range.

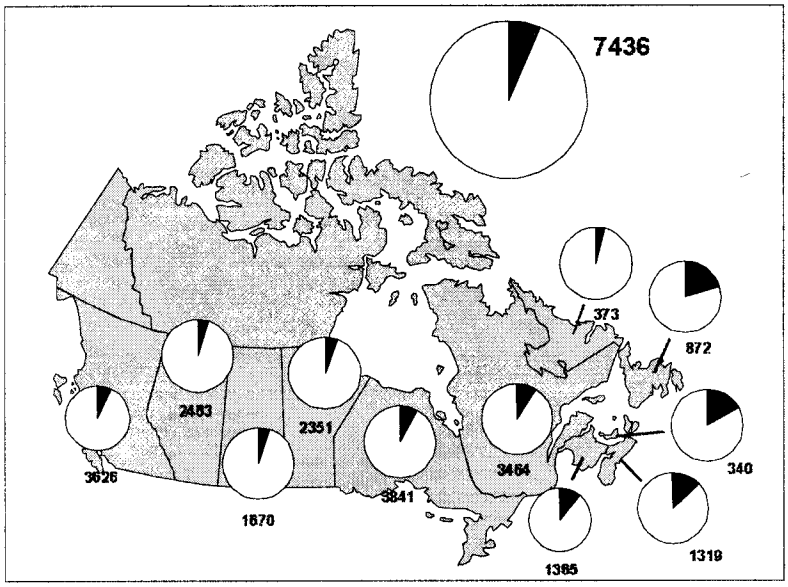

Figure 2. Total number of species of Coleoptera in Canada and the number of species present in each province (data from Bousquet 1991). The proportion of non-indigenous Coleoptera species present in each region is denoted in black. Numbers are the total number of Coleoptera species in each region.

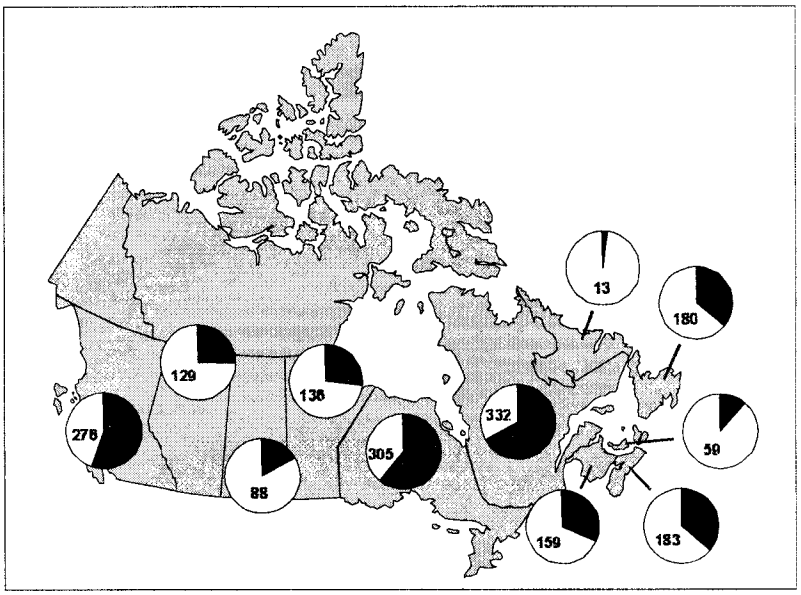

Figure 3. The proportion of the total number of non-indigenous Coleoptera present in Canada (n=501) found in each region of the country is denoted in black (data from Bousquet 1991). Numbers are the total number of non-indigenous Coleoptera species in each region.

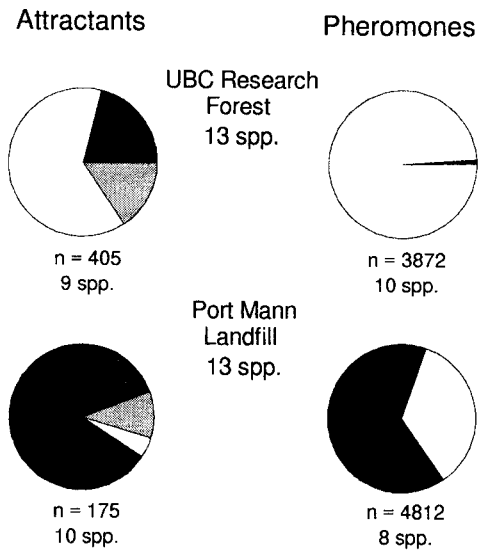

Figure 4. Relative abundance of native species (white), non-indigenous species recorded by Bousquet (1991) and Wood and Bright (1992) (grey), and non-indigenous species discovered in these studies (black) responding to traps baited with attractants (ethanol, α-pinene, dipentene, methyl salycilate) or pheromones (lineatin, sulcatol, chalcogran, ipsdienol) at two locations in the Fraser Valley, near Vancouver British Columbia between 16 March and 16 July 1999.

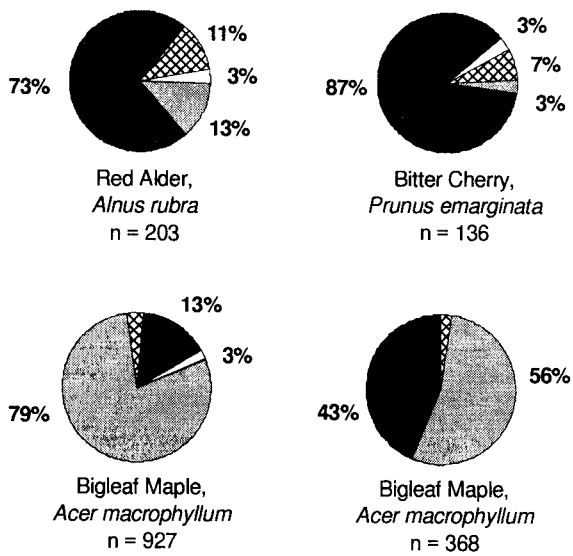

Figure 5. Relative abundance of native species (white), non-indigenous species recorded by Bousquet (1991) and Wood and Bright (1992) (grey), and non-indigenous species discovered in these studies (black) reared from the noted field attacked tree species collected at the Port Mann Landfill site, Surrey, B.C. in 1997. Cross hatching indicates the presence of males of two non-indigenous xyleborine ambrosia beetles that could not be identified accurately and thus could not be accurately placed in any category.

Summary

We have provided a brief review of the status of non-indigenous species as pests in the forests of Canada. Recent research findings related to the introduction and establishment of invasive bark and woodboring insects associated with solid wood packaging that demonstrate that non-indigenous species continue to arrive on our shores and establish in our forests as a consequence of international trade are presented. The recent introductions discovered during these studies in a limited area of southwestern British Columbia have doubled the number of non-indigenous Scolytidae known to be established in the province. Interceptions from solid wood packaging indicate that species will likely continue to accumulate in the near future. Because we lack an *a priori* knowledge of the biology and ecology of these invasive species in their new environments, we cannot predict the potential impacts they may cause, either individually or cumulatively, on our forest ecosystems.

To address the issue of non-indigenous introductions and their impacts we need to:

(1) increase our capability to quantify (more than monitor) the flow of insect species (and other organisms) in and out of the country and within national boundaries (e.g., across ecosystem boundaries);
(2) improve our capacity to identify species;
(3) study the establishment and distribution of non-indigenous species in native ecosystems to better understand their effects on ecosystem function;
(4) provide advice to government agencies responsible for plant quarantine issues; and
(5) foster international cooperation to share information on species of concern (specimen exchange, cooperative research, shared databases).

It is our hope that such efforts coupled with the adoption and enforcement of new regulations on solid wood packaging will stem the flow of invasive bark and woodborers into North American forests.

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Influence of Insect Defoliators on Seedling Establishment of Four Species of the Fagaceae Family in Northern Japan: Leaf Area Loss and Survivorship of Seedlings

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ABSTRACT Following defoliation of Siebold's beech (*Fagus crenata*) and three deciduous oak species (*Quercus crispula*, *Q. serrata*, and *Q. variabilis*), foliage at lower positions had greater leaf area loss than foliage at higher positions, and seedlings had greater leaf area loss than adult trees. Both foliage quality and gravity were probably related to these events. The percentage of leaf area loss influenced seedling mortality. However, there was a great difference between Siebold's beech and the oaks in leaf area loss of their respective seedlings. Current-year seedlings of *F. crenata* had greater leaf area loss than older seedlings. However, current-year oak seedlings had less leaf area loss than older oak seedlings. Possible causes for these differences include foliage quality related to the amount of carbohydrate supplied from cotyledons to current-year seedlings and phenological escape caused by late flushing of current-year oak seedlings.

INSECT FOLIVORY AFFECTS host plants both directly by reducing photosynthesis and indirectly by increasing chances of infection from diseases. Because young seedlings are small and have a small number of leaves, they often lose most of their leaves to insect attacks even when insect density is not very high. Seedlings living under the canopy usually experience great stress because light is limited. These facts suggest that insect folivory has a stronger impact on seedlings than on larger trees. Manual defoliation experiments involving seedlings have demonstrated that insect folivory reduces seedling growth and enhances mortality in *Quercus rubra* (Wright et al. 1989), *Q. douglasii* (Hook and Arn.) (Welker and Menke 1990), and *Liriodendron tulipifera* (Madgwick 1975). On the other hand, plants chemically and physically defend themselves against herbivores (e.g., Karban and Baldwin 1997).

Population outbreaks of folivorous insects sometimes occur in forests and almost all the trees are defoliated. However, foliage loss due to insect folivory was estimated to be around 10% at most of the total canopy in latent years (Bray 1964, Whittaker and Woodwell 1968, Gosz et al. 1972, Mattson and Addy 1975). The beech caterpillar (*Syntypistis punctatella* (Motschulsky)) (Lepidoptera: Notodontidae) and some sawfly species sometimes defoliate beech trees completely in northern Japan (Kamata 2000), but the total loss due to insect defoliation in latent years was estimated to be around 10% of the total canopy biomass (Kamata and Igarashi 1996). However, it was not rare for seedling leaves to have severe insect damage even when overhead canopy foliage was fed on minimally in latent years. This phenomenon suggests that beech seedlings are apt to have more insect folivory than canopy

Pages 56-64 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.

leaves. Folivorous insects often fall from canopy leaves because of such elements as wind and rainfall and thus escape from attacks by natural enemies. It is therefore easy to speculate that the leaves of seedlings, which are located near the forest floor, have more damage due to fallen insects than upper leaves. It is also possible that the foliage of current-year seedlings is more palatable to folivores than canopy leaves. However, there have been no reports that studied this phenomenon. If this phenomenon is universal, then both the phenomenon and its causes are quite interesting and lend themselves to many ecological hypotheses.

In this paper, Siebold's beech and three deciduous oak species are investigated. We compared leaf area loss of adult trees, current-year seedlings, and older seedlings. Seedling mortality was also investigated in relation to seedling age. These relationships were compared among tree species.

Materials and Methods

Study Sites. Study sites were located in natural secondary forests of Iwate (Site A: 40° N, 141° E, 700 to 800 m above sea level) and Ishikawa (Site B: 36 ° 30' N, 136 ° 40' E, 160 to 200 m above sea level) (Fig. 1). The study site in Iwate is located in cool temperate forests mainly occupied by Siebold's beech (*Fagus crenata*) and a deciduous oak (*Quercus crispula*). The study site in Ishikawa is warmer than the Iwate site and is occupied by two other deciduous oak species (*Q. serrata* and *Q. variabilis*).

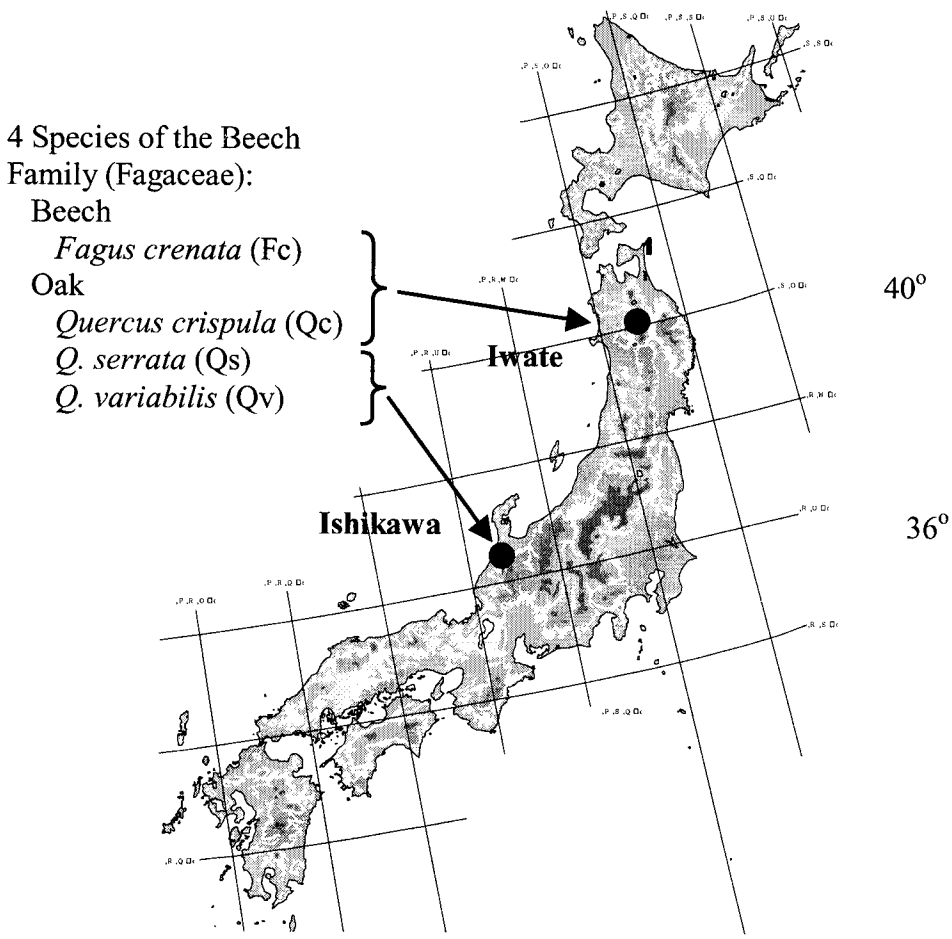

Figure 1. Study sites.

Methods. At Site A, two plots were established in 1996; four quadrants, two per plot, were established after snow melt (mid May). At site B, four quadrants for *Q. serrata* and 10 quadrants for *Q. variabilis* were established in late April of 1998. The size of each quadrant was 1 m x 1 m. Inside the quadrant, all current-year seedlings of the target species were numbered. At Site A, current-year seedlings were numbered in 1996. In 1997, these numbered seedlings were investigated to determine both folivory and mortality in the second year. At Site B, 1-year-old seedlings were also numbered in late April of 1998. Leaf area loss and mortality of both current-year seedlings and 1-year-old seedlings were investigated in the same year (1998).

Branches (ca. 1 m in length) were sampled at heights of 1 to 3 m and > 5 m. All leaves were scanned by an electronic scanner and the percentage of insect damage was calculated using the following equation:

$$\% \text{ Damage} = (\text{Area of insect damage}/\text{Area of original leaf}) \times 100$$

At site B, ca. 100 leaves were marked at each of three different heights (8, 12, and 16 m) for each of the two species. Photographs of marked leaves were taken during every site visit. The percentage of insect damage for each leaf was calculated using the same method mentioned above.

Results and Discussion

F. crenata. Figure 2 shows the survivorship curves of beech seedlings in the two plots (Plots 1 and 2) at Site A. Tendencies were similar between these two plots: most of the mortality occurred during the rainy season from mid June to mid July. No significant difference was found in the survival time of the current-year seedlings between the two plots (Cox-Mantel test, $P>0.05$).

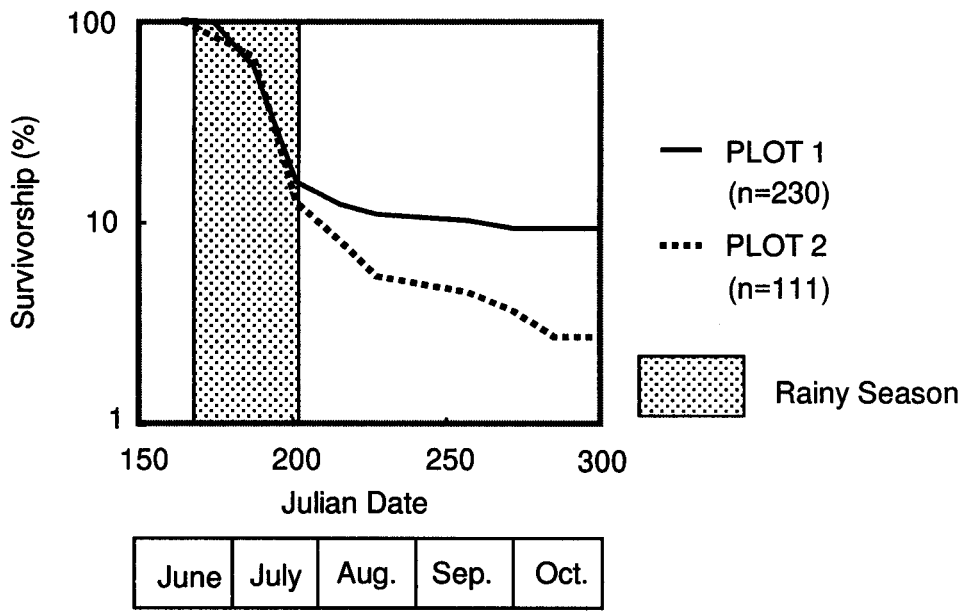

Figure 2. Survivorship curve of current-year seedlings of *Fagus crenata*.

Figure 3 shows the cumulative distribution curve of seedlings in relation to leaf area loss. Curves biased in the upper left indicate that leaf area loss was small. Leaf area loss was compared between dead and live seedlings. Significant differences in leaf area loss were found on July 5th, July 19th, and August 2nd, when mortality was great. This result indicates that dead seedlings had greater leaf area loss than live seedlings and suggests that leaf area loss promoted seedling mortality.

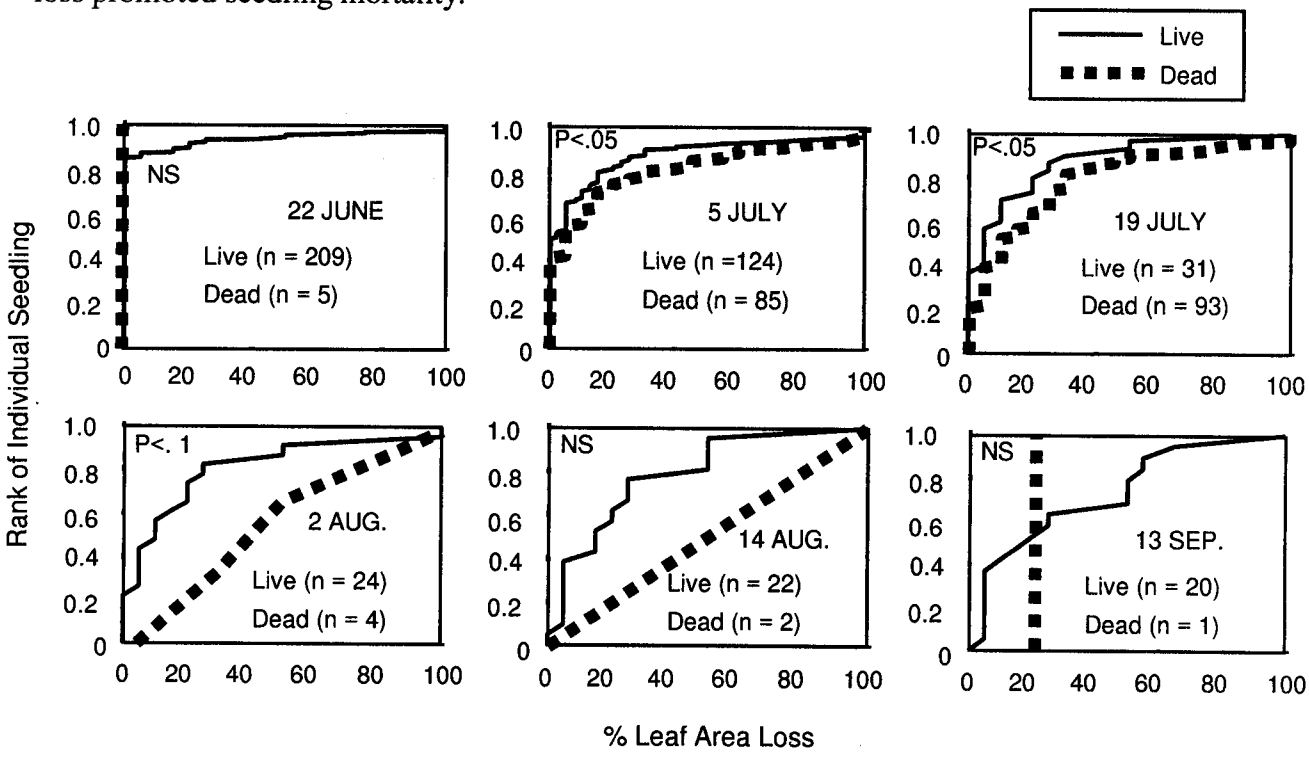

Figure 3. Percent leaf area loss due to insect defoliators and seedling mortality of current-year seedlings of *Fagus crenata* in the two plots of Iwate. The Kolmogorov-Smirnov 2-sample test and Mann-Whitney's U test were applied for detecting the difference in leaf area loss between the live and dead seedling groups.

Leaf area losses were compared among current-year seedlings, older seedlings, and adult trees. In order to study the effect of height on leaf area loss in adult trees, leaves were sampled at heights of 1 to 3 m above the ground and above 5 m. In order to exclude the effect of height on leaf area loss in seedlings, seedlings shorter than 20 cm were selected for this investigation. Figure 4 shows the cumulative distribution curve of individual leaves in relation to leaf area loss. With respect to leaf height, leaves in lower positions had greater leaf area losses; seedlings had greater leaf area losses than adult trees, and between the two groups of leaves sampled at different heights in adult trees, leaves in lower positions also had greater leaf area losses. These results indicate that leaf position is one of the factors that determine leaf area loss by insect folivory. However, current-year seedlings had greater leaf area losses than older seedlings, even though their heights were almost the same. This indicates that in addition to height, foliage quality influences insect folivory.

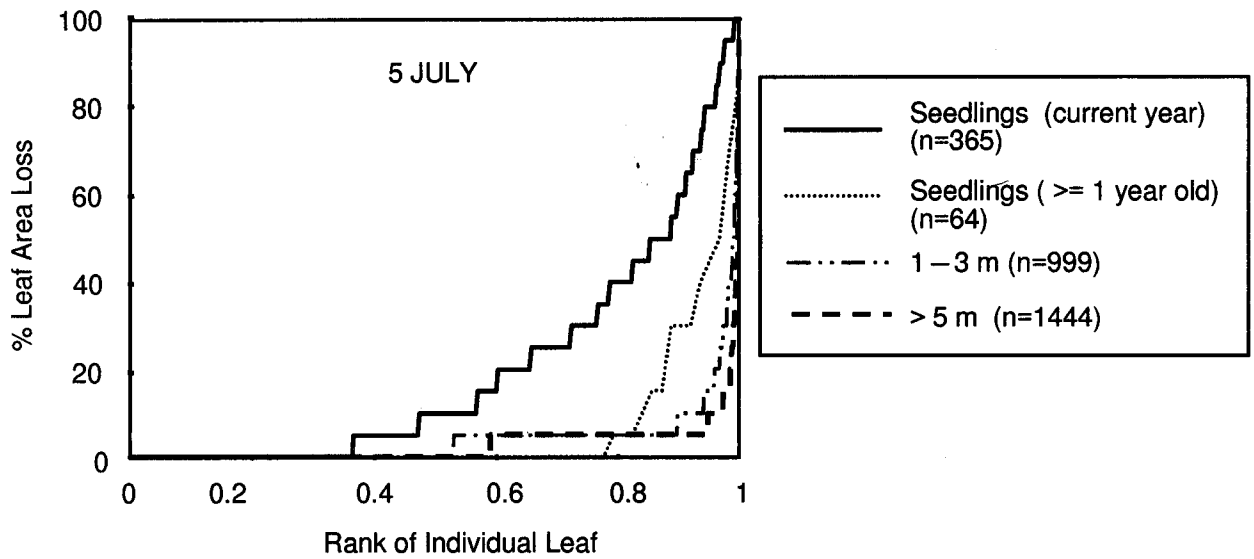

Figure 4. Percent leaf area loss of *Fagus crenata* due to insect folivory for both seedlings and adult trees. Leaf area losses due to insects were compared among leaves at different heights and among seedlings of different ages. Data on 5 July 1996 are shown.

The results for *F. crenata* are summarized below:

(1) Beech foliage located at lower heights had greater leaf area losses due to insect defoliators, suggesting the possibility that (1) more defoliators are distributed at lower heights because they fall by means of gravity and (2) foliage at lower heights is more palatable to insect defoliators than foliage at higher heights.

(2) Seedlings had greater leaf area losses than adult trees.

(3) Current-year seedlings had more severe leaf area losses than older seedlings even though their heights were almost the same, suggesting that in addition to height, foliage quality was related to the event.

(4) Leaf area loss influenced the survival of current-year seedlings.

Three *Quercus* Species. Figure 5 shows the leaf area loss of two deciduous oak species (*Q. variabilis* and *Q. serrata*) at Site B with respect to foliage height. It is clear for both species that foliage in lower positions was heavily defoliated. Seedlings of these two oak species had more severe leaf area losses than their respective adult trees. Figure 6 shows leaf area loss in relation to seedling age and mortality. The effects of seedling age and mortality on leaf area loss were tested by 2-way ANOVA. Both variables were statistically significant, but their interaction was not. These results were the same for *Q. crispula* (Fig. 7). These results suggest that current-year oak seedlings of all three species had less leaf area loss than older seedlings, which was completely the opposite of the results for *F. crenata*. Dead oak seedlings had more leaf area loss than live seedlings, which corresponds with the result for *F. crenata*. The percentage leaf area loss significantly influenced seedling mortality (logistic regression, $P<0.001$).

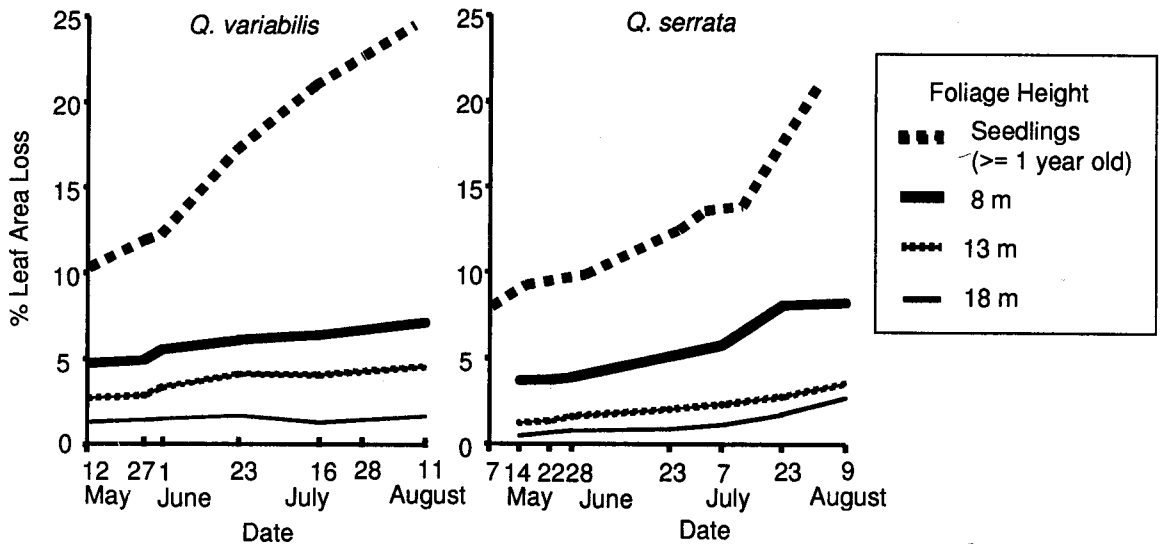

Figure 5. Seasonal changes in percent leaf area loss due to insect folivory of two oak species (*Q. variabilis* and *Q. serrata*) in relation to foliage height.

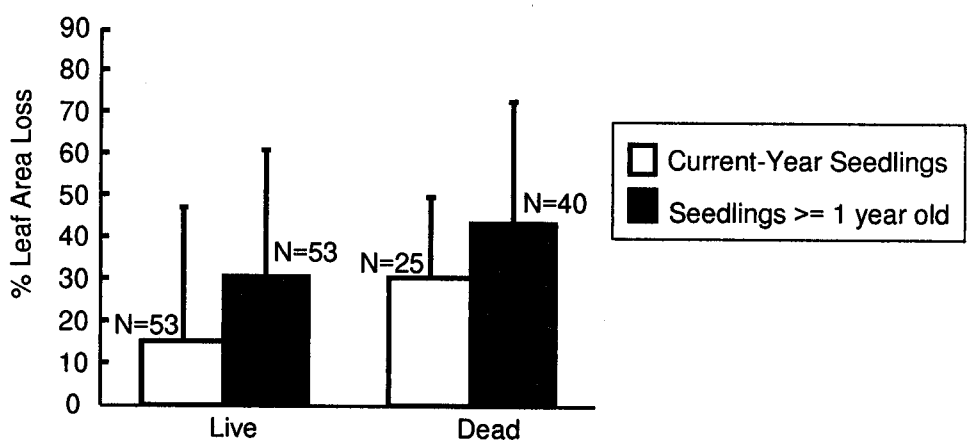

Figure 6. Influence of seedling age and mortality on leaf area loss due to insect folivory of *Quercus variabilis*. Both mortality and seedling age significantly influenced leaf area loss (ANOVA, $p<0.05$), but their interaction did not ($p>0.05$). Leaf area loss significantly influenced seedling mortality (logistic analysis, $p<0.05$), but seedling age did not ($p>0.05$).

Carbon and Defense. For both the three deciduous oak species and Siebold's beech, foliage at lower heights had greater leaf area losses, and leaf area loss influenced seedling mortality. Among the oak species and Siebold's beech, however, there was a difference in insect folivory between current-year seedlings and older seedlings. Current-year seedlings of oaks had less leaf area loss than older seedlings, and the mortality of current-year seedlings was lower. In contrast, current-year seedlings of Siebold's beech had greater leaf area losses, and mortality at age 0 was higher than that of older seedlings.

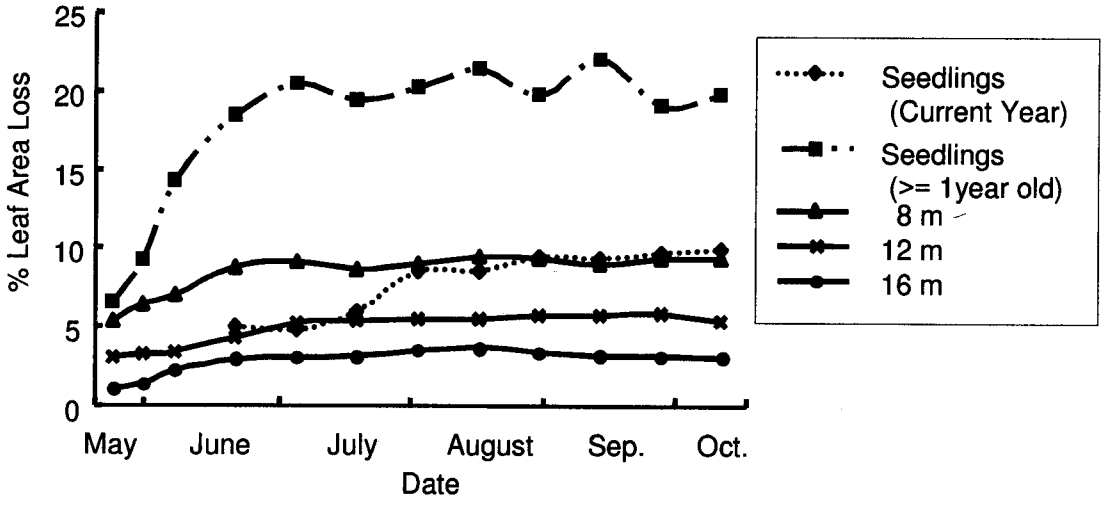

Figure 7. Seasonal changes in percent leaf area loss due to insect folivory of *Quercus crispula* in relation to foliage height and seedling age.

One of the plausible causes to explain this difference between Siebold's beech and oaks is foliage quality (Fig. 8). For Siebold's beech, nitrogen concentration was higher but tannin concentration was lower in the foliage of current-year seedlings compared to the foliage of older seedlings. The results were completely different for the oaks. No significant difference was found in nitrogen concentration between current-year and older seedlings, but current-year seedlings contained more soluble tannin. We speculate that this is related to the amount of carbohydrate supplied from cotyledons. Cotyledons of Siebold's beech seedlings drop almost two weeks after germination whereas those of oaks remain attached to seedlings for several years. Great amounts of carbohydrates are supposed to be supplied from an acorn to a current-year oak seedling. However, older seedlings must synthesize carbohydrates by themselves, or they can use a stock of carbohydrates from the previous year. The photosynthetic rate is low under the light-limited conditions found on the forest floor beneath tree canopies. The C/N ratio of the foliage is likely to become low under such circumstances, so that the foliage of older oak seedlings becomes a more palatable food for defoliators than the foliage of current-year seedlings.

Phenological Escape of Current-Year Seedlings of *Q. crispula*. Another plausible cause for low leaf area losses in current-year oak seedlings is phenological escape. For *Q. crispula*, a concurrent species of Siebold's beech, current-year seedlings had much less leaf area loss than older seedlings (Fig. 7). The mortality of current-year *Q. crispula* seedlings was also significantly lower than for older seedlings (Fig. 9).

We compared the phenology of canopy flush and seed germination between Siebold's beech and *Q. crispula* with respect to seasonal changes in the abundance of insect defoliators in the canopy (Fig. 10). Defoliator abundance was estimated using dry weight of fallen frass. In 1997, canopy flushing of Siebold's beech started around May 5th, and the first peak of canopy defoliators occurred in early June. This first peak was caused by flush feeders. The second peak was caused mainly by the outbreak species *Syntypistis punctatella* (Lepidoptera: Notodontidae). Because this graph shows these events during an endemic year, the second peak was not so high. This second peak has been known to vary on an order magnitude of 4, corresponding to the density cycles of the outbreak species (Kamata and Igarashi 1996, Kamata 2000). Most Siebold's beech seeds germinated simultaneously at almost the same time as the first peak of canopy defoliators. In contrast to Siebold's beech, *Q. crispula*

canopies flushed almost 10 days later, so the first peak of defoliators (mainly flush feeders) were a bit behind the beech. There was a great difference in the timing of seed germination. Strictly speaking, these oaks had germinated their root before winter. The timing of leaf flush of current-year oak seedlings was late and varied greatly among individuals; leaf flush started in late June and ended in late August, with a peak in early July. Because the timing of leaf flush of current-year oak seedlings was late and greatly behind the peak of flush feeders, these seedlings could phenologically escape from defoliators for the first year.

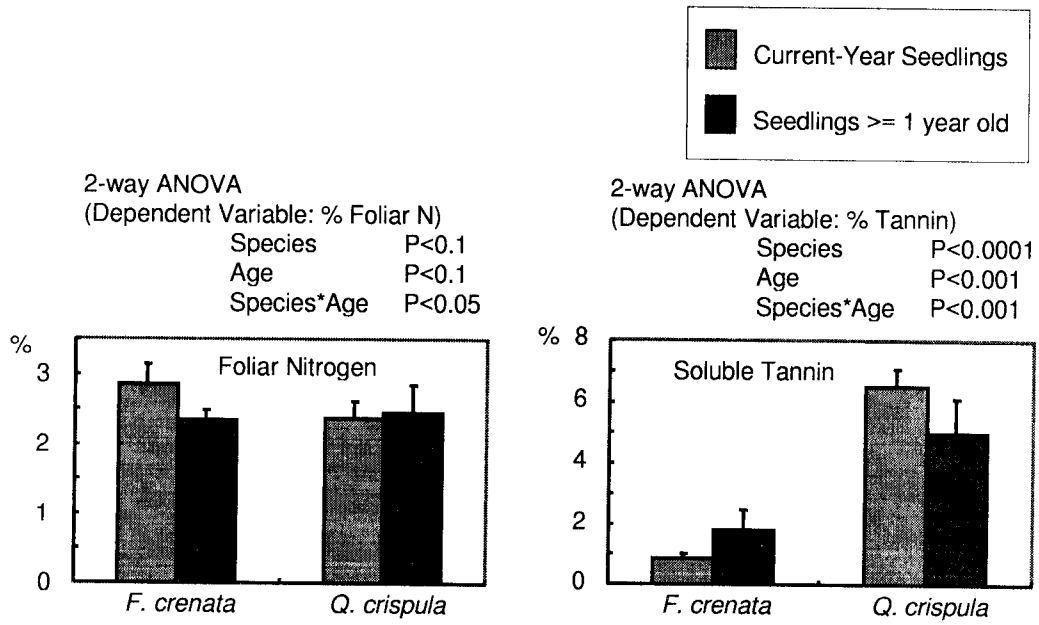

Figure 8. Foliage chemical properties of *Fagus crenata* and *Quercus crispula* in relation to seedling age.

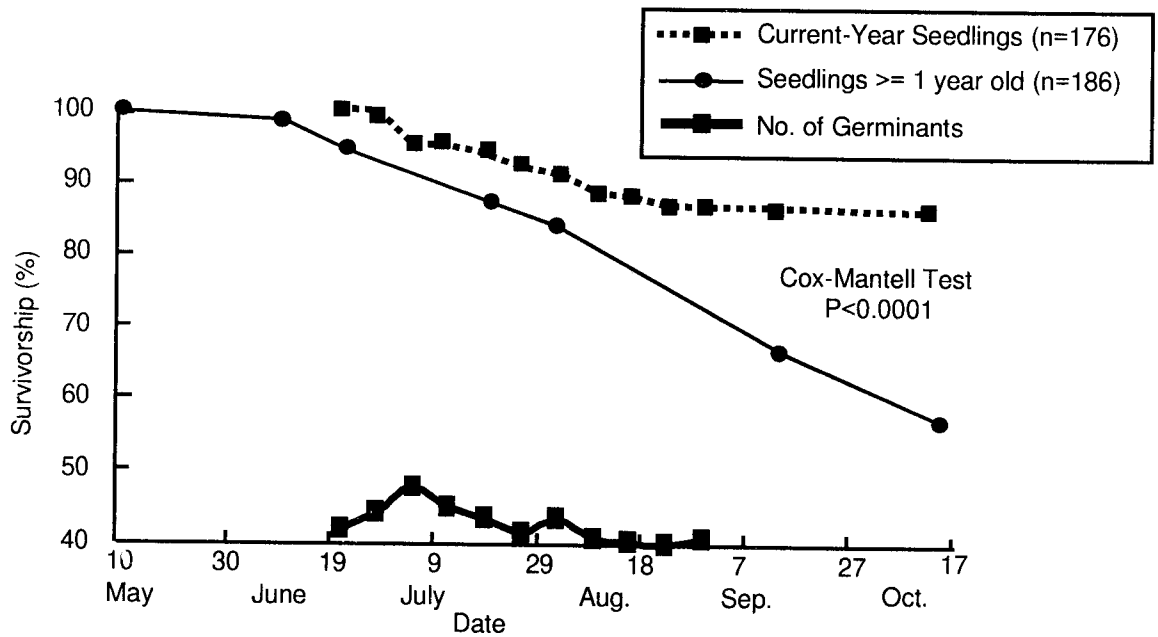

Figure 9. Survivorship curve of *Quercus crispula* seedlings in relation to their age.

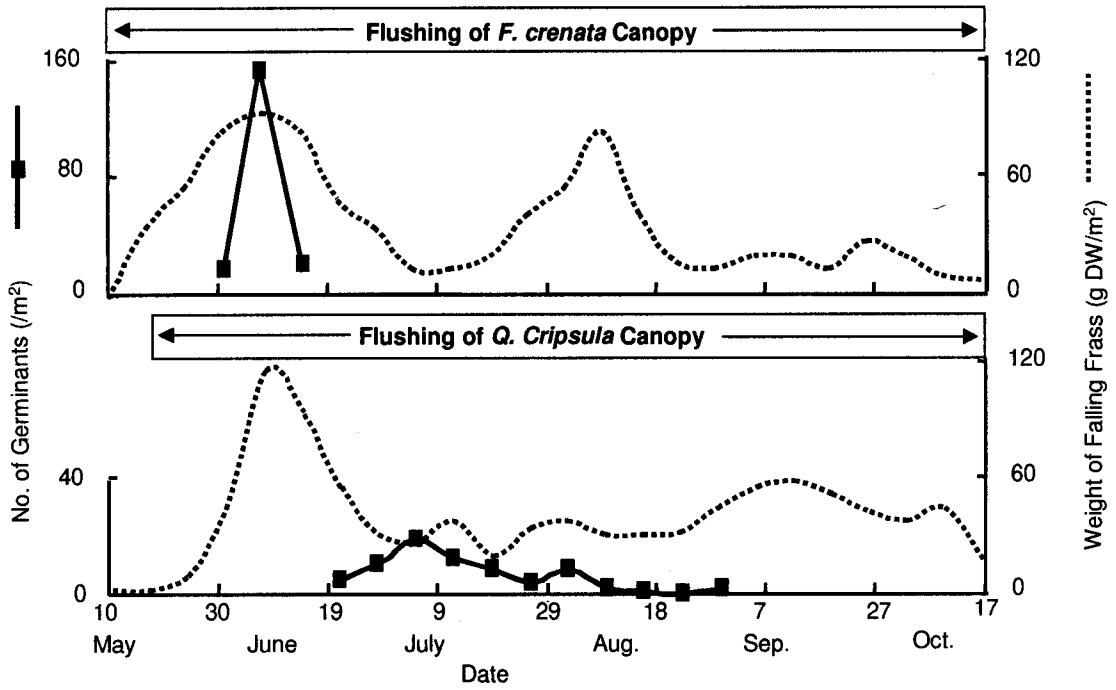

Figure 10. Seasonal changes in falling frass under *Fagus crenata* and the concurrent oak *Quercus crispula* and seasonal changes in the number of germinants of both species.

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European Parasitoids of the Pine False Webworm (*Acantholyda erythrocephala* (L.)) and Their Potential for Biological Control in North America

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ABSTRACT The pine false webworm (*Acantholyda erythrocephala*) is a pine defoliator of Palearctic origin introduced into North America early in the 20th century. A literature search and field surveys showed that the parasitoid complex of the pine false webworm is much richer in Europe than in North America. The potential for introducing European parasitoids into North America is evaluated here. The most promising biological control agent is the tachinid *Myxexoristops hertingi*, a larval parasitoid that lays microtype eggs on pine needles. The release of *M. hertingi* is proposed. Other larval parasitoids, particularly the ichneumonid *Xenoschesis* sp. and the egg parasitoid, *Trichogramma* sp., also show some potential but further studies are required before considering them for release into North America.

THE PINE FALSE webworm (PFW) (*Acantholyda erythrocephala* (L.)) (Hym.: Pamphiliidae) is a Palearctic insect, distributed from Japan to Britain and from Lapland to Italy. It was first observed in the United States in 1925 (Wells 1926) and in Canada in 1961 (Eidt and McPhee 1963). It reached pest status in the late 1970s when heavy damage was observed in young red pine (*Pinus resinosa*) plantations in Ontario (Syme 1981). In 1993, the first outbreaks occurred in mature red pine stands. In New York State, the first severe defoliation was noticed in the early 1980s; since then, the PFW has become a persistent and increasing problem in white pine (*Pinus strobus*) plantations in the Adirondack Mountains (Asaro and Allen 1999, Allen 2000). Although most defoliation reports have come from Ontario and New York, the PFW is in several states in the northeastern United States, Quebec, Alberta, and Newfoundland (Howse 2000). In addition to white and red pine, nearly all pine species are occasionally attacked. Persistent outbreaks, as observed in North America, cause severe growth loss (Allen 2000). Tree mortality often occurs after 5 to 7 years of heavy defoliation due to secondary pests such as bark beetles. Even low populations of the PFW can be particularly destructive in Christmas tree plantations, reducing the market value of the trees.

In contrast, the PFW is considered a minor pest in its area of origin. Outbreaks are rare and usually of short duration (2 to 3 years). Notable exceptions include an 8-year outbreak in the 1960s in eastern Austria (Schmutzenhofer 1974) and populations in southern Poland that remained at semi-outbreak levels for a decade in the 1980-1990's (M. Kenis, unpublished). In the late 1990s, unusually heavy outbreaks started in northwestern Italy in 40-year-old white pine plantations situated far from the natural distribution of pine species. As in North America, *A. erythrocephala* is found on most pine species, with the exception of Mediterranean species. The heaviest outbreaks were observed in plantations of *P. strobus*, *P. sylvestris*, and *P. nigra*. In addition, defoliation is often observed on isolated *P. mugho* and *P. cembra* in gardens, particularly in the Southern Alps (Hellrigl 1996).

Pages 65-73 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.

The biology and ecology of *A. erythrocephala* has been studied by several authors (e.g. Schwerdtfeger 1941, 1944; Schmutzenhofer 1974; Lyons 1994, 1995, 1996; Asaro and Allen 1999). Its life history can be summarized at follows. Adults emerge from the soil in spring, from March (Italy) to May (Canada). Mating and oviposition start soon after emergence. Eggs are laid in rows of one to ten on 1-year-old pine needles. Hatching occurs 3 to 4 weeks later and newly hatched larvae start feeding at the base of the needles, then construct silken webs within which they feed. On average, a larva destroys about 50 needles of *P. sylvestris*, most of them being only partly consumed. Males go through five instars and females go through six instars. From May to July, mature larvae (eonymphs) drop to the soil and build a pupal cell below the humus layer, usually at depths of 3 to 12 cm. After a summer diapause, most eonymphs transform to pronymphs, but some go into prolonged diapause for 2 to 3 years. The rate of prolonged diapause varies among years and with latitude. Pronymphs pupate in spring and adults emerge a few weeks later.

Very little is known about the population dynamics of the PFW in Europe, but natural enemies, particularly parasitoids and pathogens, have been commonly observed and have sometimes been associated with the collapse of outbreaks (e.g. Schwerdtfeger 1941, Rumphorst and Goossen 1960, Jahn 1967, Schmutzenhofer 1974). In North America, however, natural enemies are rare and of low incidence (Lyons 1995, Asaro and Allen 1999). Considering the differences between Europe and North America in terms of both natural enemy impact and outbreak frequency and duration, a biological control program was set up with the aim of introducing European natural enemies into North America. This paper presents information on PFW parasitism in North America and Europe as well as data on the main parasitoid species and an evaluation of their potential as biological control agents. More precise data on parasitoid collection and rearing will be presented elsewhere (Kenis and Kloosterman, in preparation).

Parasitoid Complex of *A. erythrocephala* in North America

The parasitoid complex of the PFW in North America is shown in Table 1. Egg parasitoids are nearly absent. The polyphagous species *Trichogramma minutum* Riley has occasionally been reared from PFW eggs in Ontario (Lyons 1995, Bourchier et al. 2000). Strains of *T. minutum* and *T. platneri* Nagarkatti have been used for inundative releases against the sawfly with some success (Bourchier et al. 2000).

Table 1. Parasitoids of *Acantholyda erythrocephala* in Canada and the USA

	Canada	USA
Egg Parasitoid		
Trichogramma minutum Riley (Trichogrammatidae)	X	
Larval Parasitoids		
Ctenopelma erythrocephalae Barron (Ichneumonidae)		X
Homaspis interruptus (Provancher) (Ichneumonidae)		X
Olesicampe sp. (Ichneumonidae)	X	
Sinophorus megalodontis Sanborne (Ichneumonidae)	X	

Sources: Canada: Bourchier et al. 2000; Lyons 1995, 1999
USA: Asaro and Allen 1999; Barron 1981

Four ichnemonid larval parasitoids were observed on the PFW in Canada and the USA. *Sinophorus megalodontis* Sanborne and *Olesicampe* sp. were reared from eonymphs in Ontario (Lyons 1995, 1999; Bourchier et al. 2000) and *Homaspis interruptus* (Provancher) was found parasitizing the PFW in New York (Asaro and Allen 1999). In addition, *Ctenopelma erythrocephalae* Barron was observed ovipositing in eggs of the PFW in New Jersey (Barron 1981). All these species are apparently of Nearctic origin and none of them seem to have an important impact on sawfly populations, probably because they are poorly adapted to their novel host. Larval parasitism has not exceeded 10%, even after 15 years of continuous outbreaks. *H. interruptus* is also known from another *Acantholyda* sp. and a *Cephalcia* sp. (Barron 1990), whereas the regular hosts of the three other parasitoid species are not known.

Parasitoid Complex of *A. erythrocephala* and Congeneric Species in Europe

Table 2 presents the parasitoid species found in the literature or during our own surveys in Poland, Italy, and Switzerland. The parasitoid complexes of the two congeneric species *A. posticalis* Matsumura (= *nemoralis* Thomson) and *A. hieroglyphica* (Christ) are added since they could represent alternative hosts for parasitoid collections should *A. erythrocephala* populations not be available in Europe. Comparing the parasitoid complexes of closely related hosts might also give important information on parasitoid specificity. Although the literature data on parasitoids of *Acantholyda* spp. were checked for the most obvious mistakes, the list presented in Table 2 has to be considered with caution because it probably contains taxonomic errors, such as different names referring to the same species or a single name referring to two species.

As expected, the parasitoid complex of the PFW is much richer in Europe than in North America. At least four to five egg parasitoids and 8 to 10 larval parasitoids attack *A. erythrocephala* in Europe. *A. posticalis* has a parasitoid complex that is similarly rich, with several species overlapping. Only three species were reared from *A. hieroglyphica*, probably because few studies focused on this species.

Egg Parasitism. Several gregarious *Trichogramma* species are reported from the PFW and other *Acantholyda* spp. in Europe. Schwerdtfeger (1944) mentions high parasitism by *T. evanescens* Westwood on *A. erythrocephala* in Germany in the 1940s and Burzynski (1961) reports *T. embryophagum* (Hartig) as a parasitoid of *A. erythrocephala* in Poland. Both species are also known to attack *A. posticalis* (Herting 1977). Recently, an undescribed *Trichogramma* sp. of the group *fasciatum* was found attacking outbreak populations of *A. posticalis* and low-density populations of *A. erythrocephala* in the Valle d'Aosta, northeastern Italy. This species is univoltine, overwinters in host eggs, and is more specific than the majority of its congeneric species. Screening tests were made on four Lepidopteran species frequently used as rearing hosts for *Trichogramma* spp. (Bourchier et al. 2000). The *Trichogramma* sp. refused to oviposit in *Anagastes kuehniella* (Zeller), *Actebia fennica* (Tauscher), and *Choristoneura fumiferana* (Clemens), whereas oviposition was observed on *Lambdina fiscellaria* (Guenée) but no development occurred. In additional tests (Kenis and Kloosterman, unpublished), females rejected eggs of two diprionid pine sawflies, *Diprion pini* L. and *Gilpinia frutetorum* F. The species most closely related to the undescribed *Trichogramma* sp., both ecologically and morphologically, is *T. cephalciae* Hochmut & Martinek, a parasitoid mainly associated with *Cephalcia* spp., another pamphiliid genus

Table 2. Parasitoids of *Acantholyda erythrocephala*, *A. posticalis*, and *A. hieroglyphica* in Europe; data is from the literature (L) and own surveys (S)

	A. erythr.	*A. postic.*	*A. hierogl.*
Egg Parasitoids			
Trichogramma sp. (Trichogrammatidae)	S	L,S	
Trichogramma cephalciae Hochmut & Martinek (Trichogr.)		L	
Trichogramma embryophagum (Hartig) (Trichogrammatidae)	L	L	
Trichogramma evanescens Westwood (Trichogrammatidae)	L	L	
Trichogramma semblidis (Aurivillius) (Trichogrammatidae)	S	S	
Aprostocetus sp. (Eulophidae)		S	
Neochrysocharis formosa (Westwood) (Eulophidae)	L,S	L,S	
Mesopolobus subfumatus (Ratzeburg) (Eulophidae)		L,S	
Larval Parasitoids			
Ctenopelma lucifer (Gravenhorst) (Ichneumonidae)		L	
Ctenopelma nigrum Holmgren (Ichneumonidae)	L	L	
Holocremnus heterogaster Thomson (Ichneumonidae)	L		
Homaspis rufinus (Gravenhorst) (Ichneumonidae)	L	L	
Notopygus sp. (Ichneumonidae)	S	S	
Olesicampe monticola (Hedwig) (Ichneumonidae)	L		
Netelia oscellaris (Thomson) (Ichneumonidae)	L		
Sinophorus sp. (Ichneumonidae)	S		
Sinophorus crassifemur (Thomson) (Ichneumonidae)	L	L	
Xenoschesis sp. (Ichneumonidae)	S		
Xenoschesis fulvipes (Gravenhorst) (Ichneumonidae)	L	L	L
Euexorista obumbrata (Pandellé) (Tachinidae)		L	
Exorista larvarum (L.) (Tachinidae)		L	
Myxexoristops bonsdorffi (Zetterstedt) (Tachinidae)		L,S	
Myxexoristops hertingi Mesnil (Tachinidae)	L,S		
Nemorilla maculosa (Meigen) (Tachinidae)			L
Pseudopachystylum gonioides (Zetterstedt) (Tachinidae)	L	L	
Undetermined Tachinidae			L

Sources: *A. erythrocephala*: Kenis and Kloosterman (unpublished surveys in Poland, Italy and Switzerland); Burzynski 1961; Eichhorn 1988 (review); Hellrigl 1996; Herting 1964, 1977 (review); Jahn 1967; Joakimov 1921; Pschorn-Walcher 1982 (review); Rumphorst and Goossen 1960; Schmutzenhofer 1974; Schwerdtfeger 1941, 1944; Thompson 1944 (review)
A. posticalis: Kenis and Kloosterman (unpublished surveys in Italy); Casale and Campò 1977; Eichhorn 1988 (review); Herting 1977 (review); Hochmut and Martinek 1963; Pschorn-Walcher 1982 (review); Thompson 1944 (review)
A. hieroglyphica: Herting 1977 (review); Pschorn-Walcher (1982 (review)

that feeds mainly on spruce. *T. cephalciae* has also been occasionally reared from *A. posticalis* (Hochmut and Martinek 1963). This species is partly univoltine and apparently specific to Pamphiliidae, but is morphologically distinguishable from undescribed *Trichogramma* sp. (Pintureau, Stefanescu, and Kenis, in preparation). Another species, the multivoltine, polyphagous *T. semblidis* (Aurivillius) was reared occasionally from the same

populations of *A. posticalis* and *A. erythrocephala* in Italy (Kenis and Kloosterman, in preparation).

Burzynski (1961) and Kenis and Kloosterman (in preparation) reared the solitary eulophid *Neochrysocharis formosa* Westwood (=*Achrysocharella ovulorum* Ratzeburg) from *A. erythrocephala* in Poland. *N. formosa* is a polyphagous parasitoid also known from *A. posticalis* (Casale and Sampò 1977; Herting 1977; Kenis and Kloosterman, in preparation) and pine diprionid sawflies (e.g. Pschorn-Walcher and Eichhorn 1973).

Larval Parasitism – Ichneumonidae. Several ichneumonid species are reported from *A. erythrocephala* and congeneric species (Table 2), but usually only one or two species are mentioned per host population. The ichneumonids most commonly associated with *A. erythrocephala* belong to the genera *Xenoschesis* and *Sinophorus*. In previous studies, they were usually identified as *X. fulvipes* (Gravenhorst) and *S. crassifemur* (Thomson) (e.g. Schwerdtfeger 1944, Schmutzenhofer 1974), two species better known as parasitoids of *Cephalcia* spp. However, a closer examination of *Xenoschesis* sp. from Poland and Italy and *Sinophorus* sp. from Poland (Kenis and Kloosterman, in preparation) revealed morphological differences when compared with specimens reared from *Cephalcia* spp. Since the phenology of *Cephalcia* spp. is at least one month later than that of *A. erythrocephala* and *A. posticalis*, it is likely that the two host genera support different, closely related parasitoids. A similar taxonomic problem arises with *Ctenopelma lucifer* (Gravenhorst), the main parasitoid found in *A. posticalis* outbreaks in the Valle d'Aosta, Italy (Casale and Sampò 1977). Recent observations in the same area suggest that it is not *C. lucifer*, but *Notopygus* sp., a species also reared from *A. erythrocephala* in Poland (Kenis and Kloosterman, in preparation).

Two other ichneumonid species worth mentioning are *Olesicampe monticola* (Hedwig), a parasitoid usually associated with *Cephalcia* spp. that was found parasitizing 44% of the larvae of an isolated population of *A. erythrocephala* in South Tyrol, Italy (Hellrigl 1996), and *Holocremnus heterogaster* Thomson, the dominant parasitoid during an *A. erythrocephala* outbreak from 1915 to 1917 in Bulgaria (Joakimov 1921).

Ichneumonid parasitoids of *Acantholyda* spp. attack eggs or larvae and kill their host in the pupal cell, either before or after the winter. In most cases, ichneumonids are able to follow their host into prolonged diapause (Kenis and Kloosterman, unpublished). Eggs and young larvae are frequently encapsulated in the host haemolymph.

Larval Parasitism – Tachinidae. Only two tachinid species are reported from *A. erythrocephala* (Table 2). *Pseudopachystylum gonioides* (Zetterstedt), a species frequently reared from *A. posticalis* in Central Europe, has also been cited as a parasitoid of *A. erythrocephala* (Herting 1977). However, the most regularly encountered tachinid parasitoid of *A. erythrocephala* is *Myxexoristops hertingi* Mesnil. It is found throughout the entire European distribution of its host and has often been mentioned as the main parasitoid of the PFW; Rumphorst and Goossen (1960) suggested that the fly was the main cause of the collapse of an outbreak in Germany. *A. posticalis* and the closely related *Cephalcia* spp. are attacked by the congeneric species *M. bonsdorffi* (Zetterstedt) and *M. abietis* Herting, respectively (Herting 1964, Eichhorn 1988), suggesting high host specificity in this genus. *M. hertingi* was found in low density populations on isolated *Pinus cembra* in the Swiss and Italian Alps. Specimens were also reared from the closely related host *Acantholyda pumilionis* (Giraud) in the same areas (Kenis and Kloosterman, in preparation). However, these had a much more rapid development, with large larvae found in mature host larvae dropping to the soil, which suggests the possible existence of sibling species.

M. hertingi lays over 1,000 microtype eggs on pine needles that are ingested by sawfly larvae. Parasitoid development occurs when the eonymph is in the soil. The winter is passed as a mature maggot in the dead host skin. In spring, the maggot climbs to the soil surface to build a puparium. Adults emerge after about a month and mate soon after emergence. *M. hertingi* puparia are sometimes heavily attacked by hyperparasitoids such as a gregarious diaprid wasp *Trichopria* sp. that killed over 20% of the puparia in an outbreak in Italy in 1999 (Kenis and Kloosterman, in preparation).

In recent years, we have put much emphasis on the development of a rearing method for *M. hertingi*. Although possible, rearing *M. hertingi* in the laboratory proved to be very difficult for two reasons: (1) the low rate of mating success and (2) the poor development of tachinids after egg ingestion (Kenis and Kloosterman, in preparation).

Biological Control Potential

There is general agreement on the most important attributes of a good biological control agent to introduce against an exotic pest (e.g. Cock 1986). In particular, the natural enemy should (1) have an important impact on the host in the region of origin, (2) be host specific, (3) be well synchronized with the host, (4) have a high searching capacity, (5) be well adapted to a wide range of environmental conditions, and (6) occupy an empty ecological niche in the natural enemy community of the pest in the region of introduction. The tachinid *M. hertingi* combines all these attributes. Literature and field surveys showed that it is the most abundant and frequently encountered parasitoid of the PFW in Europe. Its broad distribution indicates that it has a wide climatic range and the observation of isolated PFW populations being attacked in the Alps suggest that the fly has a good search capacity. There is no tachinid or other late larval parasitoid reported from the PFW in North America. *M. hertingi* is a univoltine parasitoid and is well synchronized with its host. Finally, *M. hertingi* is apparently very specific and is probably restricted to one or two *Acantholyda* spp. Therefore, we recommend *M. hertingi* for introduction into North America.

The difficulty in rearing *M. hertingi* suggests that releases in North America may have to be made with field collected material. Since outbreaks in Europe are scarce, every opportunity should be taken to collect *M. hertingi* when sizeable populations are available. However, efforts should be made to improve laboratory mating techniques because establishment in North America would more likely be achieved by releasing mated females than unmated flies.

Ichneumonids, particularly the most common species *Xenoschesis* sp., may represent additional candidates. Ichneumonids have long been considered less specific than *M. hertingi* because the same species were reported from *Acantholyda* spp. and *Cephalcia* spp. However, recent observations showed that a complex of sister species was involved that was probably more specific than previously thought. Further studies, however, are needed on the taxonomy, specificity, biology, and ecology of the main species before considering them for introduction. In particular, the high rates of encapsulation often observed in Europe may hamper their establishment or efficiency in North America.

Finally, the undescribed *Trichogramma* sp. would merit further studies. In contrast to most other *Trichogramma* spp., it is univoltine and would not require an alternate host to become established in North America. Host specificity would need to be further evaluated but preliminary observations suggest that this species is more host specific than most of its

congeneric species. However, its real impact and occurrence in Europe as well as its taxonomic status need to be further assessed.

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Preliminary Results on the Efficacy of Stored TM BioControl-1®

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ABSTRACT Douglas-fir tussock moth nucleopolyhedrovirus (OpNPV) was produced and stored in various sized packages during the 1980s under the registered name of TM BioControl-1®. This virus is an important component of the pest management system for this tussock moth. In this paper, preliminary results of a collaborative project between the USDA Forest Service and the Canadian Forest Service to test the efficacy, or shelf life, of stored TM BioControl-1® are presented. Bioassays were done using 1-day-old third instar Douglas-fir tussock moth larvae inoculated with different concentrations of virus preparation. Comparisons of LD50 and LD90 values indicated a trend of higher values for samples stored for 6, 10, and 13 years than for virus that was stored for 4 years or was freshly produced. Potency ratios suggested a loss in potency with longer storage. There appeared to be no difference in LD values or potency in samples from different package sizes from the same lot.

FROM THE EARLY 1980s to 1995, the USDA Forest Service undertook an ambitious project to produce, register, and store Douglas-fir tussock moth nucleopolyhedrovirus (OpNPV) for use against the Douglas-fir tussock moth (DFTM). Numerous lots of OpNPV were produced during this time and stored at -10 °C at USDA Forest Service facilities in Corvallis, OR. The multicapsid isolate of OpNPV was registered in the United States in 1976 under the name TM BioControl-1® (Martignoni 1978, 1999). The same product received registration in Canada in 1983 along with the same virus produced in *Orgyia leucostigma* under the name Virtuss® (Otvos et al. 1998). This virus is now an important component of the pest management system that was developed for the Douglas-fir tussock moth (Shepherd and Otvos 1986, Otvos and Shepherd 1991). Considerable time has elapsed since the original production and storage of TM BioControl-1® lots. A collaborative project between the USDA Forest Service and the Canadian Forest Service was initiated in the summer of 1998 to test the efficacy, or shelf life, of the stored TM BioControl-1® product. This is a preliminary report of early results of these efficacy tests in this on-going project.

Douglas-fir Tussock Moth. The Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) (Lepidoptera: Lymantriidae) is a native defoliator and causes periodic damage in the interior dry-belt coniferous forests of British Columbia, Canada and the western United States. Outbreaks occur every 7 to 11 years and persist up to 4 years (Mason and Luck 1978, Harris et al. 1985). Although DFTM larvae feed on the foliage of several tree species, the primary hosts in British Columbia and the U.S. are Douglas-fir (*Pseudotsuga menziesii* variety *glauca* Biessen (Franco)) and *Abies* spp. (Beckwith 1978, Shepherd 1985). Severe economic damage may occur during outbreaks. There may be significant tree mortality due to defoliation as well as top kill, growth reduction, and secondary attacks by insects and fungi (Wickman 1978, Alfaro et al. 1987).

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History of TM BioControl-1® Samples. Production of TM BioControl-1® occurred at the USDA Forest Service facility in Corvallis, OR. Fifth instar DFTM larvae were infected with OpNPV, reared until death, and frozen. Over the course of 9 years, three private companies were contracted to process the virus-killed larvae and remove excess insect parts. The cadavers were lyophilized to remove moisture, resulting in a high potency, small particle size, virus-containing powder capable of being mixed as an insecticide and sprayed through ground and aerial spray equipment. The finished product was a wettable powder meeting the requirements of the registered product TM BioControl-1®. The packaging was to be suitable for long-term storage at -10°C and ease of use in field locations where control measures were required. Packages of TM BioControl-1® are kept in cold storage at the Forestry Sciences Laboratory in Corvallis.

The infectivity titre (LC50) of the processed product was determined by the USDA Forest Service on advance samples provided by the contractors. This was done at Corvallis using the diet surface contamination technique. Second instar Goose Lake colony tussock moth larvae were exposed to several different concentrations of the virus sample. The Goose Lake colony, which originated from northern California field-collected DFTM, has been maintained in the laboratory under controlled conditions since the mid 1960s. The virus dilutions were applied to the surface of the artificial diet to determine how much of the preparation was required to cause 50% of the test insects to die (LC50) (Martignoni and Iwai 1977, Martignoni 1999).

Ten lots of TM BioControl-1® were produced and stored between 1985 and 1995. These lots were placed in 1,243 packages and contained the equivalent of approximately 400,000 acre doses (Hadfield and Magelssen 1995). From these packages, 47 samples were selected for efficacy testing. The selection was based on lot number, time in storage, and package size (Table 1). We are testing the effects of the following variables on the efficacy of the stored products: (1) time in storage, (2) package size, (3) company processing the virus-infected insects, and (4) potency against strains of DFTM from different geographical regions. This paper presents preliminary results of the bioassays conducted in the first year.

Materials and Methods

Selection of Samples for Testing. Of the 1,243 packages stored, 17 different package sizes, representing small, medium, and large packages, were sampled for bioassays. Twenty-gram samples were weighed out and sent to the Pacific Forestry Centre in Victoria, B.C., for testing. Fifteen of the package sizes had three samples each and two had one sample each for a total of 47 samples. The 47 samples were ranked in terms of time in storage, package size, and acre dose available.

To date, three large bioassay runs, each using approximately 4,500 larvae (for a total of approximately 14,000 larvae) have been completed employing larvae from the following sources: (1) Goose Lake DFTM colony, (2) wild DFTM reared from egg masses collected in California, and (3) wild DFTM reared from egg masses collected in British Columbia.

Egg masses of DFTM have to be stored at cold temperatures (5°C) to break diapause. Storage from 4 to 7 months is ideal to give maximum hatching rate while storage for longer periods results in a decrease in larval hatch (Beckwith 1978). Each large bioassay run takes approximately 2 to 3 months to complete. We are reporting here on some preliminary data from the first large bioassay run using the Goose Lake strain.

Table 1. List of the 20-gram samples removed for efficacy determination from TM BioControl-1® packages in storage at Corvallis

Lot #[a]	g/Pkg[b]	# Pkgs	Total Acre Doses	# 20-g Samples	Date Stored
1	1,200	1	480	1	1985
2	2,150	18	18,000	3	1986
3	1,830	13	13,000	3	1986
4a	368	124	24,800	3	1986
4b	1,840	33	33,000	3	
5a	368	54	10,800	3	1986
5b	1,840	26	26,000	3	
6	180	170	17,000	3	1989
7a	31.7	485	48,300	3	1990
7b	158.5	100	50,000	3	
7c	317	50	50,000	3	
8a	202	1	690	1	1991
8b	293	68	68,000	3	
9b	58	57	5,700	3	1993
9c	580	9	9,000	3	
10a	124.7	10	1,000	3	1995
10b	1,247	24	24,000	3	

[a] Lot 1 processed by USDA Agricultural Research Service
Lots 2-5 processed by Reuter
Lots 6-7 processed by Espro
Lots 8-10 processed by Crop Genetics

[b] Package size: small = <100g/pkg, medium = 100-999g/pkg, large = >1,000g/pkg

Bioassays with Goose Lake Strain DFTM. Five samples, representing four different time periods in storage and three package sizes (small, medium, and large) were selected for the first large bioassay run. These samples were: lot 2 (TM2) stored 13 years, lot 6 (TM20) stored 10 years, lot 9 (TM36 and TM37) stored 6 years, and lot 10 (TM43) stored 4 years (Table 2). All of these samples represented lots with medium to high acre doses in storage. In addition, TM36 and TM37 were from the same lot and represented small and medium package sizes.

Table 2. History of TM BioControl-1® samples used in the 1999 bioassay reported here

Lot #	Sample #	Year Stored	Time in Storage (yr)	Package Size (g/pkg)
2	2	1986	13	2,150
6a	20	1989	10	47
9b	36	1993	6	58
9c	37	1993	6	580
10b	43	1995	4	1,247

Bioassay Protocol. To obtain DFTM larvae, Goose Lake colony (maintained at the Pacific Forestry Centre since March 1996) eggs were washed three times with a 0.1% sodium hypochlorite (2% bleach) solution to reduce potential virus contamination, rinsed three times with distilled water, and allowed to air dry. The eggs were hatched and larvae reared at 25°C, 50 to 60% RH with a photoperiod of 16:8 [L:D]. Larvae were reared in groups of 10 on artificial diet in petri dishes (Thompson and Peterson 1978). Newly molted third instar larvae were selected from the colony and starved for 16 to 20 hr before the bioassay.

Virus Preparation. Twenty mg of each of the five TM BioControl-1® samples to be tested in the first bioassay were weighed out and 20 ml of distilled water were added. Samples were stirred for 2 hr and viral samples prepared in triplicate. One week prior to inoculation, serial dilutions were made and stored at 4°C. The USDA Forest Service had already counted the polyhedral inclusion body (PIB) concentrations of these samples and these counts were available in the original bioassay data provided to us. However, as a check, haemacytometer counts of PIBs were done on five of the TM BioControl-1® samples. The PIBs/ml calculated were the same as the original PIB counts done at Corvallis. A fresh OpNPV virus sample, used as a positive control, was prepared prior to the bioassay by homogenizing Goose Lake DFTM larvae previously inoculated with OpNPV and reared until death. The fresh OpNPV sample was prepared 2 weeks prior to use and stored at 4°C; dilutions were discarded after 3 months. The homogenate was filtered through cheesecloth, centrifuged several times, and resuspended in distilled water. PIB counts were done using a haemacytometer to quantify the virus.

Inoculation. A diet plug inoculation bioassay technique, similar to that of Kaupp and Ebling (1990), was used. Diet plug bioassay is superior to diet surface contamination because it eliminates any variation in the distribution of PIBs on the diet surface and negates differences in larval feeding rates and interactions among larvae reared in the same container.

Serial viral dilutions ranging from 2.5 to 300 PIBs/µl were used in our bioassay. One µl of each viral dilution or control (distilled water) was added to a small diet plug (3 to 4 mg) inside each well of a 24-well tissue culture plate. The diet plugs were large enough to fully absorb the 1 µl of liquid. Immediately after inoculation, one third instar larva was placed into each well to feed on the treated diet plug. Five virus concentrations and one control were tested for each of the TM BioControl-1® samples as well as the fresh OpNPV sample (positive control). Bioassay of the five dilutions of each TM BioControl-1® sample, the fresh preparation of OpNPV, and an untreated control were replicated three times. For each viral dilution or control, 48 larvae were tested.

Larvae were held in darkness for 24 hr with the inoculated diet plug at 25°C, 50 to 60% RH. Larvae that consumed the entire diet plug were placed in individual cups (Solo P100, Solo Cup Co., Urbana, IL 61801-2895) with a fresh cube of diet and returned to the same growth chamber. Larvae that did not consume the entire diet plug were discarded. Because of the high virulence of OpNPV, it was necessary to rear the larvae individually after inoculation to avoid cross infection. Separate growth chambers, set at the same rearing conditions, were maintained for the control and viral-infected insects to guard against viral transmission to the control insects. Diet was changed at least weekly or more often if required. Larvae were reared until adult emergence or death and were examined daily and had their mortality recorded. Only those larvae that died from NPV infection, as determined by gross pathology or microscopic examination, were included in the analysis.

Data Analysis: Preliminary Data. The equations of the dosage mortality curves and LD values with associated 95% fiducial limits were calculated using PROC PROBIT analysis (SAS Institute 1989-1996). Each replicate at day 14 post inoculation (or day 21) was tested as a separate preparation to verify that there was no difference in the replicates. If there was no difference, data for the three replicates were combined. Estimates of LD50 and LD90 for each TM BioControl-1® sample and the fresh OpNPV sample were calculated. LD values at day 14 and day 21 were compared to see if lethal doses changed over time. LD50 and LD90 values were examined for significant differences (no overlap of the 95% fiducial limits).

Potency ratios comparing each TM BioControl-1® sample to the fresh OpNPV preparation were calculated. Also, potency ratios were calculated comparing each TM BioControl-1® sample to Lot 10 (TM43).

Preliminary Results

Within Sample Variation of LD50 and LD90. There were no significant differences between LD50 values at day 14 compared to day 21 for any of the TM BioControl-1® samples tested or for the fresh OpNPV sample. There were no significant differences between LD90 values at day 14 compared to day 21 for any of the TM BioControl-1® samples tested or for the fresh OpNPV sample. Therefore, we decided to continue the analysis using day 14 data only.

Between Sample Comparisons of LD50 and LD90. There were no significant differences in LD50 values when the fresh OpNPV sample was compared to any of the TM BioControl-1® samples (Fig. 1). However, there was a clear trend of higher LD50 values for lots stored longer than 4 years. When the LD50 value of lot 10 (TM43), which was stored for 4 years, was compared to the other TM BioControl-1® samples, it was significantly lower than lot 2 (TM2) stored 13 years; the LD50 values for the other three samples were between these two values.

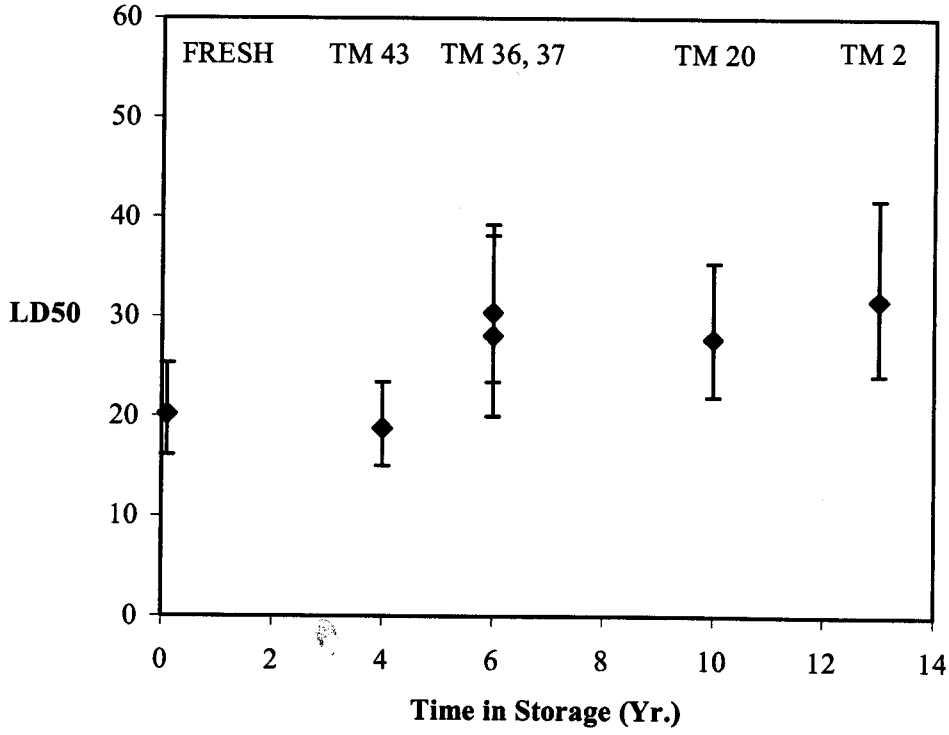

Figure 1. LD50 values with 95% fiducial limits at day 14 of the bioassay with the Goose Lake strain of Douglas-fir tussock moth larvae plotted against time in storage. Data from each bioassay fit the probit model (p>0.05).

Comparisons of LD90 values (Fig. 2) showed that the fresh OpNPV sample was significantly different from one sample (TM36) stored for 6 years. There was a trend of higher LD90 values for lots stored for 6 and 13 years compared to freshly produced OpNPV. When the LD90 value of lot 10 (TM43) was compared to the other TM BioControl-1® samples, it was significantly lower than lots stored for 6 and 13 years but not the lot stored for 10 years.

When looking at the effect of package size within a lot stored for 6 years, no significant differences were found in LD50 and LD90 values for a small package (TM36) compared to a medium package (TM37).

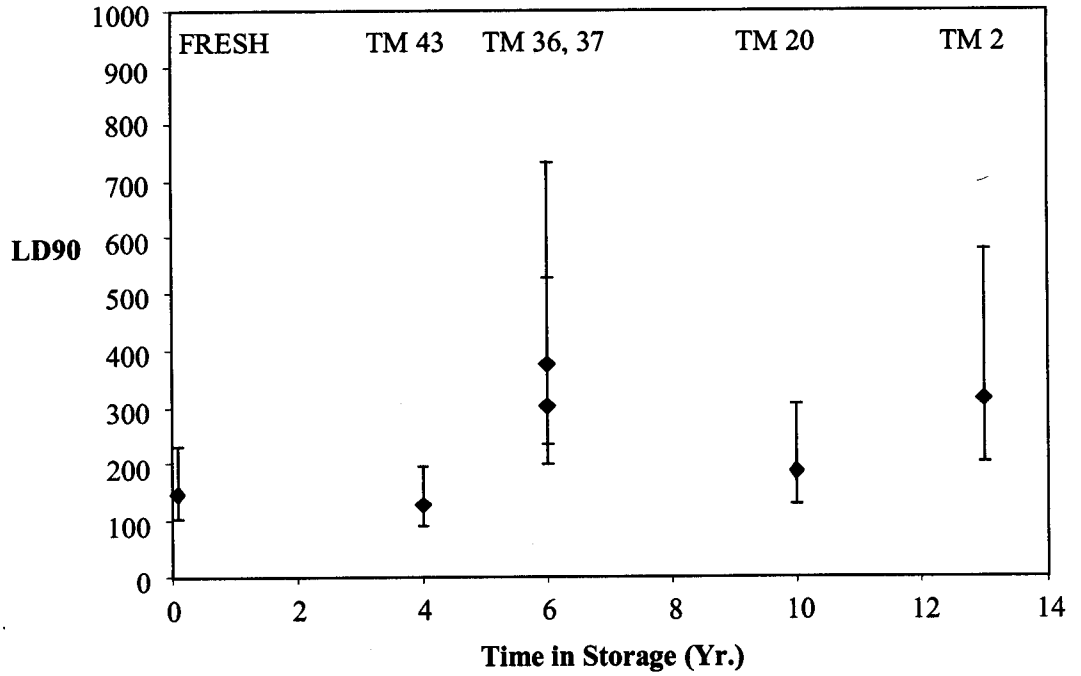

Figure 2. LD90 values with 95% fiducial limits at day 14 of the bioassays with the Goose Lake strain of Douglas-fir tussock moth larvae plotted against time in storage. Data from each bioassay fit the probit model (p>0.05).

Potency Ratios. Copies of the original bioassay data, using the advance samples from the processors, were obtained from Roy Magelssen[1]. Direct comparisons of the LC50 values from the original bioassays done in Corvallis on the advance samples from the processors and our LD50 data cannot be done because two different bioassay techniques (diet surface contamination and diet plug) and different instars (second and third) were used in the two bioassays. However, comparisons of potency ratios within the two data sets obtained by the two bioassay techniques can be done. The relative potency of two stimuli is defined as the ratio of equally effective doses (Finney 1952). The relative potency provides a convenient description of the differences among samples.

Potency Comparisons and Rankings. In our current Goose Lake bioassays, potency ratios were calculated by comparing each TM BioControl-1® sample to the freshly prepared OpNPV sample (Table 3). Potency ratios were used to rank the effectiveness of the different lots tested. One sample tested from lot 10 stored for 4 years was greater in potency than the freshly prepared sample of OpNPV. All other samples were less potent than fresh OpNPV.

Using our Goose Lake bioassay results, potency ratios were obtained by comparing TM BioControl-1® samples without the fresh OpNPV sample (Table 4). Lot 10 stored for 4 years was used as the basis for the comparison since the LD values were not significantly different from those of the fresh OpNPV sample and lot 10 was in storage for the least amount of time. In addition, original LC50 data from surface contamination bioassays done at the time of processing of TM BioControl-1® were re-analyzed to produce potency data and a ranking of the lots was done (Table 4). Again, potency comparisons were done using lot 10 as the basis for the comparison.

[1]Roy Magelssen, USDA Forest Service, Pacific Northwest Region, Forest Insect and Disease Service Centre, Wanatchee, WA.

Table 3. Comparison of potency data among lots calculated from day 14 LD50 values using the fresh OpNPV as the basis of comparison with TM BioControl-1® samples

Years Stored	Lot #	TM BioControl-1 Sample®	Potency Ratio
13	2	2	0.6
10	6	20	0.7
6	9	36	0.7
6	9	37	0.7
4	10	43	1.1
0		FRESH OpNPV	1.0

Table 4. Comparison of potency data among the different lots calculated using the original bioassay data from the processor's advance sample and potency data calculated from the current Goose Lake bioassays; Lot 10 was used as the basis for the comparisons

Lot #	Original Potency Ratio	Current Potency Ratio
10	1.0	1.0
6	1.2	0.7
9	0.8	0.7
2	0.5	0.6

Rankings obtained from data when the samples were first processed indicate that lot 10, lot 9, and lot 6 were quite potent but that lot 2 was considerably less potent than the other lots. This indicates that even at the time of processing, there was a difference in potency among the different lots. This fact is very important when interpreting current bioassay data with respect to length of storage of the samples. The comparison of potency ratios, calculated using data from the current bioassays, indicated that lot 9, lot 6, and lot 2 are less potent that lot 10.

Lot 6 was originally more potent than lot 10. In the advance bioassay data from Corvallis, lot 6 was contaminated with CPV. There may be synergistic effects between these two viruses (Tanada 1956).

Discussion

Our preliminary results indicate that storage affects efficacy directly. When LD50 values from the current bioassay were compared, the sample of fresh OpNPV and the sample from lot 10 (stored since 1995) were not significantly different. However, for samples stored longer than 4 years, there was a trend of higher LD50 values. Higher LD50 values mean that more product (a higher dose) is required to achieve the same level of larval mortality.

Comparing LD90 values, there was also a trend of higher LD90 values in lots stored longer than 4 years when compared to fresh OpNPV and lot 10. Comparisons of both LD50 and LD90 values suggested a trend of higher values for samples stored longer than 4 years. Additional bioassay data of stored samples will be used to determine if the trend shown by these preliminary results can be confirmed.

These preliminary results indicated no difference in potency among the viral samples from different package sizes within a lot and this is encouraging. The different virus samples bioassayed and their data analyzed to date are not large enough to determine conclusively if processing by different companies had an effect on potency. Preliminary results on lot 2 suggested that it was never as potent as lot 10, 9, or 6 and we offer no explanation for this difference.

Other studies with stored tussock moth virus show similar results. Martignoni (1978), using the diet surface contamination technique, reported a shelf life of 5 years for Douglas-fir tussock moth NPV when the virus was stored in a cool, dry place. Kaupp and Ebling (1993), using a diet plug inoculation bioassay with second instar whitemarked tussock moth larvae and Virtuss®, have similarly concluded that virus potency decreased in storage at 4°C. A 46% loss in infectivity was observed after 2 years in storage and Virtuss® stored up to 10 years showed up to a 25-fold decrease in infectivity. This decreasing potency with storage was also reported by other authors for different insects using different bioassays. Cunningham (1970), using balsam foliage dipped in virus suspensions, found that eastern hemlock looper NPV, stored for 6 years at 4°C, showed a 200-fold loss of pathogenicity to third instar larvae compared to freshly produced virus. Lewis and Rollinson (1978) found similar results with stored gypsy moth NPV. These authors reported that suspensions of NPV retained their potency for 5 years under refrigeration, for 2 years at room temperature, for 1 year as air-dried powder stored at 4°C, and for 6 months as air-dried powder stored at 38°C in diet contamination bioassays using second instar gypsy moth larvae. Neilson and Elgee (1960), investigating the effect of storage on NPV virulence on second and third instar larvae of the European spruce sawfly, reported similar results. Using foliage contaminated with virus suspension, they reported that when virus was stored at 4.5°C, loss of potency occurred beyond 5 years with the greatest change in virulence after 9 years in storage and total inactivation after 12 years.

All the above studies reported some loss of activity of the virus with storage. Our preliminary results suggest that storage has affected the efficacy of stored TM BioControl-1®. There seemed to be a trend of viral potency loss with storage. Additional bioassays will be conducted to confirm our results to date regarding how length of storage, package size, and processing affect viral efficacy. In addition, we will also conduct experiments on the effectiveness of TM BioControl-1® against DFTM from different geographical regions.

Acknowledgments

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Impact of the Texas Leaf-Cutting Ant (*Atta texana* (Buckley)) (Order Hymenoptera, Family Formicidae) on a Forested Landscape

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ABSTRACT *Atta texana* (Buckley), the Texas leaf-cutting ant, rapidly expanded in a harvested forested landscape on sandhills characterized by droughty soils, causing mortality of planted loblolly pine (*Pinus taeda* (L.)). The site, composed primarily of Quartzipsamments soils classified as thermic coated Typic Quartzipsamments in the Tonkawa soil series, accounts for approximately 5,000 ha in Nacogdoches, Rusk, Panola, and San Augustine Counties in eastern Texas, USA (Dolezel 1980). These soils are characterized by low fertility, rapid permeability, and extreme acid reaction. These sandhills are resistant to erosion and are considered important ground water recharge areas. The distribution of *A. texana* central nest mounds and foraging areas was examined using aerial photography, digital orthophotographic quarter quadrangles (DOQQ) (scale 1:6000), and global positioning satellite (GPS) data. Plant nutrition of *A. texana* nesting areas was examined. Previous soil texture analysis of the central nest mound and adjacent landscapes is presented.

FROM 1973 TO 1975, approximately 1,400 ha in the Tonkawa soils (Typic Quartzipsamments) were clearcut, followed by extensive site preparation (Tracey et al. 1991). Removal of all organic matter and surface litter from the site exposed the bare mineral soil to the sun and wind, decreasing the moisture holding capacity of the soil and increasing surface temperatures (Kroll et al. 1985). The clearcutting disturbance of the study site quickly resulted in ideal *Atta texana* habitat.

Atta species densities are normally higher in secondary than in primary vegetation (Haines 1978). Nest dimensions are significantly correlated with distances foraged by leafcutters (Fowler and Robinson 1979) and *Atta* species foraging patterns are influenced by the availability and locations of preferred plant species in its territory (Waller 1986). Adaptations in their pattern of nest distribution enable ants to use the food available in the habitat more effectively and reduce the unfavorable results of competition among societies, which limit their reproduction and numbers (Cherrett 1968).

Though long considered serious pests in both natural and plantation ecosystems, the basic biology of leaf-cutting ants is not completely understood. Leaf-cutting ants are exclusively New World species, ranging from Argentina in the south to Texas in the north. The northernmost species is *A. texana*, the Texas leaf-cutting ant (Hölldobler and Wilson 1990).

A. texana shows a decided preference for nesting in sandy or sandy loam soils, but is also capable of nesting in heavy soils and those of limestone origin (Smith 1963). *A. texana* overturns the soil when excavating tunnels and chambers. When building tunnels and chambers, materials transported to the surface by ants are mixed with body fluids to form uniform pellets of soil (Weber 1966). *A. texana* constructs tunnels and chambers in the soil

Pages 85-90 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.

that are numerous and extend deeper than those of vertebrate animals. The nest area is usually marked by crescent-shaped mounds 15 to 30 cm tall and about 30 cm in diameter.

A. texana shows a decided preference for grasses, weeds, and hardwood leaves. Leaf parts are gathered and used to cultivate their food fungus. They prune the vegetation, stimulate new plant growth, break down vegetable material rapidly, and, in turn, enrich the soil (Hölldobler and Wilson 1990). *A. texana* is a forest pest because it cuts needles from both natural and planted pine seedlings. Though ant foraging occurs year round, the industrial forest impact is felt in the winter months when pines are defoliated in the absence of other forage (Moser 1967). In East Texas, this situation causes considerable loss to timber producers, especially in young plantations on droughty sites.

Methods

A. texana, by overturning the soil when excavating tunnels and chambers, has a profound effect upon organic matter and texture of the Tonkawa soil series. *A. texana* utilized created openings and disturbances to create nesting areas and benefitted from the wintering foraging on pines in their expansion. *A. texana* is found along the FM 1087 road corridor and along the edges of stream side corridors. In regeneration areas, *A. texana* reacted to the monocultural habitat and dispersed in all directions, causing massive destruction to the loblolly plantation.

The study area is located along the FM 1078 road corridor (right of way) and an area of regeneration north of camp Tonkawa, located in northern Nacogdoches and southern Rusk Counties, 10 km west of Garrison, Nacogdoches County, Texas, USA. The distribution of *A. texana* central nest mounds and foraging areas was examined using aerial photography, digital orthophotographic quarter quadrangles (DOQQ) (scale 1:6000), and global positioning satellite (GPS) data. Plant nutrition of *A. texana* nesting areas was examined. Previous soil texture analysis of the central nest mound and adjacent landscapes is presented. This study area encompasses sandy soils and loams capable of sustaining *A. texana* populations.

Results and Discussion

Currently, there are 52 openings found throughout the study area. The total study area was 78 ha, or 78,000 square meters. Total defoliation attributed to *A. texana* accounted for 16,380 square meters (21.5%) of the total study area. The immediate nesting areas or mounds accounted for 1.25% of the total area affected by *A. texana*. Not all disturbance areas contained mounds due to natural mound mortality or chemical treatment with methyl bromide.

Repeated efforts at regeneration and control of *A. texana* in the Tonkawa site have met with limited success. Low site productivity makes intensive forest silvicultural practices marginal. Plantation forestry, particularly involving pines on droughty sites, is adversely affected by *Atta* species defoliation (Cherrett 1968) with the most disastrous outbreaks of *Atta* species occurring in monoculture systems (Hölldobler and Wilson 1990).

The impact of *A. texana* nests is evident following timber harvests as nests become the dominant feature on landscapes with deep sandy soils. *A. texana* is the primary soil-improving organism in the droughty environment of the Typic Quartzipsamments or Tonkawa landscape in northern Nacogdoches County, Texas (Cahal 1993, Cahal et al. 1993). Nests extend underground to a depth of 8 m with hundreds of subterranean chambers (Moser

1963) and up to 61 cm of excavated subsoil on the nest's surface (Cahal 1993, Cahal et al. 1993, Kulhavy et al. 1998). *A. texana* significantly increases the percent clay; the percent clay in the pellets of nest mound craters was significantly higher than at the intermound surface and the control surface. When comparing percent clay by depth, the mound surface had a significantly higher percentage of clay (5.6% clay for the pellets of the nest mound crater compared to 3.9% and 3.6% at 50-cm depths and the internest surface, respectively) (Cahal 1993, Cahal et al. 1993, Kulhavy et al. 1998).

Leaf-cutting ants play an important role in soil development (Cherrett 1968, Weber 1972, Haines 1975, Alvarado et al. 1981, Fowler and Haines 1983, Cahal et al. 1993, Kulhavy et al. 1998). Leaf-cutting ants are responsible for pedoturbation, or soil mixing (Hole 1961). The subterranean network of tunnels and galleries reduces soil bulk density and increases the concentrations of soil organic matter. Ants are one of the few species that transport subsoil mineral nutrients to the surface where they can be utilized by plants (Weber 1972, Lockaby and Adams 1985).

Following defoliation and mortality of the pine plantation matrix, the patches are maintained by *A. texana* and eventually become a permanent component of the landscape. These patches can vary in size from a few hundred square meters to 6 hectares.

A single *A. texana* nest is a marvel of engineering and the dimensions are staggering. The central nest mound may be 30 m in diameter, have numerous 0.3-m diameter feeder mounds extending outwards to a radius of 80 m (Moser 1967, Cahal 1993, Kulhavy et al. 1998), and may occupy 30 to 600 square meters (Hölldobler and Wilson 1990, Cahal 1993). Larvae are raised in brood chambers, fungus is cultivated in fungal chambers, and waste material is deposited in detrital chambers. Removal of vegetation covering *A. texana* nests reduces soil moisture. *Atta* species are prodigious foragers and a large colony is capable of gathering several kilograms of leaves per day (Weber 1966).

On the Tonkawa study site, the matrix was composed of pine plantations and post oak savannas. Selective foraging by *A. texana* created patches readily apparent on aerial photography. Nest emigration (new patches) occurs by new-founding queens or translocation of existing colonies (Fowler 1981). Combining GPS and GIS with aerial photography quantifies the impacts these ants have on the forested landscape.

The relationship of *A. texana* to topography and depth above the water table is being examined to develop a landscape model to ascertain the effects of both terrain and location of the ant mounds and the influence of *A. texana* on the forest landscape. Nesting areas (mounds) are most often found on the tops and sides of ridges where the water table is deep and nests can reach depths of 8 meters (Moser 1967, Cahal et al. 1993). Generally, *A. texana* mounds are located between 1.5 m and 8 m from the water table (Moser 1963, Cahal et al. 1993).

Vegetation on active ant mounds in the Tonkawa soils (Typic Quartzipsamments) are species not preferred by *A. texana*. Post oak (*Quercus stellata)*, bluejack oak (*Q. incana*), shining sumac (*Rhus capillinum*), yucca (*Yucca louisianensis*), mockernut hickory (*Carya tomentosa*), sassafrass (*Sassafrass albidum*), muscadine grape (*Vitis rotundifolia*), and dog fennel (*Eupatorium caprifolia*) predominate on *A. texana* nests. This vegetation flourishes following site colonization by *A. texana*. To examine foliar nutrition, samples were collected on *A. texana* central nest mounds and on adjacent non-mound areas, oven dried, and ground with a Wiley mill to prepare the samples for nitric acid digestion (Mills and Jones 1991). Concentrations of a suite of nutrients associated with plant productivity (N, P, K, Ca, Mg, Mn, Cu, S, Na, Fe, As) were determined by ICP (inductively coupled argon plasma emission spectrometry), sensitive to <1 mg kg^{-1} (Walsh 1983). Each plant species was compared

individually based on location (either on-mound or off-mound), mound size, and ant activity level.

A. texana serves an important ecological function of soil amelioration and increases biodiversity, especially on the very sensitive ecosystem of the Tonkawa study area. Impact of leaf-cutting ants was greatest on planted loblolly pine. Repeated efforts at regeneration and control of *A. texana* in the study area have met with limited success. Regeneration studies on Typic Quartzipsamments indicated the best survival with Terra-Sorb®-treated loblolly pine followed by longleaf pine (Tracey et al. 1991).

Currently, the primary land use on Tonkawa soils is pine and wildlife management, although the potential for pine is low due to the droughty and infertile nature of the sand. Watermelons can be grown, but potential is low for any other cultivated crops. Recommendations include (1) encouraging native plants in openings created by *A. texana,* (2) managing for wildlife and limited recreation, (3) allowing *A. texana* to continue its biological function of soil improvement, and (4) utilizing this area for teaching forest pest management and forest entomology (Tracey et al. 1991).

Aerial photography is used to measure landscape impacts, vis-a-vis soil formation of *A. texana* (Cahal 1993, Cahal et al. 1993). Stereoscopic color infrared photographs (1:5000) of a 36- by 36-km area were used to estimate both numbers of mounds present and percentage of area defoliated by *A. texana* in the Tonkawa soil series of the Typic Quartzipsamments. Nest mound location and identification of soils, vegetation associations, and changes in mound size and location were measured and entered into a Geographic Information System using ArcView®. Central nest mounds of *A. texana* were located by using the soil survey of Nacogdoches County (Dolezel 1980), aerial observation using fixed-wing aircraft, extensive ground checking, color infrared aerial photography at a scale of 1:6000, and digital orthophotographic quarter quadrangles (DOQQ). Moser (1986) estimated timber losses due to leaf-cutting ants by examining aerial photographs of individual mounds.

For each mound, the center was identified, marked with a sequentially numbered pole, and located with a Trimble® TDC-1 GPS receiver. One-meter accuracy was obtained by taking a minimum of 100 locational positions tracking a minimum of four satellites with a positional dilution of precision (PDOP) maximum of 6. Differentially corrected GPS data were transferred to the GIS Laboratory of the Arthur Temple College of Forestry and transferred onto 1996 DOQQ imagery (1:12000). These images were georeferenced, rectified, and parallax and distortion free, which allowed GPS positions to be overlaid with location accuracy. The integration of GPS and DOQQ imagery enhance the investigation of *A. texana* because mound movement can be mapped over time and landscape patterns discerned.

Accurate mapping coupled with an interactive GIS system (ArcView®) details the landscape-wide ecological process of patch formation, change in the matrix, and alteration of the structure and function of the forest landscape on Typic Quartzipsamments soils. A thorough investigation of central nest mound changes in size and location, coupled with analysis of the associated vegetation productivity and nutrition, is essential in assessing the ecology of *A. texana* in the forested landscape.

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Insect Defoliators of *Nothofagus obliqua* (Roble) in South Chile: Two Years Monitoring Species and Their Damage

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ABSTRACT *Nothofagus obliqua* (Mirb.) Oerst is one of the most common tree species in Chile. Following severe and early defoliation during the spring and summer of 1996 and 1997, a study was conducted between 39° and 41° south latitude within the range of *N. obliqua*. Permanent plots were established in the Coastal Cordillera, Central Valley, and Andes Cordillera geographic sectors and monthly samples were taken. The main objective of this study was to study the insect defoliator complex of *N. obliqua*, including the types of damage and defoliation levels it produces with respect to space and time. This paper reports on data collected from 1997 to 1998 and from 1998 to 1999.

CHILE HAS A total of 28 million hectares of native forests: 13.5 million hectares of productive forests and 14.5 million hectares of wild, protected areas (Corporación Nacional Forestal 1997, Instituto Forestal 1997). Most of these native forests are temperate forests that are well represented in southern Chile where the soil quality and weather conditions contribute to maintain natural forests.

Nothofagus obliqua (Mirb.) Oerst., commonly called "roble," is a broadleaf, deciduous member of the Fagaceae family and is the most common tree species in central and southern Chile. Its distribution is between 33° and 41° 30' south in several geographic zones: the Andes Cordillera, the Central Valley, and the Coastal Cordillera (Donoso and Landrum 1973, Hoffman 1982, Donoso 1993). This species is represented in several forest types as roble-hualo (*N. obliqua* - *N. glauca*) (Phil.) Krasser or roble-raulí-coigue (*N. obliqua* - *N. alpina* (Poepp. et Endl.) Oerst. - *N. dombeyi* (Mirb.) Oerst.). Stands of these species are now mainly second growth forests or renewals (Donoso 1981, 1993; Rodriguez et al. 1983). *N. obliqua* is one of the most exploited species because of the quality of its wood that is used for bridges, wharfs, houses, and furniture (Pérez 1983). The annual growth rate of roble ranges between 8 m^3/ha/year under unmanaged conditions to 18 m^3/ha/year on good sites and with management. The final rotation age is 60 to 80 years (Instituto Forestal, Corporación Nacional Forestal 1998).

The biggest health threat to roble is the stem borer *Holopterus chilensis* (Coleoptera: Cerambycidae) that frequently attacks the basal stem log. Damage has been observed in 42% of the trees in unmanaged stands, especially in the Central Valley where historically there has been selective thinning (Kruuse 1981, Cabrera 1994, Diaz 1999, Peredo et al. 1999).

Because roble is a deciduous tree, the foliage begins to open in September, fully leafs out from October to November, and begins to decay in February. The folivorous insect

Pages 91-103 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.

complex has total synchrony with this leaf-out behavior, demonstrating a pattern of optimal utilization of this leaf resource from a temporal perspective.

In the last 5 years, unusually early defoliations have been observed in the X Región (the region with more roble in Chile), probably as a consequence of climatic changes (dry summers) that enhanced population irruptions of defoliators. The impressive impact of these defoliations stimulated some basic studies with the following objectives:

General Objective.

- Evaluate the complex of insect defoliatiors associated with *Nothofagus obliqua* in the X Región of Chile biologically and physically.

Specific Objectives.

- Identify the species of insect defoliators associated with *Nothofagus obliqua*
- Classify damage from insect defoliators
- Establish the species' seasonal cycles
- Evaluate the degree of defoliation and the cumulative effects on the tree species

Materials and Methods

Study Area. The study area included both adult and renewal stands of *Nothofagus obliqua* in the Valdivia and Osorno provinces in the X Región of Chile. We established three work areas: (1) the northern Valdivia province (North Zone), (2) the central Valdivia province (Central Zone), and (3) the Osorno province (South Zone) (Fig. 1). Each of these three areas was divided into three sectors: the Coastal Cordillera, the Central Valley, and the Andean Cordillera, according to the three geographic zones present in the area. Each sector had two permanent plots.

In the first sampling period (1997 to 1998), 18, 500-m^2 permanent plots were established and each tree was marked. Geographic coordinates, tree diameter and height, and the health of each tree were recorded. The exact sampling points are shown in Figure 1. Samples were taken every month beginning in September 1997 and ending in March 1998.

In the second sampling period (between August 1998 and April 1999), work was conducted in all three sectors but only in the North Zone; however, visits to all the plots established the first year were made during November 1998 and January 1999. Several sampling results lead to changes in the periodicity of those samples, but financial and human resources were also considered.

In each visit to the permanent plots, we took foliage samples from 6 trees on each plot using a telescopic fork that just reached the intermediate zones of the tree canopy (10 to 15 m in height) (Lowman 1997).

Each sample was taken to the laboratory and maintained in a refrigerated room at 4°C until it was time to count insects and evaluate damage. It was also the best place to conserve fresh foliage for rearing immature insects. For this purpose, the laboratory also had a growth chamber with controlled temperature, humidity, and photoperiod.

Laboratory Work.

Extraction of Insects (eggs, larvae, nympha, pupae, and adults). Insects were extracted from samples to (1) continue their development in climatic chambers, (2) follow their seasonal cycles, and (3) allow the emergence of parasitoids for mounting and identification. All reared material was placed in our insect collection. Some of these species are still being identified.

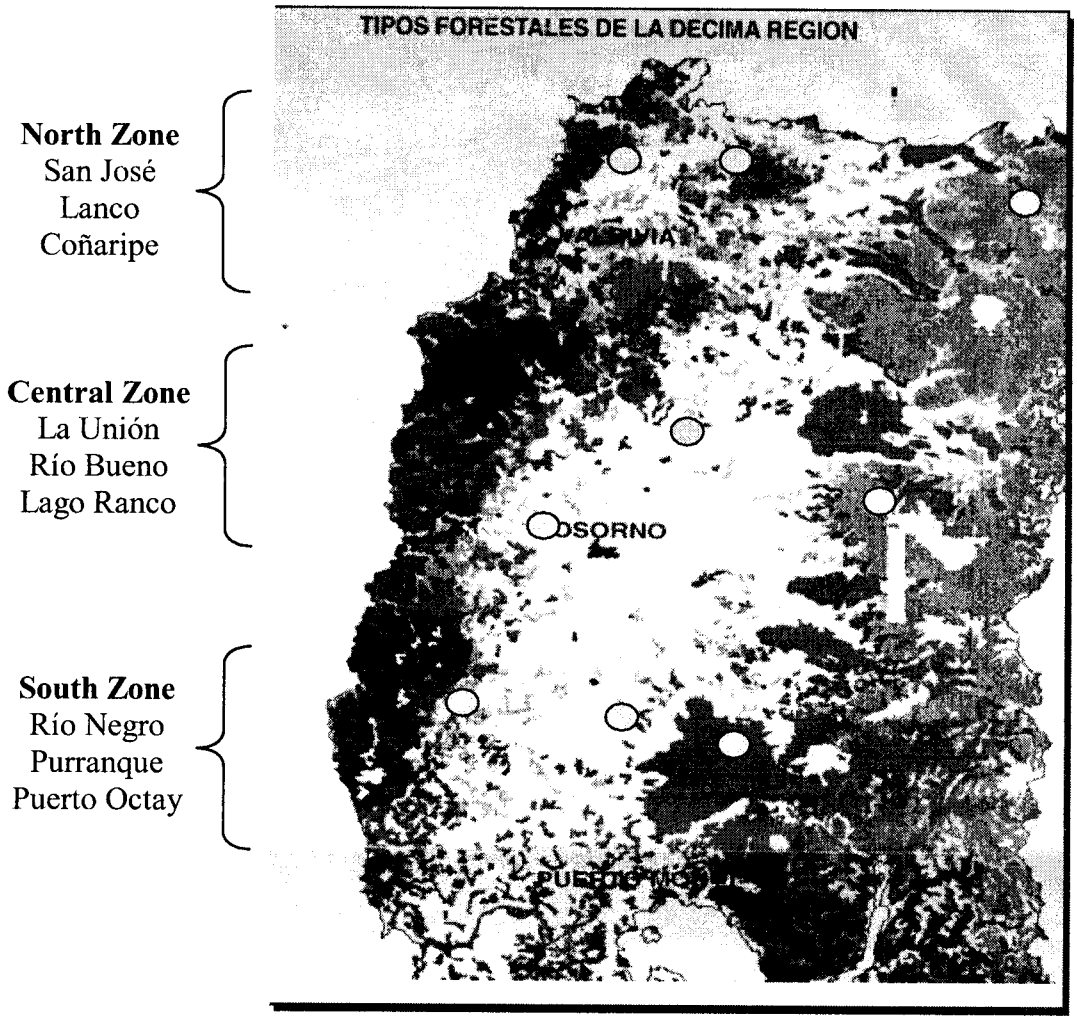

Figure 1. Distribution of the sampling plots (map source: Corporación Nacional Forestal 1997).

Classification and Quantification of Insect Damage. For this purpose, we obtained a subsample of 3 shoots on 3 trees per plot, counted all the leaves, and recorded leaf condition (damaged or undamaged) as well as the type of damage following a field guide prepared from preliminary samples. Some observations were directed to feeding behavior. We distinguished the following types of damage agents: *leaf chewers* (Type 1 consumes the entire leaf, Type 2 makes holes, and Type 3 sometimes feeds just on the leaf margin); *leaf skeletonizers*; and *leaf miners* (distinguished by the leaf mining pattern: blotch or linear).

Data Analysis. The families and species of sampled insects were analyzed and their presence in different zones and sectors was recorded. The following were also either observed or calculated: the type of damage they produced, insect stages, biological cycles, damage consistency and dominance of the species, and their temporal importance in different zones and sectors (Saiz et al. 1981). A nonparametric analysis was done using Statgraphics 2.0 Plus.

Results and Discussion

About the Species and Their Participation. The species detected in both sampling periods in all zones and sectors are listed in Tables 1 and 2. From 1997 to 1998, 9 families and 23 species were collected, whereas from 1998 to 1999, a total of 12 families and 22 species were collected.

The most common species were *Hornius grandis* (Philippi & Philippi), *Polydrossus nothofagi* Kuschel, *Omaguacua longibursae* Parra & Beèche, *Lagynopterix botulata* (Felder & Rogenhofer), and one species of Oecophoridae and Tenthredinidae (Parra and Beèche 1986, Beèche et al. 1987, Jerez and Cerda 1988, Jerez and Ibarra-Vidal 1992). The percentages of relative importance of the species for both years of sampling are illustrated in Figures 2 and 3.

Table 1. Presence of the families and species of insect defoliators for the first sampling period (1997 to 1998) by geographic zone and sector[a]

Family	Species	North Zone			Central Zone			South Zone		
		C.C.	C.V.	A.C.	C.C.	C.V.	A.C.	C.C.	C.V.	A.C.
Tettigonidae	sp. 1[b]		X	X			X			
Scarabaeidae	*Hylamorpha elegans*								X	
Chrysomelidae	*Crepidodera notata*	X	X	X	X			X	X	X
	Hornius grandis	X	X	X	X	X	X	X	X	X
	sp. 3[b]	X	X		X			X	X	X
Curculionidae	*Polydrossus nothofagi*	X	X	X	X	X	X	X	X	X
	Apion sp.	X	X		X	X	X			X
Geometridae	*Omaguacua longibursae*	X	X	X	X	X	X	X	X	X
	sp. 2[b]	X	X	X	X	X	X	X	X	X
	sp. 3[b]	X	X	X	X	X	X	X	X	X
	sp. 4[b]	X				X			X	
	sp. 5[b]	X	X	X						
	Lagynopteryx botulata	X	X	X	X	X	X	X	X	X
	sp. 7									
	Mycroclysia pristopera	X	X					X	X	
Saturniidae	*Ormiscodes* spp.							X		
	sp. 2[b]		X	X						
	sp. 3[b]		X	X	X					
	sp. 4[b]	X								
Oecophoridae	sp. 1[b]	X	X	X	X	X	X	X	X	X
	sp. 2[b]				X	X	X			
Cynipidae	sp. 1[b]								X	
Tenthredinidae	sp. 1[b]	X	X	X	X	X	X	X	X	X

[a] C.C. = Coastal Cordillera sector; C.V. = Central Valley sector; A.C. = Andean Cordillera sector

[b] In the identification process

Table 2. Presence of the families and species of insect defoliators for the second sampling period (1998 to 1999) by geographic zone and sector[a]

Family	Species	North Zone			Central Zone			South Zone		
		C.C.	C.V.	A.C.	C.C.	C.V.	A.C.	C.C.	C.V.	A.C.
Tettigonidae	sp. 1[b]	X	X	X						
Scarabaeidae	*Hylamorpha elegans*	X		X						
Chrysomelidae	*Crepidodera notata*	X					X	X		
	Hornius grandis	X	X	X	X		X	X	X	X
	sp. 3[b]	X								
Curculionidae	*Polydrossus nothofagi*	X	X	X			X			X
Geometridae	*Omaguacua longibursae*	X	X	X		X	X	X	X	X
	sp. 2[b]	X	X	X						
	sp. 3[b]									X
	sp. 5[b]	X								
	Lagynopteryx botulata	X	X	X	X	X	X	X	X	X
	Mycroclysia pristopera	X	X	X		X	X			
	sp. 9[b]		X							
	sp. 10[b]	X		X						X
Saturniidae	sp. 2[b]	X		X						
	sp. 4[b]	X	X	X						
Oecophoridae	sp. 1[b]	X	X	X	X	X	X	X	X	X
Lasiocampidae	sp. 1[b]			X						
Lepidoptera	sp. 1[b]	X	X					X		
Cynipidae	sp. 1[b]			X						
Tenthredinidae	sp. 1[b]	X	X	X					X	X
Cecidomyidae	sp. 1[b]		X							

[a] C.C. = Coastal Cordillera sector; C.V. = Central Valley sector; A.C. = Andean Cordillera sector

[b] In the identification process

Because the insect species were the same in all of the permanent plots established, work was concentrated only in the northern Valdivia zone (all sectors) for the second sampling period despite significant differences in defoliation intensity. This permitted us to refine rearing methodologies and clarify the biological cycles of the most frequent species, which was one of the objectives of the second sampling period.

Bauerle et al. (1997) recorded 16 species associated with roble in a biblographic review. Some of them did not appear in our samples, such as *Cerospastus volupis* Konow, traditionally indicated as an important defoliatior of this tree. Another defoliator that was never captured during our sampling periods was *Doina clarkei* Parra and Ibarra-Vidal (Parra and Ibarra-Vidal 1991).

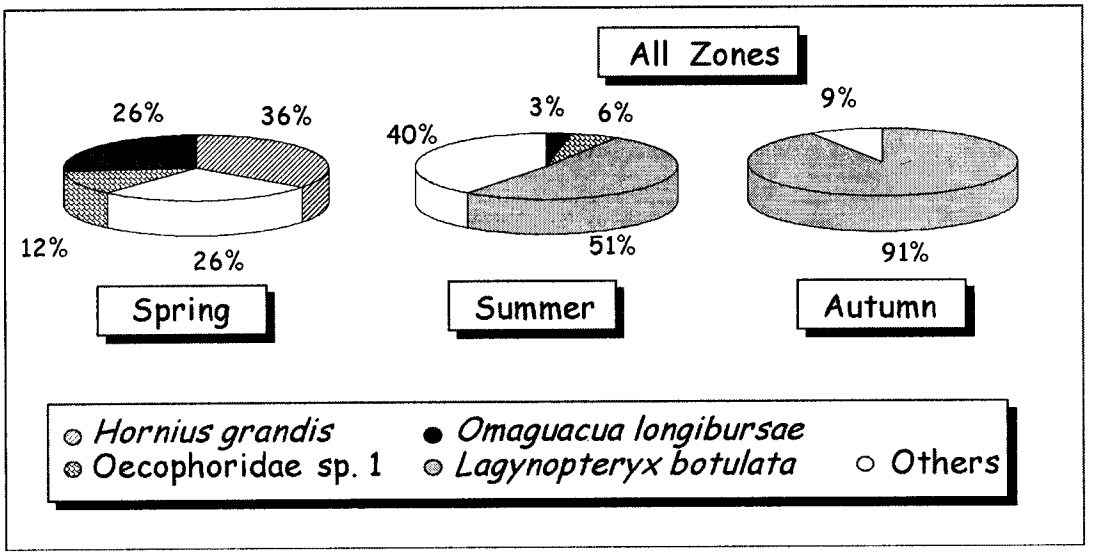

Figure 2. Percentage of relative importance of the most common species collected during the first sampling period (1997 to 1998) in all zones surveyed.

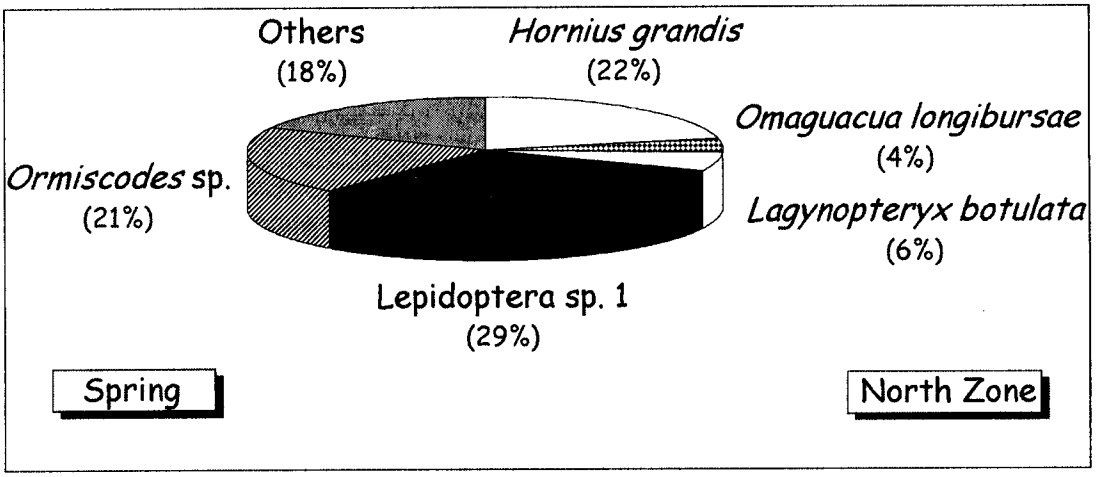

Figure 3. Representation of the main species in the second spring sampling period (1999) in the northern Valdivia (North) zone.

About the Species and Their Type of Damage. To evaluate the impact of the species, leaf damage type was recorded from 1997 to 1998 and from 1998 to 1999, respectively (Tables 3 and 4, Figs. 4 and 5). The complex of insect defoliators consumed part or all of the leaves. The insect feeding behavior, along with the insect's development, could change; sometimes they never ate all of the leaf surface. Field and laboratory observations were very time consuming and most behavioral patterns were new, especially for those species that are new or little known. Other observations relative to different life stages or instars were new for Chile.

Table 3. Types of damage and families/species involved for the first sampling period (1997 to 1998)

Types of Damage	Family	Species	Stage and Instar[a]
All-leaf Chewers (1)	Scarabaeidae	*Phytoloema mutabilis*	Adults
	Saturniidae	*Ormiscodes* sp.	Larvae[3]
		sp. 4	Larvae[3]
	Geometridae	*Omaguacua longibursae*	Larvae[3]
		sp. 2	Larvae[3]
		Lagynopteryx botulata	Larvae[3]
		Mycroclysia pristopera	Larvae[3]
Hole Makers (2)	Tettigonidae	sp. 1	Nimphae
	Chrysomelidae	*Hornius grandis*	Adults
		Crepidodera notata	Adults
		sp. 3	Adults
	Curculionidae	*Polydrossus nothofagi*	Adults
		Apion sp.	Adults
	Geometridae	*Omaguacua longibursae*	Larvae[1]
		sp. 2	Larvae[1]
		sp. 3	Larvae[1]
		sp. 4	Larvae[1]
		sp. 5	Larvae[1]
		Lagynopteryx botulata	Larvae[1]
		sp. 7	Larvae[1]
		Mycroclysia pristopera	Larvae[1]
	Tenthredinidae	sp. 1	Larvae[1]
Border-leaf Chewers (3)	Chrysomelidae	*Hornius grandis*	Larvae[2,3]
	Geometridae	*Omaguacua longibursae*	Larvae[2]
		sp. 2	Larvae[2]
		sp. 3	Larvae[2]
		sp. 4	Larvae[2]
		sp. 5	Larvae[2]
		Lagynopteryx botulata	Larvae[2]
		sp. 7	Larvae[2]
		Mycroclysia pristopera	Larvae[2]
	Tenthredinidae	sp. 1	Larvae[2]
Skeletonizers (4)	Oecophoridae	sp. 1	Larvae[1,2,3]
		sp. 2	Larvae[1,2,3]
Leaf Miners (5)	Chrysomelidae	sp. 1	Larvae[1,2,3]
Leaf-gall Makers (6)	Cecidomyidae	sp. 1	Larvae[1,2,3]
	Cynipidae	sp. 1	Larvae[1,2,3]

[a] 1 = First instars; 2 = Intermediate instars; 3 = Last instars

Table 4. Types of damage and families/species involved for the second sampling period (1998 to 1999)

Types of Damage	Family	Species	Stage and Instar[a]
All-leaf Chewers (1)	Scarabaeidae	*Hylamorpha elegans*	Adults
	Saturniidae	sp. 2	Larvae[3]
	Geometridae	*Omaguacua longibursae*	Larvae[3]
		sp. 2	Larvae[3]
		Lagynopteryx botulata	Larvae[3]
		Mycroclysia pristopera	Larvae[3]
Hole Makers (2)	Tettigonidae	sp.1	Nymphae
	Chrysomelidae	*Hornius grandis*	Larvae[1]
		Crepidodera notata	Adults
		sp. 3	Adults
	Curculionidae	*Polydrossus nothofagi*	Adults
	Geometridae	*Omaguacua longibursae*	Larvae[1]
		sp. 2	Larvae[1]
		Lagynopteryx botulata	Larvae[1]
		Mycroclysia pristopera	Larvae[1]
	Tenthredinidae	sp. 1	Larvae[1]
Border-leaf Chewers (3)	Chrysomelidae	*Hornius grandis*	Larvae[2,3]
	Geometridae	*Omaguacua longibursae*	Larvae[2]
		sp. 2	Larvae[2]
		sp. 5	Larvae[2]
		Lagynopteryx botulata	Larvae[2]
		Mycroclysia pristopera	Larvae[2]
		sp. 9	Larvae[2]
		sp. 10	Larvae[2]
	Lasiocampidae?	sp. 1	Larvae[1,2]
	Tenthredinidae	sp. 1	Larvae[2]
Skeletonizers (4)	Oecophoridae	sp. 1	Larvae[1,2,3]
	?[b]	sp. 1	Larvae[1,2,3]
Leaf Miners (5)	Chrysomelidae	sp. 1	Larvae[1,2,3]
Leaf-gall Makers (6)	Cecidomyidae	sp. 1	Larvae[1,2,3]
	Cynipidae	sp. 1	Larvae[1,2,3]

[a] 1 = First instars; 2 = Intermediate instars; 3 = Last instars
[b] ? = Lepidoptera; family and species in identification

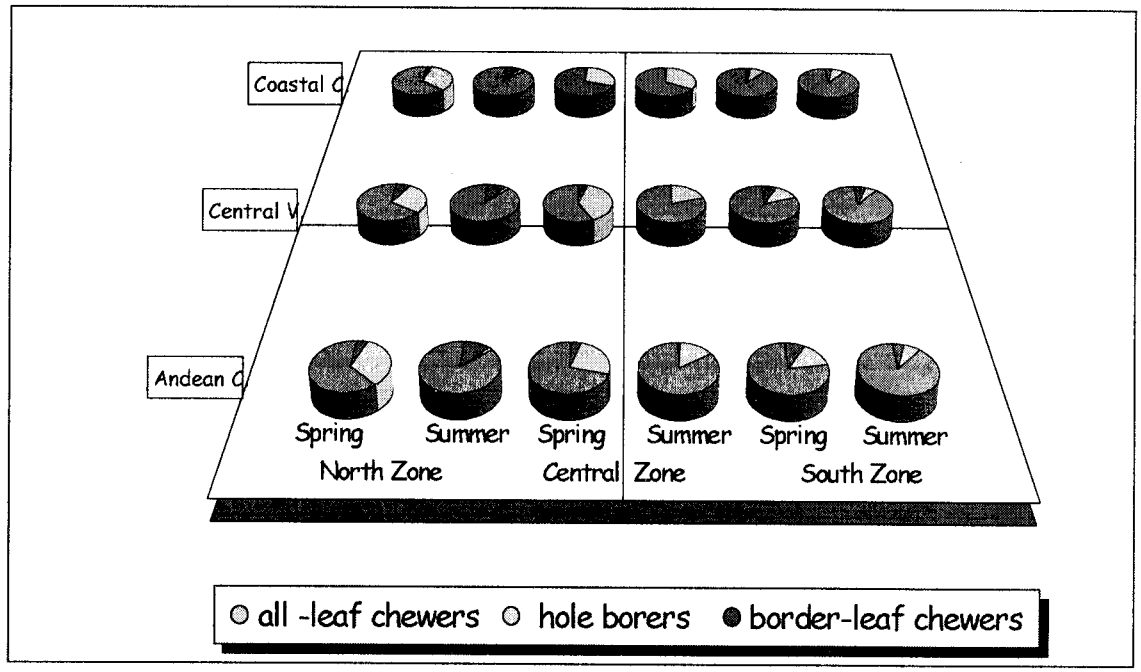

Figure 4. Types of damage during spring and summer (1997 to 1998) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

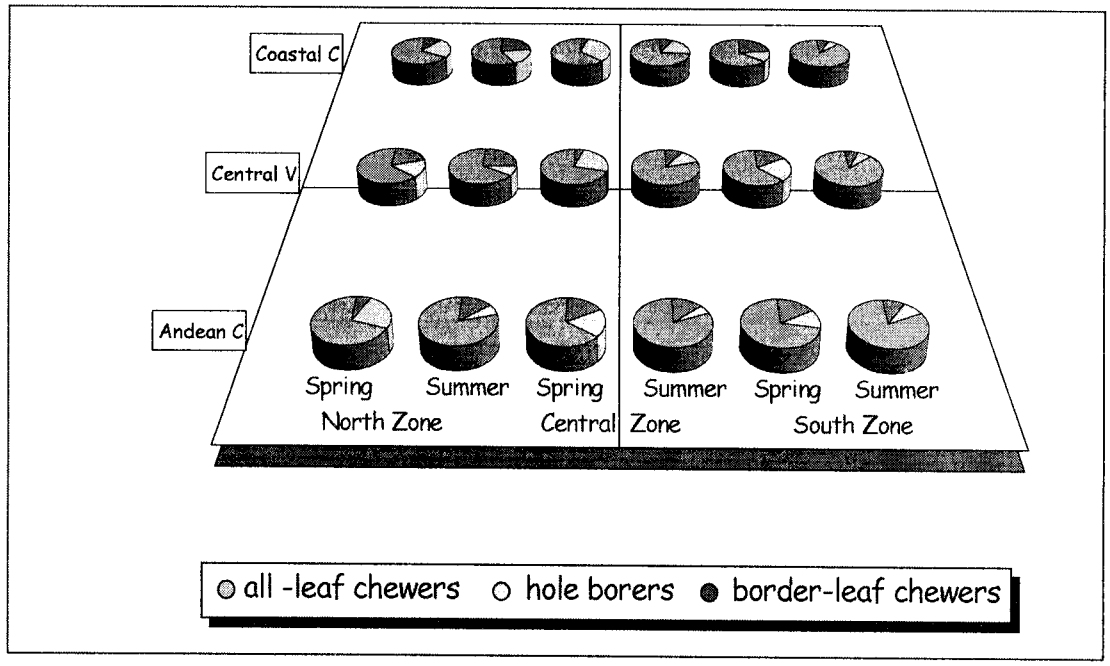

Figure 5. Types of damage during spring and summer (1998 to 1999) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

Levels of Defoliation. Figures 6 and 7 illustrate the relationship between undamaged and damaged foliage for both sampling periods. The North Zone exhibited the highest levels of defoliation that increased up to 90% in December. Peak defoliation occurred in the other zones at the end of the foliation period during March, although defoliation levels were not as high as those measured in the North Zone.

There was a decrease in defoliation in the Coastal Cordillera sector from north to south, but no trends were clear in the other sectors. This is reinforced by the significant differences between sectors and zones.

Defoliation levels were lower in the second sampling period (around 40% or less) and defoliation near 80% was observed only in the Andes Cordillera sector plots during February.

To summarize the relationship between undamaged and damaged foliage, there is a dynamic that involves (1) the feeding habits of the damage agents (insects), (2) insect population levels, and (3) foliage characteristics, influenced by climatic changes and their (insects) own temporal changes. It seemed that for each nutritional condition of the leaves, there were one or more species that exploited this resource.

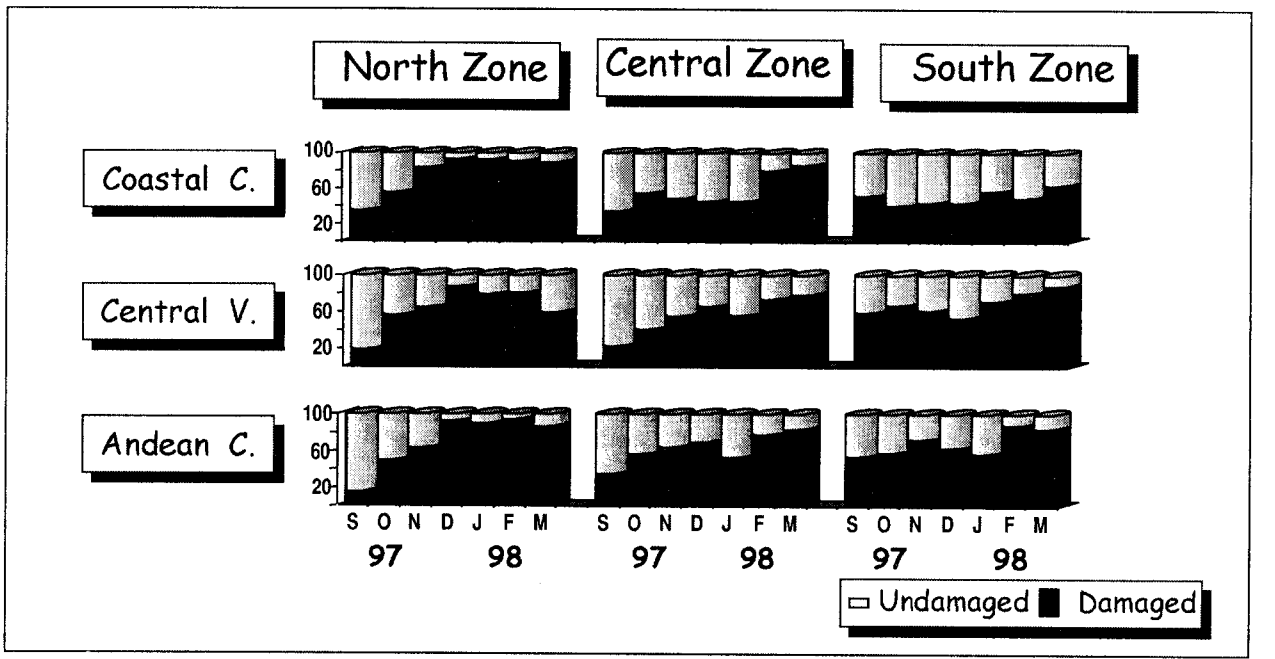

Figure 6. Relationship between undamaged and damaged foliage in the first sampling period (1997 to 1998) in all zones and sectors. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

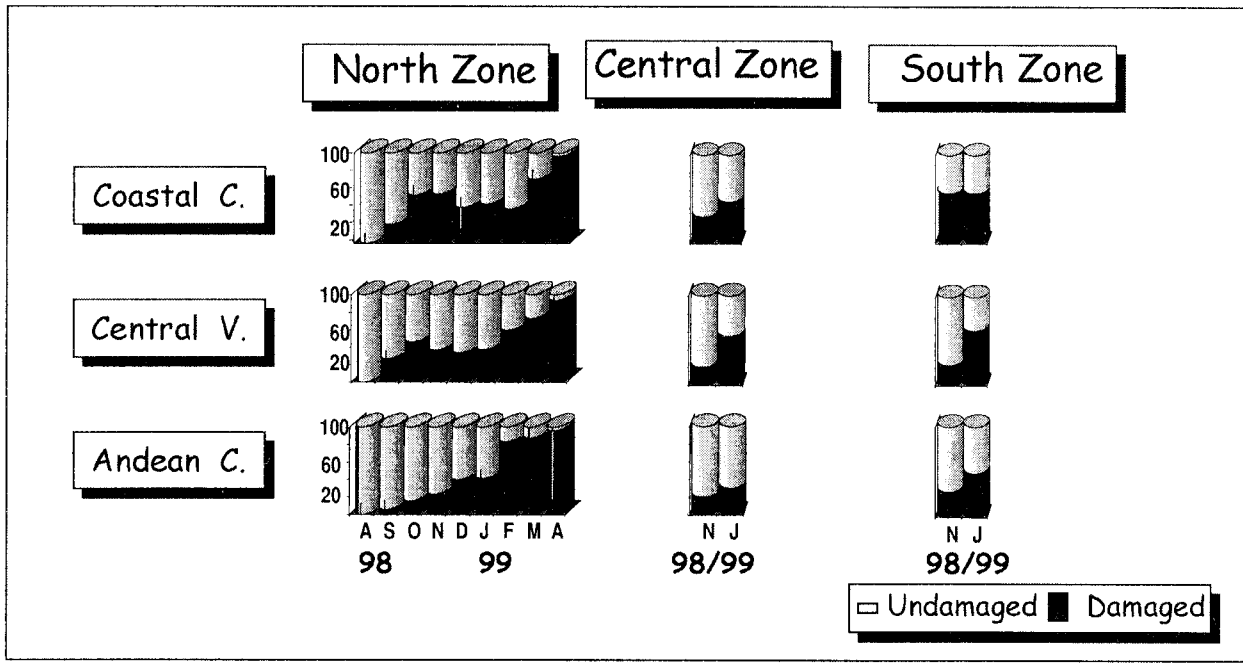

Figure 7. Relationship between undamaged and damaged foliage in the second sampling period (1998 to 1999). All sectors were sampled; however, sectors in the Central and South zones were sampled only two times: November 1998 and January 1999. Coastal C. = Coastal Cordillera sector; Central V. = Central Valley sector; Andean C. = Andean Cordillera sector

Conclusions

- No tree mortality was detected after two consecutive years of severe defoliation.
- Refoliation occurred in zones and sectors with more defoliation damage.
- All of the associated insect species were native and some were new.
- Twenty three species were collected, but only six were dominants and shared the foliage resource.
- Dominant species were present in all study areas.
- Most damage was produced by all-leaf chewers, hole borers, and border-leaf chewers.
- The study increased our knowledge of the biological cycles, life strategies, and natural enemies of roble insect defoliators.
- Defoliation increased during the study period (August to April) in synchrony with tree phenology and climatic conditions.
- There were no significant differences in leaf damage between zones and their sectors in spring and summer of the first sampling period.
- There were significant differences in leaf damage among the two sampling periods for zones, sectors, and seasons.

Future Studies

In a third study period, several new approaches are being implemented:

- Collecting monthly canopy samples using a new methodology to compare the insect fauna and their distribution at different tree heights
- Documenting foliar nutritional changes and how these affect leaf quality and therefore associated insects
- Dendrochronological studies to document historical defoliation events

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Outbreak of *Cephalcia arvensis* (s.l.) (Hymenoptera, Pamphiliidae) in Czechia from 1997 to 1999

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ABSTRACT In 1997, a local outbreak of the spruce web-spinning sawfly (*Cephalcia arvensis* (s.l.)) appeared in Czechia. The total infested area of Norway spruce (*Picea abies* (L.) Karst.) stands covered about 650 ha. Because the stands were seriously endangered by heavy defoliation, it was decided to protect them with an aerial treatment of diflubenzuron in 1998 and, to a lesser extent, in 1999. Observations of the insect's biology obtained during the outbreak are briefly summarized in this paper.

THE SPRUCE WEB-SPINNING sawfly (*Cephalcia arvensis* (s.l.)) is one of three economically important species of the genus *Cephalcia* living on Norway spruce (*Picea abies* (L.) Karst.) in Czechia. In the 1980s, *C. arvensis* caused heavy defoliation of the spruce stands in an area of several hundreds of hectares in northeastern Bohemia. A further outbreak followed here at the end of the 1990s.

Materials and Methods

The outbreak was located near the village of Česká Čermná in northeastern Bohemia (Longitude 16°14′, Latitude 50°23′). It occurred mostly in older, artificially established pure Norway spruce stands situated on slopes and plateaus at an altitude of about 500 to 650 m. The main climax tree species here is European beech (*Fagus sylvatica* L.). Characteristics of the locality are summarized in Table 1.

An increase in the web-spinning sawfly population was first detected in 1996; the following year (1997) was considered the beginning of the outbreak. The infested area almost precisely coincides with an outbreak that occurred from 1982 to 1988 (Martinek 1991). Thus, the present epidemic may be regarded as a local repeated outbreak.

In 1998 and 1999, observations in the outbreak area focused on the following problems: (1) identifying the spectrum of spruce web-spinning sawfly species involved in the infestation (with emphasis on the epidemic taxon), (2) life activities of the epidemic population, and (3) questions connected with the importance of the outbreak to forestry, including control efforts.

Voucher specimens of the examined material are deposited in the collection of the first author.

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Results and Discussion

Taxonomic Identity of the Epidemic Population. In the 1980s, two outbreaks of *Cephalcia arvensis* (s.l.) were first recorded in Czechia. Because populations in single outbreak areas had different adult emergence times, they have been called the spring and summer forms, respectively, of *Cephalcia arvensis* (Panzer, 1805). Detailed information on these forms is given by Křístek and Švestka 1986, Martinek 1991, and Battisti 1993.

Table 1. Characteristics of a *Cephalcia arvensis* (s.l.) outbreak in Czechia from 1997 to 1999

Locality:	Česká Čermná environment (Long. 16°14', Lat. 50°23')	
Habitat:	hill country at an altitude of 480 to 640 m	
Area infested:	600 to 700 ha	
Age of stand:	60 to 80 years	
Major tree species in the area:	*Picea abies* (L.) Karst. (predominant),	
	Larix decidua Mill., *Pinus sylvestris* L., *Fagus sylvatica* L.	
Tree species infested:	*Picea abies* (L.) Karst.	
Population of *Cephalcia arvensis* (s.l.)		
Density of larvae in the soil (total number of eonymphs and pronymphs per m^2):	average	200 to 300
	max. 1998	1,300
	max. 1999	570
Percentage of potential swarmers:	1998	72.6%
	1999	67.6%
Main swarming period of adults:	1998	April 14 to 18
	1999	April 20 to 25
Occurrence of males and females:	moderate protandry (several days)	
Fecundity:	17 eggs on average (n = 21)	
Egg laying:	on older (stiff, brush-like) needles in a row from 1 to 4 eggs	
	(most frequently 2 to 3: 67.6% of cases)	
Hatching of larvae:	1998	end of May to beginning of June
	1999	end of May to beginning of June
Larval feeding:	end of May to mid July	
	older needles (they avoid young shoots)	
	gregarious (1 to 4 larvae)	
Falling period of larvae:	end of June to mid July	
Depth of hibernation in the soil:	1997/98	3 to 5 cm (n = 172)
	1998/99	5 to 8 cm (n = 76)
Voltinism:	prevalence of one-year generation (60 to 70%)	
Occurrence of accompanying species of the genus *Cephalcia* Panzer in the outbreak area		
Cephalcia abietis (L.)	numerous	
Cephalcia annulicornis (Hartig)	single	
Cephalcia alpina (Klug) (= *fallenii* (Dalman))	Sporadic	

The population in the outbreak area near Česká Čermná from 1982 to 1988 and from 1997 to 1999 represents the spring phenological form according to the literature cited above. Morphological features of the adults conform to the diagnosis of the species *Cephalcia arvensis* (Panzer, 1805) as described in the revision by Beneš (1976) and van Achterberg and van Aartsen (1986). This species, however, appears to be a complex of several closely related species (Battisti and Zanocco 1994) so that the taxonomic status of the *C. arvensis* population in the outbreak area remains open.

Species Spectrum of the Genus *Cephalcia* Panzer. Besides the predominant species *C. arvensis*, an additional three species of spruce web-spinning sawfly were found in the outbreak area. They were, in decreasing order of abundance, *Cephalcia abietis* (Linnaeus, 1758), *Cephalcia annulicornis* (Hartig, 1837), and *Cephalcia alpina* (Klug, 1808). The total percentage of these three species did not exceed 1 to 2% in either year.

Notes on Bionomics. Some biological attributes of the *C. arvensis* epidemic population in northeastern Bohemia are summarized in Table 1. Some attributes differ from the data obtained from other localities in Europe where epidemic populations of *C. arvensis* have been studied (Pschorn-Walcher 1982; Křístek and Švestka 1986; Battisti 1993, 1994). These differences are undoubtedly due to a different taxonomic identity of the Bohemian population.

On the other hand, data received by Martinek (1991) from the same locality from 1982 to 1988 have been confirmed and provided the following observations:

- swarming began very early (second half of April)
- 1 to 3 (4) eggs were laid in one row on a needle
- the preferred egg laying site was older, stiff brush-like needles in the upper, sun-exposed parts of the crowns
- larvae fed exclusively on older needles
- larvae from the same egg mass were gregarious
- larvae hibernated in the upper layer of the soil, out of the mineral horizon
- one-year generation was prevalent, regardless of prevailing weather conditions during the year

Economic Importance of the Outbreak. In places where population densities of swarmers exceeded an average of 300 specimens per m^2, the number of eggs laid in tree crowns was higher than the critical number (indicating severe defoliation). There were more than 50 (critical number) and not infrequently up to 100 to 200 eggs per 1-m section of a branch. When sample trees were felled (n = 30), it was found that a high density of eggs occurred relatively evenly throughout the stand. For *C. abietis*, on the other hand, the uneven, mosaic character of an infestation is typical, and only a portion of the trees in a stand is severely defoliated. Therefore, it may be concluded that outbreaks of *C. arvensis* can be more dangerous than those of *C. abietis*, a well-known species infesting large areas in central Europe.

The area infested with *C. arvensis* was treated with a ULV spray containing 0.2 litres of Dimilin 48 SC (active ingredient diflubenzuron) per hectare. On May 25, 1998, 600 ha were treated; on May 26th of the following year (1999), only 120 ha were treated. The treatment resulted in larval mortality between 80 and 90%. A comparable effectiveness was obtained when this preparation was used against *C. abietis*.

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Predicting Pine Sawfly Population Densities and Subsequent Defoliation with Pheromone Traps

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ABSTRACT Field trials were conducted from 1989 to 1993 in Finland to develop a monitoring and prediction method using pheromone traps for European pine sawfly (*Neodiprion sertifer* Geoffr.) population densities and needle defoliation. Three traps per site were baited with 100 µg of (2*S*,3*S*,7*S*) - 3,7 - dimethyl - 2 - pentadecyl acetate (diprionyl) at sites representing advanced pine stands. The number of overwintering eggs per sample branch was used to evaluate the effectiveness of using pheromone traps to estimate sawfly populations. The relationships between the number of males in traps, the number of eggs per branch in the subsequent generation, and the number of needle-year classes after the subsequent growing season were highly correlated. The risk threshold for moderate to heavy defoliation was around 1,000 males/trap. Our results suggest that after some minor improvements, a pheromone-based monitoring system for the European pine sawfly would provide an effective tool for integrated pest management programs and successful forest management in coniferous pine-dominated forests.

THE EUROPEAN PINE sawfly (*Neodiprion sertifer* Geoffroy) (Hym., Diprionidae) is a common pest of pine in Eurasia and North America (Pschorn-Walcher 1982, Smith 1993). The species occurs in Finland up to the northern timberline, where the main host is Scots pine (*Pinus sylvestris* L.) (Viitasaari and Varama 1987). *Neodiprion sertifer* overwinters in the egg stage, larvae consume mature needles from June to July until pupation, and new adults emerge from August to early October. Outbreaks in Fennoscandia can reach over hundreds of thousands of hectares, including pine forests from seedlings to mature trees. Populations have extensive, large-scale peak densities every 20 to 30 years, but regional outbreaks can occur every 5 to 6 years. Scattered local outbreaks abound almost every year (Juutinen and Varama 1986, Hanski 1987).

Defoliation by European pine sawfly seldom kills trees, but it decreases tree increment considerably (Austarå et al. 1987, Lyytikäinen-Saarenmaa 1999). Tree mortality after an outbreak period was approximately 4% of the total number of trees in defoliated stands (Juutinen 1967, Tiihonen 1970), but the mortality level can be as high as 50% in young plantations (Austarå et al. 1987). Height growth decreased between 26% and 63%, volume growth decreased between 33% and 50%, and radial growth decreased between 20% and 84% after sawfly damage (Austarå et al. 1987, Britton 1988, Sanchez-Martinez and Wagner 1994). After moderate defoliation by *N. sertifer* in Finland, radial growth losses were estimated to be 20% on average (Tiihonen 1970) and height growth

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losses were 29% (Lyytikäinen-Saarenmaa 1999); however, there is a great need for a comprehensive examination of these questions. Defoliation is likely to reduce tree growth and timber yield, but these aspects have quite often been considered to be less important than potential tree mortality. However, economically significant reductions in increment might occur even after a single defoliation period and even when densities remain below those required to initiate a secondary attack by scolytid bark beetles. The grim reality is that *N. sertifer* causes serious consequences to forestry; in Finland alone, the estimated economic value of growth losses might reach up to 6.0 million USD (60 USD/ha) after a single-year, large-scale outbreak (P. Lyytikäinen-Saarenmaa and E. Tomppo, unpublished data).

The current sampling methods used to estimate European pine sawfly population densities include counting overwintering egg clusters in early spring or cocoons in mid summer. They may roughly detect population trends and predict damage but are time and labor consuming (Allen et al. 1986). It is essential to accurately predict the risk of sawfly epidemics and defoliation intensity in order to be prepared in time for outbreaks. Using pheromone traps to provide estimates of population trends and manage peak densities is available for many other insect pests, particularly within the orders Lepidoptera and Coleoptera (Howse et al. 1998). The most obvious aspect of pheromone-based sampling systems is to produce a quantitative relationship between trap catches and immature stages of the following generation(s) of pests. However, previous attempts to use pheromone-baited traps for monitoring purposes have provided contradictory results.

In the early 1990s, a new method for identifying and synthesizing the *N. sertifer* sex pheromone, (2*S*,3*S*,7*S*) -3,7 - dimethyl - 2 - pentadecyl (diprionyl) acetate or propionate (Högberg et al. 1990), launched development of monitoring and control programs in Scandinavia (Anderbrant 1993, Jönsson and Anderbrant 1993, Anderbrant et al. 1995, Wedding et al. 1995, Östrand et al. 1999). The first long-term monitoring study for predicting population densities of *N. sertifer* using pheromone traps was conducted in young pine plantations (Lyytikäinen-Saarenmaa et al. 1999). The development of a predictive tool that warns forest managers and forest owners of European pine sawfly outbreaks would be of considerable practical importance in pest management programs.

Our objective was to study the effectiveness of using pheromone-baited traps to estimate forthcoming population levels of the European pine sawfly and predict defoliation risks in naturally regenerated advanced Scots pine stands. This was done by comparing the number of sawfly males captured in traps in the fall with the number of eggs per pine branch of the subsequent generation. The correlation between trap catches and subsequent defoliation was also studied.

Materials and Methods

Sites and Sampling. The study was conducted from 1989 to 1993 in naturally regenerated forests representing the advanced stand development class (mid rotation and mature Scots pine stands) on dry or dryish forest sites in south and central parts of Finland. In 1989, mean tree age was 46.3 years (± 20.2 SD) and mean tree density was 1,888 stems/ha (± 1,015 SD). The estimated average annual height growth was 0.21 m (± 0.06 SD). The total number of sites for each year varied from 6 to 32 (Table 1); they were monitored for 1 to 4 years until local populations collapsed. Three monitoring traps were placed at each site in the form of a triangle. The distance between traps was approximately 50 m. The stand

characteristics of experimental sites were, in most cases, measured after the growing season of the first monitoring year using a circular sample plot survey method. The position of each pheromone trap was used as the middle point for a circular plot for a total of three plots on each site. The plot radius was chosen depending on stand density and so that there were at least 20 pines in a plot. The data from the three circular plots were averaged for each site to produce an estimate of stand parameters (Table 1).

Table 1. Means of stand characteristics of the sites, numbers of males captured per trap, and numbers of subsequent overwintering eggs per branch in each year of the study. For details of stand characteristics, see the Materials and Methods section. Standard deviations of the stand characteristics are shown in parenthesis.

	1989	1990	1991	1992
Number of sites	32	31	6	7
Basal area (m^2ha^{-1})	16.9 (4.6)	17.0 (3.6)	20.6 (4.3)	19.7 (1.7)
Mean diameter (cm)	14.5 (4.6)	15.3 (4.7)	15.0 (4.6)	16.7 (5.7)
Mean height (m)	11.8 (3.4)	12.1 (3.4)	13.0 (4.7)	13.8 (4.4)
Number of males/trap	186.0 (160.5)	446.0 (593.8)	132.2 (174.8)	203.9 (160.6)
Number of eggs/branch	37.8 (52.6)	91.6 (221.7)	5.4 (8.3)	3.7 (4.3)

Diameter at breast height was measured for all trees; every fourth tree was chosen for height measurement to an accuracy of $\pm$0.5 m using a Suunto hypsometer. The diameter and height of each tree were projected for other years of the monitoring period using a diameter increment model developed by Pukkala (1989) and a height increment model developed by Nyyssönen and Mielikäinen (1978). Tree basal area per hectare was then calculated for each year as well as mean diameter and mean height, both weighted by basal area.

Branch samples (0.5 m) were collected early each year from 2 to 4 sample trees per site at about the middle point of the triangle in order to count the number of overwintering egg clusters and eggs and to estimate the degree of defoliation. Nine branch samples were collected per tree (three samples each from the upper, middle, and lower third of the crown) and placed in sealed plastic bags in an outdoor shelter. Egg-bearing shoots were kept in water at room temperature for approximately 1 to 2 weeks before the number of eggs was counted. The eggs represented the subsequent generation and were compared to trap catches. The degree of defoliation was determined by estimating the number of remaining needles to an accuracy of a quarter of a needle-year class one year after each trap catch. Scots pine has approximately 2.5 to 4 needle-year classes in southern and mid Finland.

Sawfly Monitoring. The population density of sawfly males was measured by placing three Lund-I sticky traps about 2 m above ground. Traps were baited with (2*S*,3*S*,7*S*) - 3,7 - dimethyl - 2 - pentadecyl acetate (Högberg et al. 1990) applied on dental cotton roll dispensers. The substance was of a high stereoisomeric purity (> 99 %) and contained less than 0.01% of the antagonist (2*S*,3*R*,7*R*) - isomer (Anderbrant et al. 1992b). The traps were baited with 100 µg diprionyl acetate that gave an average release rate of 2.8 µg/d from the cotton roll dispensers over a 30-day period and, on average, a double release rate for a 2-week period (Anderbrant et al. 1992a). The trapping period started in early August each year and extended to mid October. Baits and sticky bottoms were renewed either every second week (1989) or every fourth week (1990 to 1992).

Data Processing. Data were processed applying analysis of variance (ANOVA) and linear regression analysis (BMDP Statistical Software 1994). A square root transformation (Sokal and Rohlf 1981) was applied to improve normality and homoscedasticity of the parameters when necessary. The figures present the original, untransformed data. The average trap catch of three traps was used in analyses. The differences between years in number of eggs per branch and trap catch were tested by one-way ANOVA. The relationships between trap catch and number of eggs in the subsequent generation and stand parameters were determined by linear regression analyses.

Results

Both trap catch and the number of eggs per branch reached peak values in 1990 (Table 1). ANOVA revealed significant differences in trap catch between years ($F = 2.96$; $df = 3,72$; $P = 0.038$), but not in egg number ($F = 0.99$; $df = 3,72$; $P = 0.404$). When trap catch was regressed linearly with number of eggs per branch in the subsequent generation, using combined data from all years, the coefficient of determination was high (76%) (Fig. 1). The relationships were never significant within a single year.

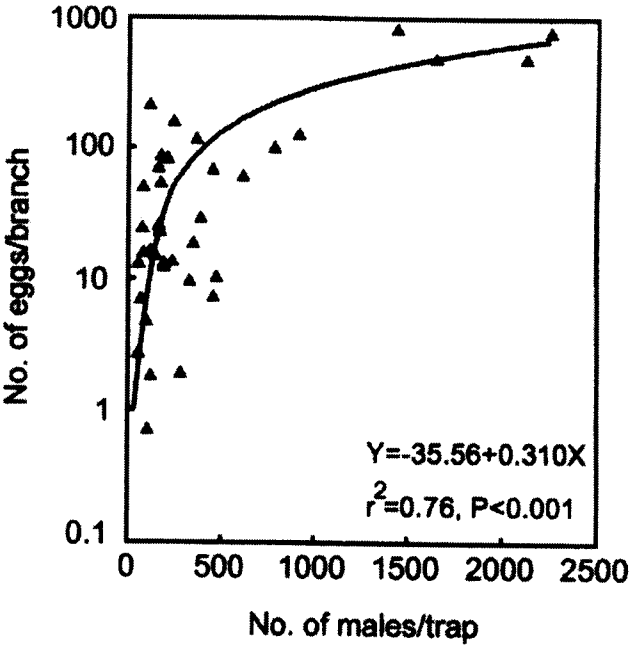

Figure 1. Relationship between the number of *Neodiprion sertifer* males captured in traps baited with 100 μg diprionyl acetate and the number of eggs per branch in the subsequent generation.

Trap catch data were divided into two groups before analyzing relationships with the number of needle-year classes after a subsequent growing season: low male density (< 400 males/trap) and high male density (> 400 males/trap). When male density was low, the

relationship between trap catch and number of needle-year classes was not significant (Fig. 2A). However, the regression line indicated a negative relationship trend between these factors. On the contrary, a different pattern was revealed at high male densities. The relationship between trap catch and number of needle-year classes after the subsequent growing season had a highly significant negative correlation. It is obvious that a risk threshold for moderate to heavy defoliation (and thus a loss of almost all but current year needles) may occur when the number of males caught exceeds 1,000 per trap (Fig. 2B). However, the data from the four sites with the highest male densities should be regarded with caution. These four sites were heavily defoliated in 1990. Nuclear polyhedrosis virus (NPV) was applied in the summer of 1991 prior to the last estimation of the number of needle-year classes in winter. This might have caused a drop in defoliation intensity. Without NPV application, defoliation levels would have been even higher.

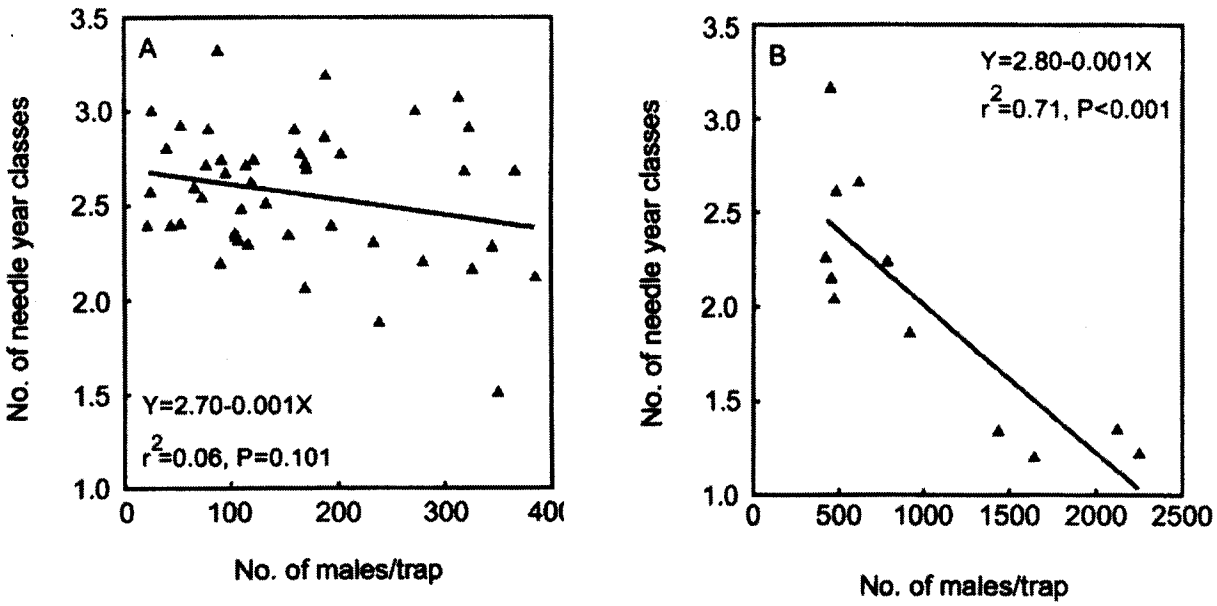

Figure 2. Relationship between the number of *Neodiprion sertifer* males captured in traps baited with 100 μg diprionyl acetate and the number of needle-year classes after the subsequent growing season from 1989 to 1993. (A) male density < 400 males/trap; (B) male density > 400 males/trap.

Discussion

European pine sawfly populations had one peak year (1990) and afterwards rapidly declined toward endemic levels. However, our study period was relatively short and resulted in an inability to follow long-term population trends. The number of males in traps was still quite high despite the low number of eggs per branch in the subsequent generation (Table 1). This relatively high level in male numbers could be a consequence of an immigration of males from nearby forest stands (Sweeney et al. 1990) or the termination of a prolonged diapause after high population densities associated with epidemics (Juutinen and Varama 1986). Moreover, virus epizootics may alter the sex ratio of the surviving population to create a male biased population (Lyons 1964).

The number of eggs per branch in the subsequent generation showed a strong relationship with the number of males in traps, indicating the ability of traps to give a proper estimate of future population densities. Generally, the accuracy of the prognosis would be better if several sites with moderate to high sawfly densities were available, particularly when densities are increasing (Lyytikäinen-Saarenmaa et al. 1999). Egg parasitism might hamper European pine sawfly density estimates in some years because egg mortality can be as high as 90% after the population's peak (Juutinen and Varama 1986). The number of eggs per sample branch was used to estimate needle damage risks. During the early stage of epidemics, when stands have only suffered slight defoliation, about 250 to 300 healthy eggs per branch (length 0.5 m) are needed for almost all mature needles to be consumed during the subsequent growing season (Juutinen and Varama 1986). The corresponding egg number during the second outbreak year is only around 100 healthy eggs per branch. Several of our sites included those risk threshold densities of eggs, particularly in 1989 and 1990. Therefore, when predicting the number of eggs and forthcoming defoliation using the number of males caught in pheromone traps, we can be one (or even more) step ahead and have more time to prepare and plan for control measures. These results are promising, suggesting that pheromone traps can be applied as part of integrated pest management programs after some improvements of the method.

Trap catch correlated well enough with the number of eggs in the subsequent generation, and obviously with larvae causing the damage, as also observed earlier (Lyytikäinen-Saarenmaa et al. 1999). It is generally accepted that the amount of growth loss after defoliation is roughly proportional to the amount of foliage defoliated (Sanchez-Martinez and Wagner 1994, Lyytikäinen-Saarenmaa 1999). Defoliation of pines early in the growing season usually causes a reduction in current growth, but in some cases even higher reductions will follow a year or several years later (Lyytikäinen-Saarenmaa 1999). Increment losses, including height, radial, and volume growth, could be estimated by knowing the number of remaining needle-year classes. It is possible to predict the degree of defoliation using the average number of males caught, which represents pine sawfly population density in an area.

Searching for a threshold value of defoliation risks is the main question in pest management programs. According to our results, having less than 400 males per trap does not create risks for remarkable needle damage, but at higher male densities (> 400 males per trap), considerable forest damage is likely. Our results suggest that having at least 1,000 males per trap implies a need for control methods, e.g. virus application and intensive observation of a pest situation. If the number of sawfly males greatly exceeds 1,000 per trap,

loss of all old needles (and, in some cases, part of the current needles) can be expected. Our data contained only a few sites with such high population levels, which normally appear in epidemics. It is likely that additional observations from sites with high population levels would indicate a lower threshold value than mentioned above. The pheromone trap method may help to predict defoliation in the near future, providing more accurate damage estimates than traditional methods. Our method could also very easily be included into the framework of integrated pest management and modern decision support systems, linking pest and forest ecosystem management.

When pest densities are at a risk threshold, the value of growth loss and killed trees normally equals the maximum amount of money spent on control measures to prevent insect damage (Austarå et al. 1987). The risk threshold fluctuates depending, for example, on the geographic location of the area, stand age, price of standing timber, transport costs of timber, and domestic and international trade. It is possible to estimate the economic value of growth losses based on the proportion of tree species in the area, timber volume in the stand, annual increment, average intensity of insect defoliation, percentage of killed trees, and timber value. A model that predicts defoliation and increment losses and evaluates the losses using pheromone trap catches would be highly practical for forest managers and forest owners. After improvements, our pheromone-based monitoring system for the European pine sawfly would provide an effective tool for integrated pest management programs and successful forest management in coniferous pine-dominated forests.

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Effects of Gypsy Moth Defoliation in Oak-Pine Forests in the Northeastern United States

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ABSTRACT Dendrochronology data from two oak-pine (*Quercus-Pinus*) forests in the northeastern United States (New Jersey and Massachusetts) were examined to understand the influence of defoliation on radial ring width of highly preferred trees (*Quercus*) and slightly less preferred trees (*Pinus*). Over a 5-year period, defoliation from gypsy moth (*Lymantria dispar* L.) ranged from 2.4% to 86.4% and mortality was nearly 50% of *Q. alba* stems in Massachusetts. The effect of individual tree defoliation, although generally negative, differed slightly among all the oak species. Stand-level defoliation negatively influenced growth of oaks and pines on both sites. There was no compensatory response apparent in the radial growth of pitch pine. The effect of defoliation was also evident in the relative production of earlywood and latewood with a pronounced dominance of earlywood production in host trees during the same year as defoliation and often in the following year.

AS A NON-NATIVE, polyphagous species in North America, the gypsy moth (*Lymantria dispar* L.) can negatively influence many forest types. Its preferred host are oaks (*Quercus* spp.), the dominant overstory tree species in the eastern United States. Pines (*Pinus* spp.) generally are considered less likely to be defoliated by gypsy moth than oaks (Liebhold et al. 1995), although defoliation of pines has been widely observed and documented (Brown et al. 1988, Gottschalk and Twery 1989, Montgomery et al. 1990). When gypsy moth larval densities are high and defoliation is widespread, shifting to a less preferred host is common. Oak-pine forests, therefore, may be classified as susceptible to gypsy moth. Oak-pine forests are also typically found on the most xeric portion of the landscape capable of supporting forests.

Site factors may exacerbate defoliation-related stress and may account for increased mortality in forests with high defoliation. Although some research findings support this assumption, Davidson et al. (1999) suggest that the evidence is contradictory, and that at least an equal number of studies have demonstrated that trees growing on poor sites have less mortality than those on good sites. Gansner (1987) suggested that poor quality trees were physiologically adapted to stress conditions and therefore could endure defoliation.

Dendroecological techniques can be useful in assessing the effect of insect outbreaks, but have been used primarily to reconstruct historic patterns of outbreaks (Fritts and Swetnam 1989). In western North America, western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak histories have been developed through many studies (Thomson and VanSickle 1980; Swetnam and Lynch 1989, 1993; Weber and Schweingruber 1995). Extensive chronologies have been developed to determine the long-term impact of defoliation, such as radial growth losses of trees and forests (Brubaker 1978, Wickman 1980, Mason et al. 1997).

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Few studies have used dendrochronology to examine the effects of hardwood defoliators in the eastern United States. With the exception of research by Baker (1941), Campbell and Garlo (1982), and Muzika and Liebhold (1999), there is a noticeable absence of dendrochronological research examining the effects of defoliation on deciduous trees. In this paper, we use data from a study conducted in the 1970s to examine the effect of gypsy moth defoliation on both pines and oaks in two areas of the northeastern United States.

Methods

The data used in this study were collected as part of the USDA Forest Service Intensive Plot System (IPS) from 1972 to 1978 (Reardon 1976). Data were collected in six areas throughout the northeastern United States. For this study, however, we focused on the two areas that were dominated by oak-pine forests. Area 1 was located on Cape Cod, Massachusetts, and Area 2 was located along the Atlantic coast in New Jersey. These areas contained coastal stands that were dominated by white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), and pitch pine (*Pinus rigida*). Each area consisted of five to eight sites that were relatively homogenous in soil type and overstory species composition. Within each site, there were five 0.04-ha plots from which data were collected on a wide array of parameters relative to gypsy moth populations, individual tree defoliation, and crown condition. All trees within the plots were identified, height and diameter were measured, and vigor and defoliation were evaluated. Defoliation was measured as a percentage loss of canopy and was estimated following gypsy moth feeding in the summer (Table 1).

Table 1. Defoliation estimates (%) of overstory trees for the two study areas for each of 5 years. Defoliation estimates represent averages across the sites at each area.

Year	Massachusetts	New Jersey
1972	79.7	67.3
1973	56.3	86.4
1974	10.6	21.9
1975	4.7	15.0
1976	2.4	3.4

In the winter of 1976-1977, an increment core was taken from each living tree on every plot. Ring widths were measured at Virginia Polytechnic Institute and State University soon after the cores were extracted. Most of the cores were measured through the most recent 25 years, although a few had longer series. Only species with at least 10 individuals per site were retained for analysis. Total radial increment was measured on all trees and earlywood and latewood were differentiated.

All cores consisted of at least 25 annual growth rings; the most reliable chronologies existed for the years from 1952 to 1976. We graphically cross dated each series and eliminated series that may have had missing rings. The raw tree-ring series were standardized to correct for an age-related growth trend. Because of the relative shortness of the series, we fit unique linear regressions for each tree and used the residuals as the standardized

increment. Detrending eliminated the effect of individual tree age and resulted in a series that represented the relative growth level for each year.

Detrended ring widths were used for analysis of defoliation effects; we used averages for each species at each site. Defoliation data were available for only the last five years of each series (1972 to 1977). Overall, there were five species used in the analysis (white oak, scarlet oak, chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), and pitch pine). Stepwise linear regression was used to test the effect of defoliation on radial increment. The dependent variable was normalized, detrended increment for each tree in each year. Increment was normalized by dividing the detrended (residual) increment by the standard deviation of the detrended values. Normalization was performed in order to remove among-tree variation in increment variance. Independent variables used in the stepwise regressions were: (1) individual tree defoliation in the same year as increment (defoliation), (2) individual tree defoliation in the prior year (lag defoliation, or defoliation (t-1)), (3) average stand-level defoliation in the same year as increment (stand defoliation), and (4) stand-level defoliation in the previous year (lag stand defoliation, or stand defoliation (t-1)). A P value of 0.05 was used as the criterion for including either defoliation or lag defoliation in the regression model.

Using earlywood and latewood measurements, we calculated the proportion of earlywood and used it as the dependent variable in stepwise regression for all trees of a given species pooled across all sites. We used the same independent variables as described above. The proportion of earlywood was transformed, then detrended because of the influence of age on early and latewood width (Zhang et al. 1994).

Results and Discussion

Previous research indicated that both study areas were dominated by oak with 10 to 15% of their basal area in pitch pine (Montgomery et al. 1990). Defoliation estimates were comparable between the two areas and reflected gypsy moth populations in outbreak years (1972 and 1973) with a dramatic decline in populations within a few years following extensive defoliation. The temporal sequence in defoliation suggests that the outbreak occurred in Massachusetts initially and a year later in New Jersey. Among all six areas in the original study, these two oak-pine forests incurred the greatest amount of defoliation.

Mortality within each area was determined as a percentage of dead stems by species. Mortality of pine was comparable at both areas. In Massachusetts, nearly half of the white oak stems died over the 5-year period, but only 9% died in New Jersey (Table 2). As a group, the red oaks (*Q. velutina* and *Q. coccinea*) had greater mortality than white oaks in New Jersey. Overall, mortality was greater in Massachusetts than in New Jersey, despite higher levels of defoliation in New Jersey.

Stepwise regression results indicated the specific influence of each of the identified variables on ring width of each species (Table 3). Predictably, individual-tree defoliation and stand-level defoliation in a given year negatively influenced growth of pitch pine in Massachusetts and New Jersey. While that negative effect persisted in Massachusetts, previous year's defoliation did not influence pine growth in New Jersey. Similarly, stand-level defoliation in the previous year was inversely related to growth in Massachusetts but not New Jersey. As a less preferred host, pitch pine may be expected to benefit from

Table 2. Cumulative percent mortality from *L. dispar* defoliation for overstory trees over a 5-year period (1973 to 1978) at Cap Cod, Massachusetts, USA, and New Jersey, USA. "NA" indicates that no individuals of that species were present at the study area.

Species	Massachusetts	New Jersey
Pinus rigida	16.1	15.6
Quercus alba	46.3	8.7
Quercus rubra	20.4	NA
Quercus velutina	29.5	37.8
Quercus montana	NA	14.3
Quercus coccinea	NA	23.4

Table 3. Results of stepwise regression of radial increment on defoliation. Each tree had four observations corresponding to defoliation data from 1972 to 1976. See text (page 119) for an explanation of the variables. This table lists parameter estimates from the stepwise regression that indicate the direction of the relationship. A *P* value of 0.05 was used as the criterion for retaining a variable in the regression.

Species	Variables	Massachusetts	New Jersey
Pinus rigida	Defoliation	-2.201	-1.359
	Defoliation (t-1)	-0.767	*ns*
	Stand Defoliation	-1.323	-1.138
	Stand Defoliation (t-1)	-0.381	*ns*
Quercus alba	Defoliation	0.203	-0.548
	Defoliation (t-1)	-0.328	*ns*
	Stand Defoliation	0.449	-0.666
	Stand Defoliation (t-1)	-0.538	*ns*
Quercus coccinea	Defoliation	*ns*	-0.588
	Defoliation (t-1)	-1.138	-0.175
	Stand Defoliation	*ns*	-0.710
	Stand Defoliation (t-1)	-1.564	-0.216
Quercus montana	Defoliation	-	-0.793
	Defoliation (t-1)	-	*ns*
	Stand Defoliation	-	-1.045
	Stand Defoliation (t-1)	-	*ns*
Quercus rubra	Defoliation	0.227	-
	Defoliation (t-1)	-0.615	-
	Stand Defoliation	*ns*	-
	Stand Defoliation (t-1)	-0.840	-
Quercus velutina	Defoliation	*ns*	-0.417
	Defoliation (t-1)	-0.479	*ns*
	Stand Defoliation	*ns*	-0.668
	Stand Defoliation (t-1)	-0.785	*ns*

defoliation of oak species; therefore, stand-level defoliation could result in a positive influence on pitch pine growth, as has been demonstrated with non-host species (Muzika and Liebhold 1999). In the present study, increased growth in less preferred species (pitch pine) was not observed, but this most likely resulted from the high intensity of defoliation that included less preferred species themselves and depressed their growth.

Oak species were predictably, but variously, influenced by defoliation. Only scarlet oak demonstrated a consistent and negative effect of defoliation, but only in New Jersey. Defoliation in the year of growth and the previous year, both at the individual-tree and stand level, affected scarlet oak growth increment in New Jersey. The fact that defoliation positively influenced white oak increment in Massachusetts may be explained by the high mortality rate of that species. With nearly 50% white oak mortality, the individuals that did not die also did not reduce increment, likely reflecting a different cohort, i.e. the survivors may have been considerably younger than those that died. Reductions in radial growth are uncommon in younger trees. Furthermore, stand-level defoliation positively affected white oak growth in Massachusetts, suggesting enhanced or compensatory growth of the remaining cohort. In New Jersey, where white oak mortality was lower (Table 2), individual tree defoliation and stand defoliation both negatively influenced radial growth.

Most other oak species were negatively affected by defoliation in either study area. Unexpected findings include a positive influence of current-year, individual-tree defoliation on red oak and white oak growth. The previous year's individual-tree defoliation and previous year's defoliation at the stand level both negatively affected red oak increment, however. It is possible that some mortality occurred in red oaks in the first year of defoliation, but survivors responded with increased growth. In subsequent years, however, growth was negatively influenced by defoliation from the year previous. The delayed, but negative, response in growth increment the year following defoliation was also evident in scarlet and black oaks in Massachusetts.

To further assess the influence of defoliation on radial increment, we examined the proportion of earlywood to latewood as a dependent variable using stepwise regression for the oak species only. We anticipated that defoliation effects on earlywood would be minimal since earlywood production is well underway by the time defoliation by gypsy moth occurs. Contrary to our expectations, there were significant positive effects of defoliation on the proportion of earlywood in all oak species in the year of defoliation and, for most oaks, in the year following defoliation (Table 4). Since total increment was often reduced in these trees, a positive effect on earlywood proportion indicated a relatively severe negative effect on latewood. Latewood production would be directly influenced by both current and previous year's defoliation, corresponding to the results of the stepwise regression. The proportion of earlywood in chestnut oak was significantly related to defoliation in the current year only.

Our findings are in general agreement with previous studies describing how defoliation by gypsy moth and other insect species affects tree growth and production of latewood. Earlier research characterizing the influence of gypsy moth on tree growth indicated that increment loss was proportional to defoliation. There is variation in the timing of the significant relationships, however. Minott and Guild (1925) found that the effect of defoliation on increment appeared to be greatest in the same year as defoliation, but noted that there may also be a decline in growth in the year following defoliation. Similarly, Baker (1941) demonstrated that throughout a 10-year period of repeated gypsy moth defoliation,

reductions in growth were strongest in the year during defoliation; there was a noticeable, although less pronounced, lag effect, i.e. reduced increment in the year following defoliation.

Table 4. Results of stepwise regression of earlywood proportion of total increment on defoliation. This table includes trees from both study areas.

Species	N	Variable	Parameter Estimate	P
Quercus alba	1,905	Defoliation	0.074	0.0001
		Defoliation (t-1)	0.047	0.0001
Quercus coccinea	955	Defoliation	0.100	0.0001
		Defoliation (t-1)	0.025	0.0005
Quercus montana	1,225	Defoliation	0.118	0.0001
Quercus rubra	1,495	Defoliation	0.107	0.0001
		Defoliation (t-1)	0.046	0.0023
Quercus velutina	360	Defoliation	0.102	0.0001
		Defoliation (t-1)	0.056	0.0004

In this study, we have shown that gypsy moth defoliation negatively influences radial increment in hosts irrespective of the quality of that host. Overall, the more highly preferred oaks were negatively influenced, but the strength of the relationship differed among species. The intermediate host, pitch pine, was negatively affected by defoliation, but the lag response varied between the two areas. The consistent relationships between the two sites indicated that generalizations about the susceptibility of oak-pine forests to gypsy moth can be established and predictions about anticipated losses in radial growth or tree mortality can be made to benefit forest management efforts.

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Modeling Seasonal Development of the Gypsy Moth in a Novel Environment for Decision Support of an Eradication Program

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ABSTRACT Observations of field-caged egg masses of the European gypsy moth (*Lymantria dispar* (L.)) on Vancouver Island, British Columbia, Canada, indicate that overwinter survival of the insect is very high in this area. Emergence of larvae in the spring occurred over a period of 4 to 5 weeks. These observations were used to validate a process-oriented phenology model that was, in turn, used to time pesticide applications during an eradication program against the gypsy moth. Based on a digital elevation model and climate normals, the phenology model was used to examine heterogeneity of seasonal development within the eradication zone and to identify areas where successful completion of the insect's life history might be unlikely because of climate.

THERE HAVE BEEN repeated introductions of gypsy moth (*Lymantria dispar* (L.) (Lepidoptera: Lymantriidae)) into British Columbia, Canada, since 1978. In many cases, capture records of single male moths in pheromone traps in one year have not been repeated in the following year despite an intensification of trapping effort. These cases indicate the population did not persist and no eradication programs were undertaken. However, there have been several occasions when detected populations have persisted and apparently increased for at least 2 years. These infestations have been treated, mostly through multiple aerial applications of *Bacillus thuringiensis* var. *kurstaki* (*Btk*) (Humble and Stewart 1994).

The introduction of exotic insects such as the gypsy moth to a new geographic area presents unique challenges for pest managers. At minimum, resource managers will want to intensify monitoring to delimit the area of actual infestation. With gypsy moth, this monitoring is done with pheromone traps and so it is necessary to know the period of male adult flight so traps can be deployed and retrieved at appropriate times. If a decision is made to eradicate the incipient population, there is then the more demanding practical problem of predicting the timing of treatment of susceptible life stages. Susceptibility to *Btk*, for example, is greatest for early larval stages. In the situation of recently introduced exotic insects, there is no historical record of seasonal development for the area and the insect is too rare to sample reliably at all life stages. Moreover, the environmental conditions in the newly infested area may be significantly different from areas where historical information is available. The result is that the phenomenological approach often used by pest managers is either unavailable or unreliable for decision making.

This paper describes a modeling approach to these problems using the recent experience involving the European gypsy moth on southern Vancouver Island in British

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Columbia, Canada, as a case study. We analyzed the phenology of all life stages of the gypsy moth using a temperature-driven model of gypsy moth development. This model was validated with field observations from southern Vancouver Island. The phenology model was then used to develop area-wide forecasts of target events in the seasonal life history of gypsy moth as described by Régnière and Sharov (1999). The results were mapped to visualize spatial variation in the timing of specific phenological events such as egg hatch and moth flight at the landscape level. These events were then used to support timing decisions made in an eradication program in 1999.

Methods

Models. Régnière and Sharov (1998) linked models of gypsy moth egg hatch (Johnson et al. 1983), early instar development (Logan et al. 1991), and late instar and pupal development (Sheehan 1992) into a composite, full-season model of gypsy moth development. They then used this composite model to demonstrate a method of simulating temperature-dependent ecological processes over a large geographic area (Régnière and Sharov 1999). For our purposes, we compared the output of three egg-hatch models: that of Johnson et al., that of Lyons and Lysyk (1989), and that of Gray et al. (1991, 1995, In press). These egg-hatch models were run using on-site temperature records, and their output was compared to observed gypsy moth egg hatch to determine the best-fitting egg-hatch model to include in the composite seasonal model.

The best-fitting egg-hatch model and the composite seasonal model were then linked to BioSIM, a system designed to generate area-wide phenology simulations based on digital elevation models, climatic normals, real-time weather observations, and temperature-dependent phenology models (Régnière 1996). BioSIM generates forecasted temperature traces that drive the phenology model to predict target events such as the date of egg hatch or moth flight. Daily air temperature records starting in 1997 for a range of locations in southern Vancouver Island and Vancouver and regular, 5-day forecasts for Nanaimo, Victoria, and Vancouver were provided by the Victoria Weather Office, Environment Canada. Standard air temperature normals (mean monthly and extreme minimum and maximum) from 1961 to 1990 were obtained from the Canadian Monthly Climate Data and 1961-1990 Normals and Monthly Averages CD-ROM (1993 issue; Climate Information Branch, Environment Canada, Ontario, Canada). A 3-arc-second digital elevation model of southern Vancouver Island was obtained from D. McKenney (Canadian Forest Service, Sault Ste Marie, Ontario). The digital elevation model was projected to Universal Transverse Mercator and the horizontal resolution was decreased to 150 m by re-sampling.

In the process of generating maps of phenology model outputs, BioSIM must simulate phenology for points other than the location of weather stations. This is done by adjusting temperatures for differences in elevation, latitude, and longitude between stations and simulation points. These adjustments were based on thermal gradients obtained by a method developed by M. Gignac (pers. comm., Department of Geomatics, Laval University, Quebec, Canada) and involve a general linear model that includes latitude, longitude, elevation, month of year, and an index of either minimum or maximum temperature.

Validation. To compare and validate predictions of the three available models of egg hatch, 76 locally collected egg masses were obtained from survey crews of the Canadian Food Inspection Agency (CFIA), Victoria, B.C., between December 1998 and February

1999. Each egg mass was placed in an individual plastic petri dish and housed outside in a ventilated cage at ground level under partial shade. Because gypsy moth egg masses are laid mostly in sheltered locations at ground level (Leonard 1972), this was our best effort to provide ambient overwintering and spring conditions for the eggs. A temperature probe (Optic Stowaway, Onset, MA) was placed among the petri dishes and provided temperature records hourly. Egg masses were observed daily for eclosion and hatching larvae were counted and removed. This gave the seasonal distribution of egg hatch for both individual egg masses as well as the population as a whole. After the emergence of larvae was completed, all egg masses from which no larvae had emerged and a random subsample of 20 egg masses from which at least some larvae had emerged were examined and the status of unhatched eggs (uneclosed but fertile, infertile or parasitized) was determined. This provided an estimate of survival of the gypsy moth eggs in the area.

An independent check on the composite seasonal model was made by comparing model predictions of the timing of adult male moth flight in 1998 to actual observations made by survey crews of the CFIA from pheromone traps monitored daily in that year. This composite model predicts seasonal appearance of the adult stage. Pheromone traps record moth flight. Therefore, we imposed an arbitrary linear relationship between air temperature and moth flight activity, with a lower activity threshold of 15°C for graphical comparison of predicted and observed male flight activity (inset, Fig. 2).

Forecasts. Area-wide forecasts of egg hatch and adult moth flight were mapped to visualize spatial heterogeneity of gypsy moth phenology on southern Vancouver Island and to advise pest managers on the timing of critical target events at specific locations. These maps also allow identification of areas where seasonality is biologically impossible for the gypsy moth on southern Vancouver Island as has been done for this same insect in northeastern North America (Régnière and Sharov 1999).

Results

Egg Hatch: Observations and Model Validation. Seventy-six unhatched gypsy moth egg masses were collected and assessed between December 1998 and May 1999. Twelve of these egg masses contained only infertile eggs and could have been from either 1998 or previous years. There was no evidence of egg parasitism. At least 1 larva hatched from each of the remaining 64 egg masses. The mean (standard error) number of gypsy moth larvae emerging per egg mass was 317.8 (±26.0). Examination of a subsample of these egg masses after hatch was complete indicated that mean survival in viable egg masses was 90%. Given that some mortality of individual eggs could be expected from handling, as these egg masses were in many cases scraped off the substrate with a knife, this is a conservative estimate of survival for gypsy moth eggs in Victoria. Thus, the gypsy moth survived the relatively warm and wet winter in Victoria at least as well as they did in climatically dissimilar places where populations have persisted for decades (Nealis et al. 1999).

The distribution of hatch within individual egg masses was protracted with larvae eclosing from the same egg mass over a 10- to 26-day period for egg masses containing more than 100 eggs. Hatch of the population as a whole, of course, was even more protracted, occurring over a 38-day period in 1999. Of the three egg-hatch models compared to this observed distribution, Gray's model fit by far the best (Fig. 1).

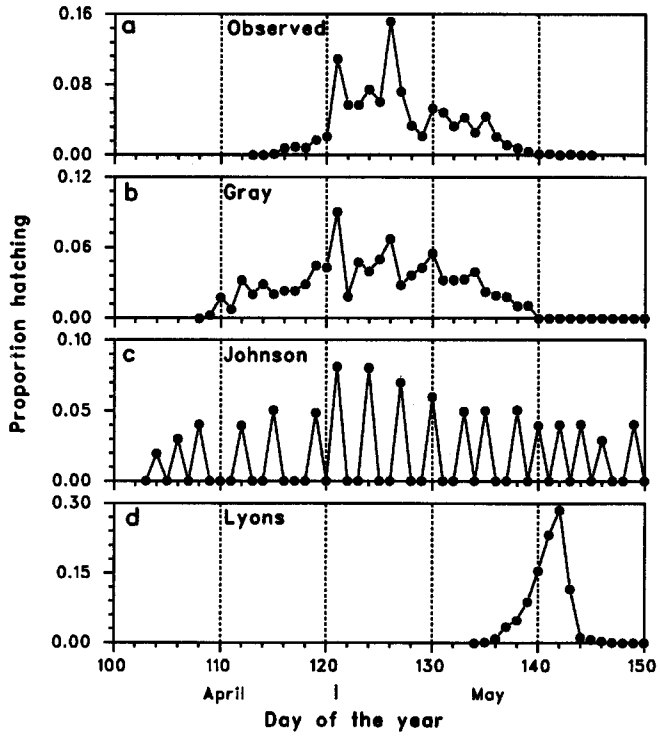

Figure 1. Comparison of observed and predicted egg hatch rates in Victoria, British Columbia, in 1999. (a) Observed. Note that individual egg hatch was not recorded for the first 6 masses to hatch. Hatch rate predicted by (b) Gray's, (c) Johnson's, and (d) Lyons and Lysyk's models.

The models developed by both Johnson et al. (1983) and Lyons and Lysyk (1989), although validated in the areas for which they were developed originally, were inadequate in forecasting phenology in the novel environment of southern Vancouver Island. In contrast, Gray's model is based on a detailed description of egg developmental physiology and, if valid, should be relatively robust to changes in regional climate. Parameters were developed from carefully controlled laboratory experiments and the model makes an explicit distinction between the phases of embryonation, diapause, and post-diapause development. Gray's model requires the date of peak oviposition as input, but is relatively insensitive to this parameter. Preliminary simulation studies suggested that early September was a likely date of peak oviposition for the south of Vancouver Island. By itself, this model permitted accurate forecasts for egg hatch in 1999 using the date of observed peak moth flight in 1998 as the peak oviposition date. When combined with sub-models for the remaining life stages compiled by Régnière and Sharov (1998), it contributed to a very good prediction of observed flight of male gypsy moths in 1998 (Fig. 2).

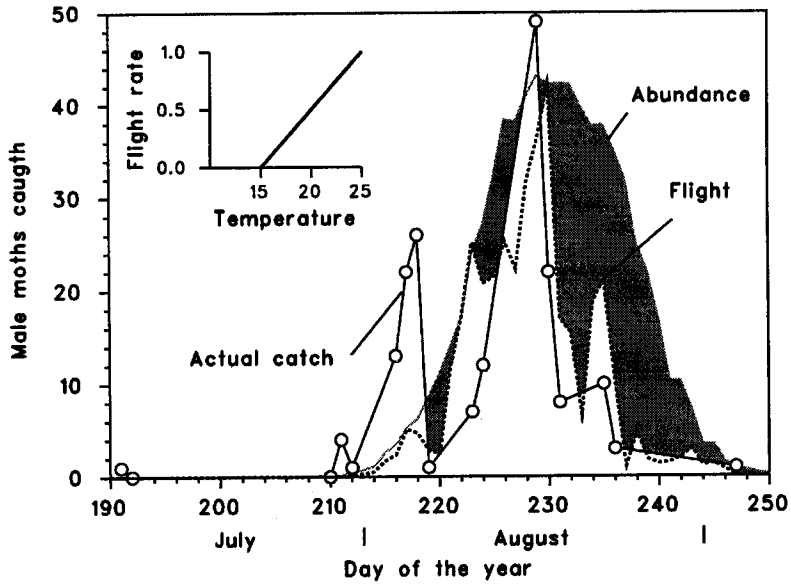

Figure 2. Comparison of predicted and observed male moth flight in 1998. Grey-shaded curve: predicted moth abundance; dotted line: predicted flight activity, the product of male abundance by the linear relationship of mean air temperature illustrated in the inset; solid line and open circles: observed daily moth catch in pheromone traps. Egg hatch simulated using Gray's model.

The importance of substituting available real-time weather observations for normal weather records when predicting target events for specific pest control operations is illustrated in Figure 3. Our reliance on 30-year normal temperatures to predict the occurrence of peak first instars or first moth flight on Vancouver Island would have been very inaccurate in both 1998 and 1999 because of specific weather patterns in those years. In 1998, a relatively warm spring and summer led to phenology that was much earlier than would have been expected from climate normals (peak first instar was 14 days in advance and the first moth flight was 20 days in advance). In 1999, spring temperatures were below normals and peak first instar was reached 8 days later than expected on the basis of normals. The remainder of the summer was near normal, so that moth flight also started nearly one week later than would have been predicted by climate normals. Had the timing of control operations in 1999 been based on 1998 phenology, the first application would have been made 20 days too early.

Maps. Maps of the date on which first instar and male moth frequency are predicted to be maximum were generated for southern Vancouver Island (Figs. 4a and b). These maps were generated using the first week of September as the peak oviposition date (day 250) for all locations and illustrate the wide range of phenology expected for gypsy moth in this relatively small geographic area. Areas where male abundance (approximately synchronous with peak oviposition) would occur after November are unlikely to permit persistence of the population for reasons of seasonality alone. Such maps provide pest managers with a means of identifying areas were gypsy moth populations are most likely to persist as well as provide specific guidelines for timing *Btk* applications and the deployment and recovery of pheromone traps.

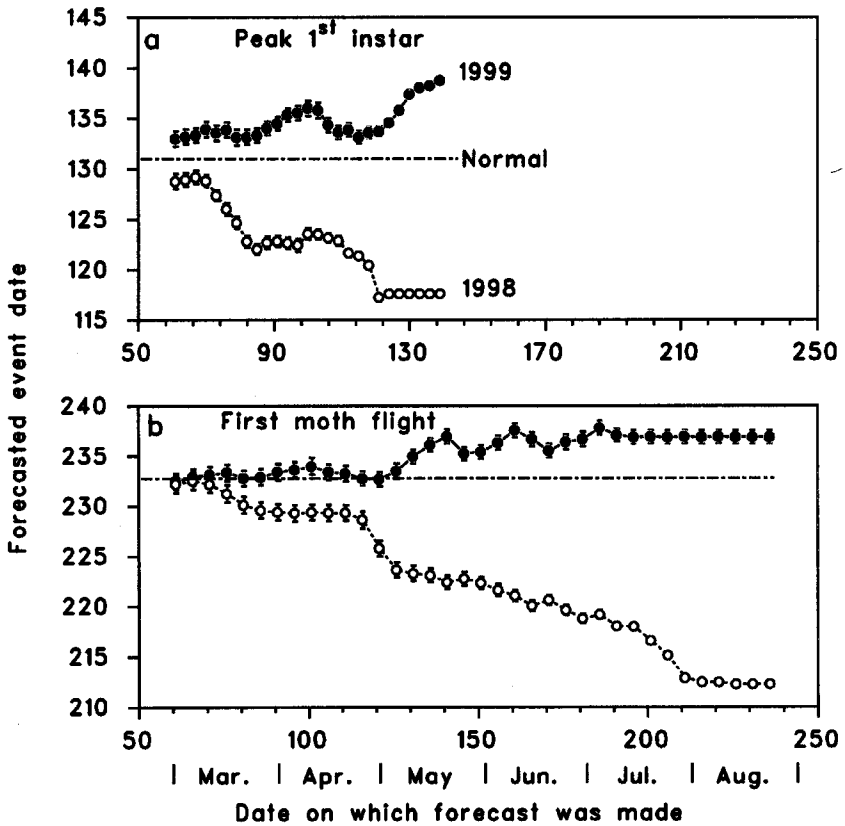

Figure 3. Evolution of the predicted date of peak abundance of (a) first instar larvae and (b) male moths in 1998 (open circles) and 1999 (closed circles) as time in the season progressed and an increasing amount of actual (real-time) data accumulated. The horizontal lines represent the predictions based solely on climatic normals. Egg hatch simulated using Gray's model.

Discussion

Phenology models provide a critical basis for a generalized approach to forecasting insect seasonality at the landscape level (Schaub et al. 1995, Régnière 1996, Régnière and Sharov 1999). The process-oriented model of egg development constructed by Gray et al. (1991, 1995, In press) provided an accurate prediction of observed hatch in Victoria in the spring of 1999. The advantage that this model has over others is its explicit description of temperature-dependent processes occurring between the time of oviposition in year *t*-1 and the time of egg hatch in the spring of year *t*. This distinction allowed the egg-hatch model to be far more sensitive to the warm winter conditions characteristic of the area of interest and was therefore important for forecasting specific target events within the unique climatic environment of southern Vancouver Island. Comprehensive modeling of diapause also permitted a biological, rather than a calendar, definition for initiating the seasonal model, namely, the actual time of oviposition the previous season.

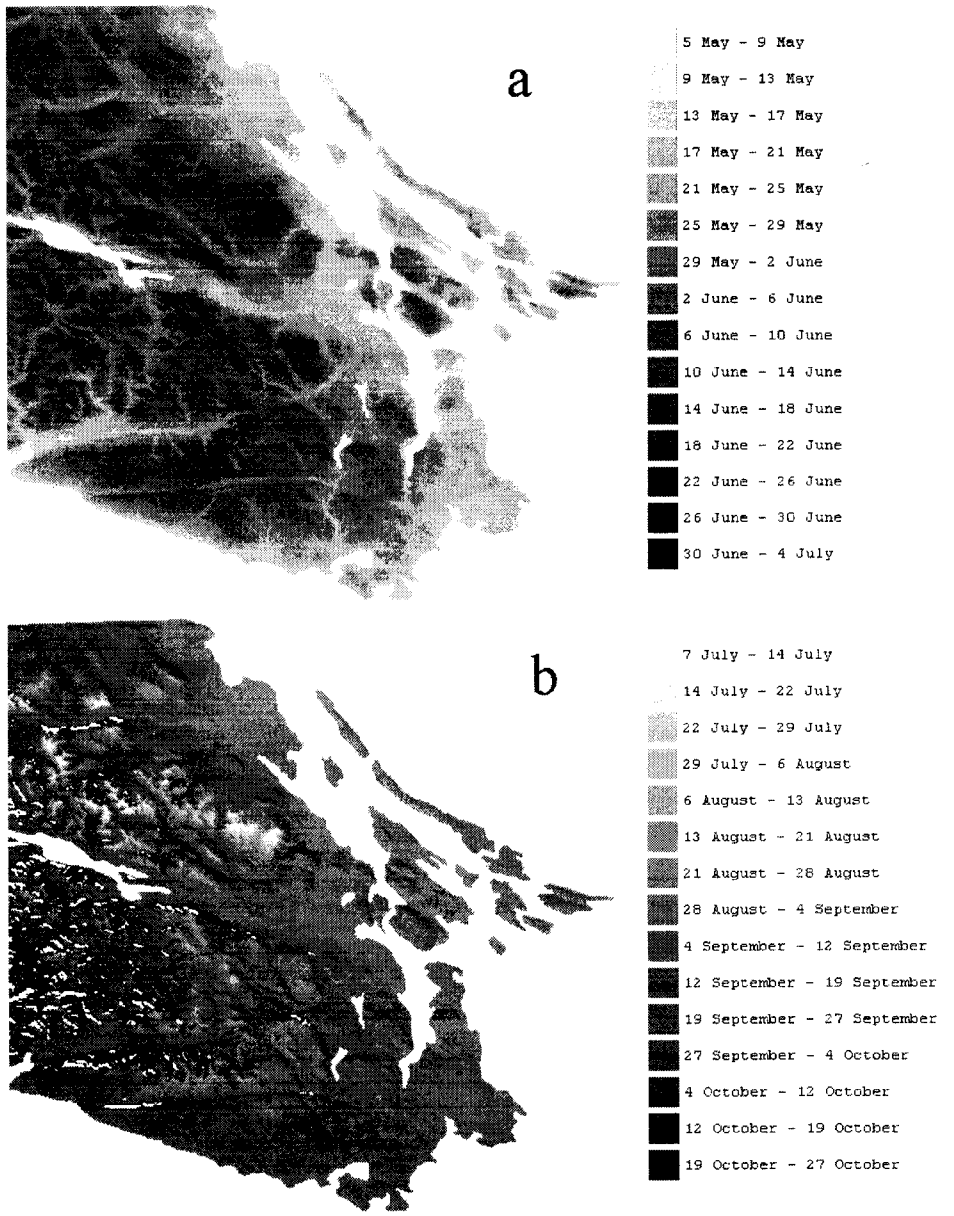

Figure 4. Maps of the predicted dates of peak frequency of (a) first instars and (b) male moths on southern Vancouver Island, based on climatic normals. Maps prepared with the BioSIM system. Egg hatch simulated using Gray's model.

Gypsy moths survived the 1998-1999 winter very well on southern Vancouver Island. The relatively mild coastal climate imposes no direct source of mortality during diapause unlike the cold winter climate in eastern Canada (Nealis et al. 1999). This climate, however, does influence the timing and distribution of critical life stages. The timing of egg hatch in the spring varies considerably over the region because of dominating maritime and topographical influences on air temperatures in the spring. This spatial heterogeneity is further modified during the summer months as a result of pronounced vertical thermal gradient inversions related to cooling near the cold ocean waters, especially in the Victoria

area. Development in low-lying areas near the sea is retarded, and the most pronounced influence of topography becomes exposure to sunshine (slope and aspect) rather than elevation. Annual weather patterns typical of Vancouver Island (relatively warm winters and relatively cool summers) can lead to a seasonal biology in which oviposition is so late that egg hatch the following spring is delayed. This further retards oviposition to the point where the population is eventually unable to maintain a viable seasonality and cannot persist.

The use of this model for decision support by pest managers has already been tested, in part. In British Columbia, recommended timing of aerial applications of *Btk* in 1999 was established from output of the composite model. The spray window was opened when the population was predicted to be mostly in the first or early second larval stages and was closed as the population approached the end of the third larval stage. Within the spray window, the three applications of *Btk* were timed individually based on daily updates of the simulations rather than on an arbitrary 10-day schedule as had been the practice in the past. Pest managers also used the forecast of moth activity to deploy and recover over 5,000 pheromone traps for timely reporting of results bearing on evaluation of the eradication program and planning the future course of action.

Acknowledgments

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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.

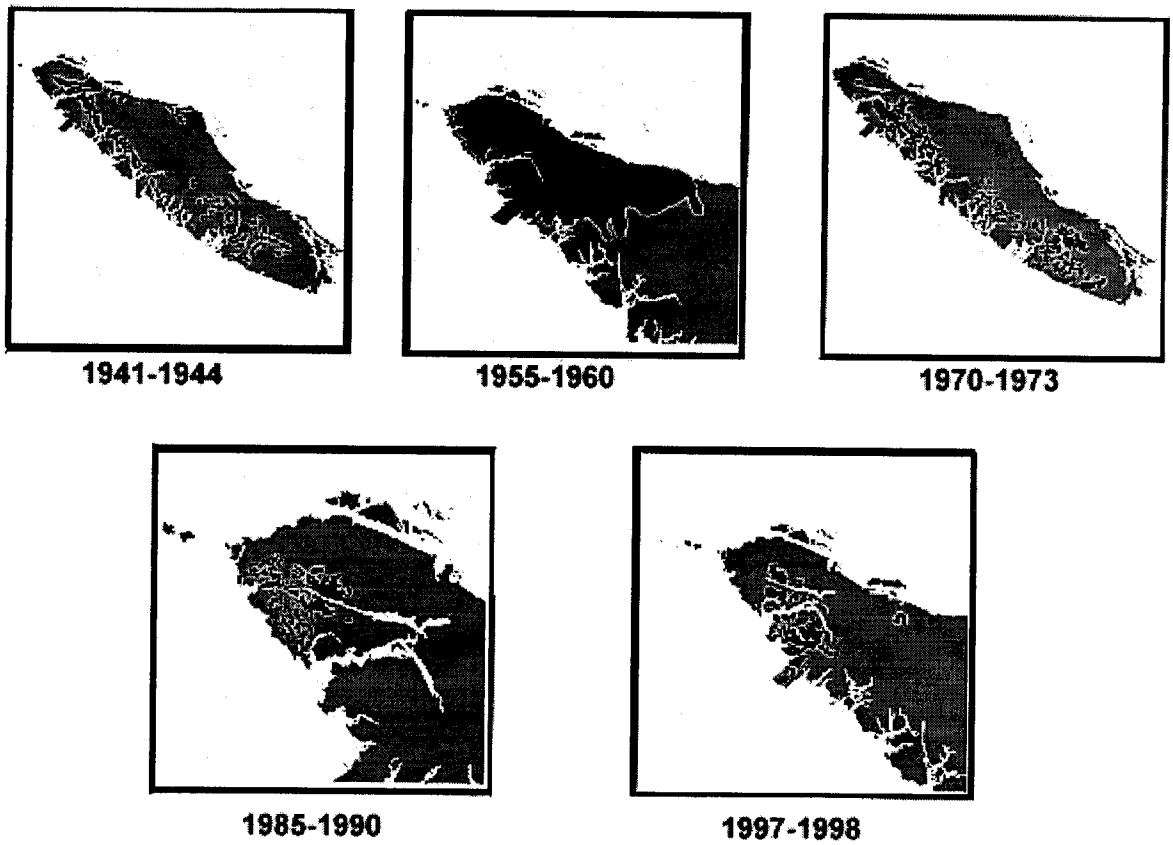

Figure 1. Outbreaks of the western blackheaded budworm on Vancouver Island (1941 to 1998).

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.

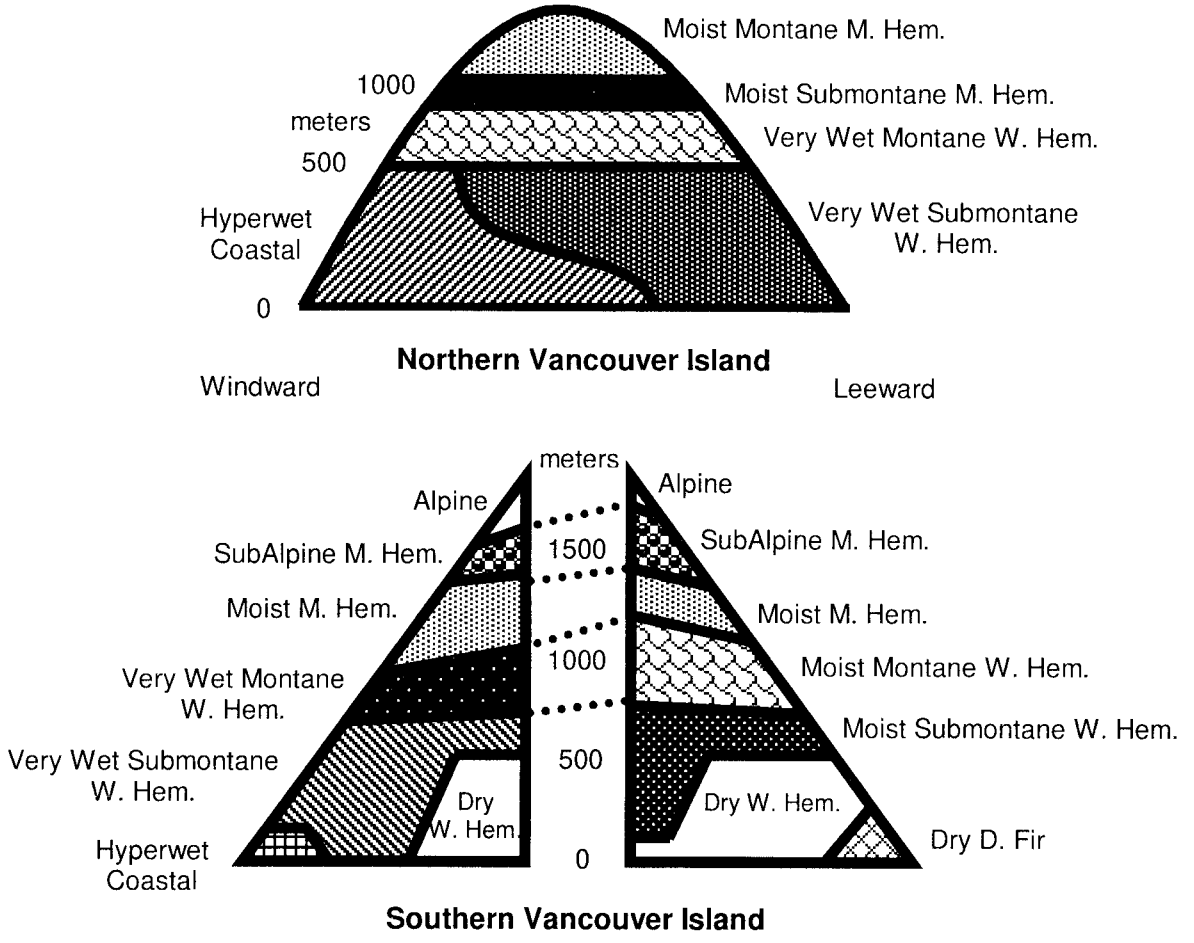

Figure 2. Elevation and distribution of biogeoclimatic units on Vancouver Island.

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).

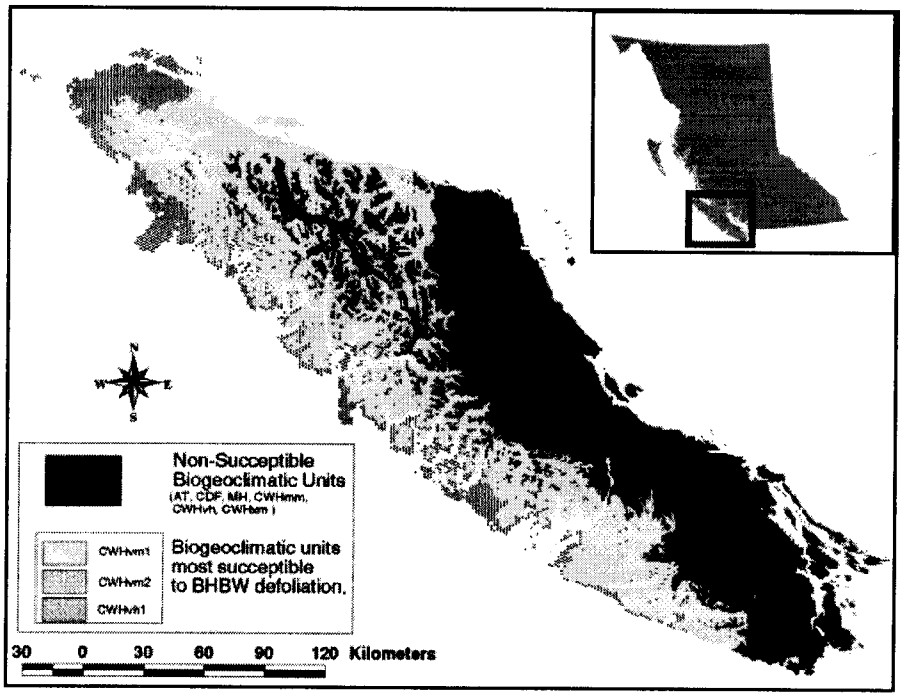

Figure 3. Biogeoclimatic units most susceptible to western blackheaded budworm outbreak on Vancouver Island.

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).

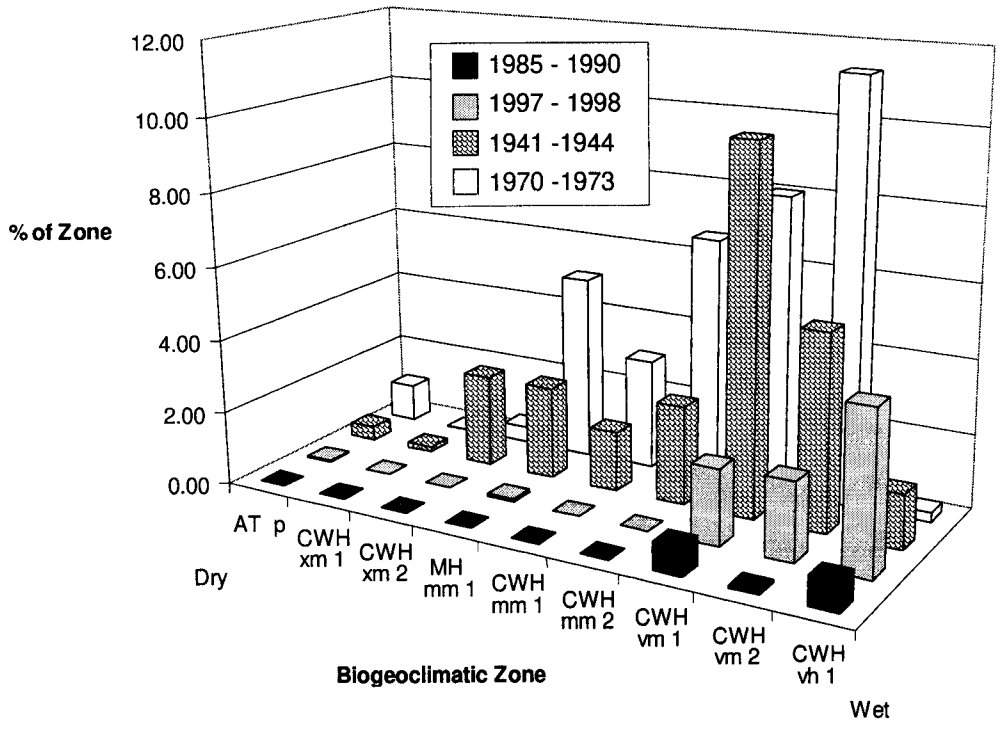

Figure 4. Comparison of the proportion of biogeoclimatic units defoliated by the western blackheaded budworm in four separate Vancouver Island outbreaks.

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

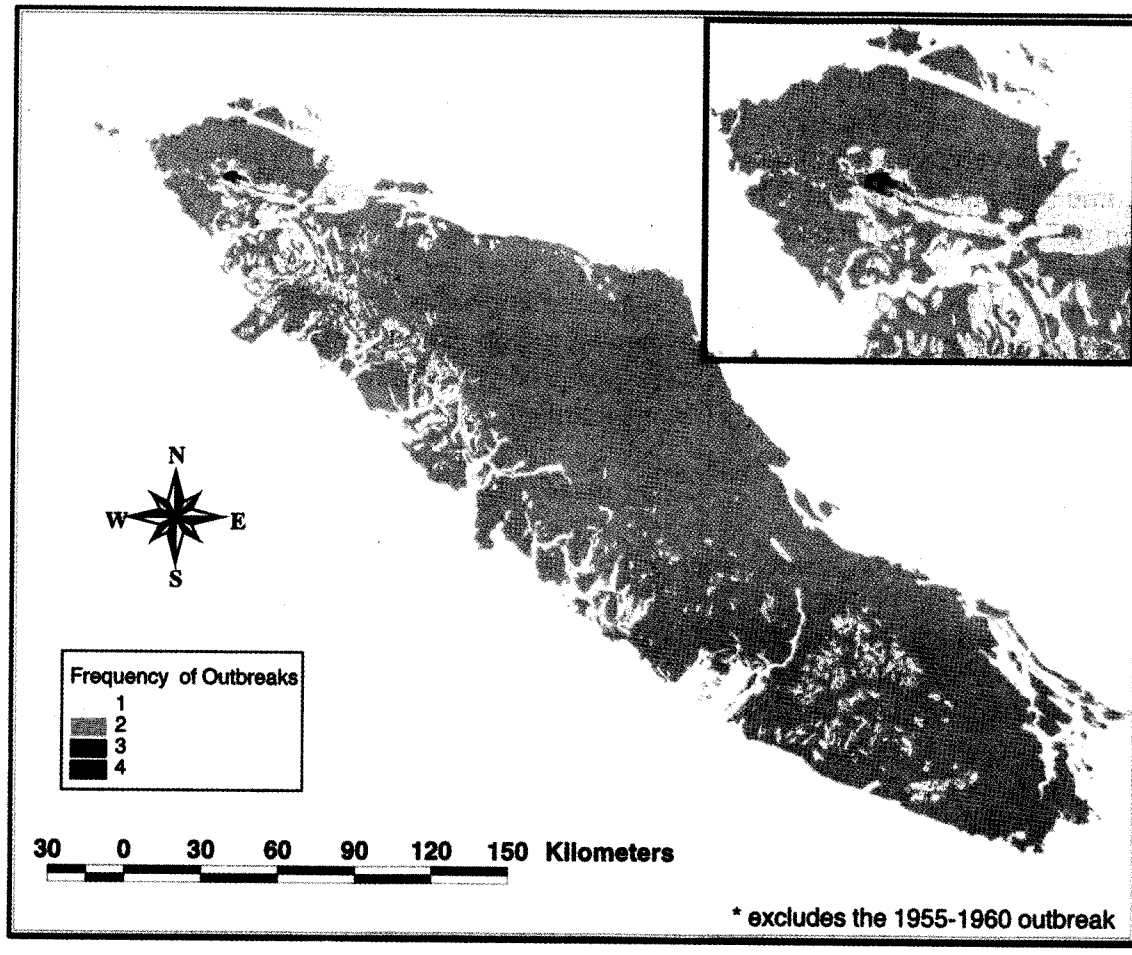

Figure 5. Outbreak frequency of the western blackheaded budworm on Vancouver Island (1941 to 1998*).

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.

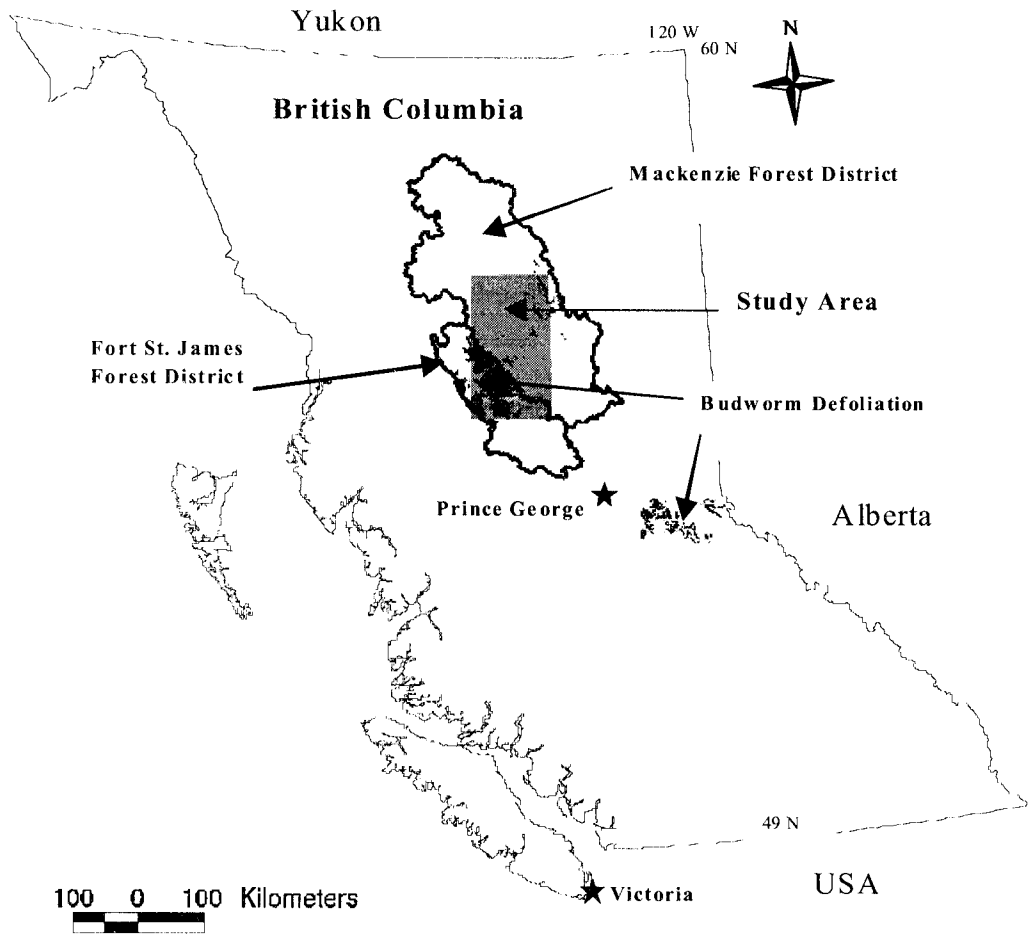

Figure 1. Location of the study area and two-year cycle budworm defoliation in British Columbia.

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).

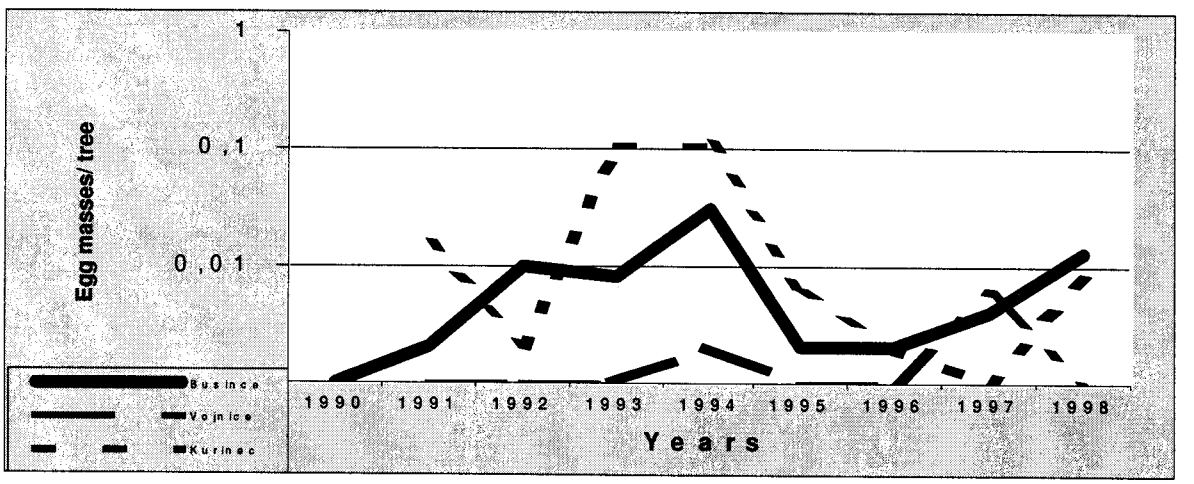

Figure 1. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Businces, Vojnice, and Kurinec plots.

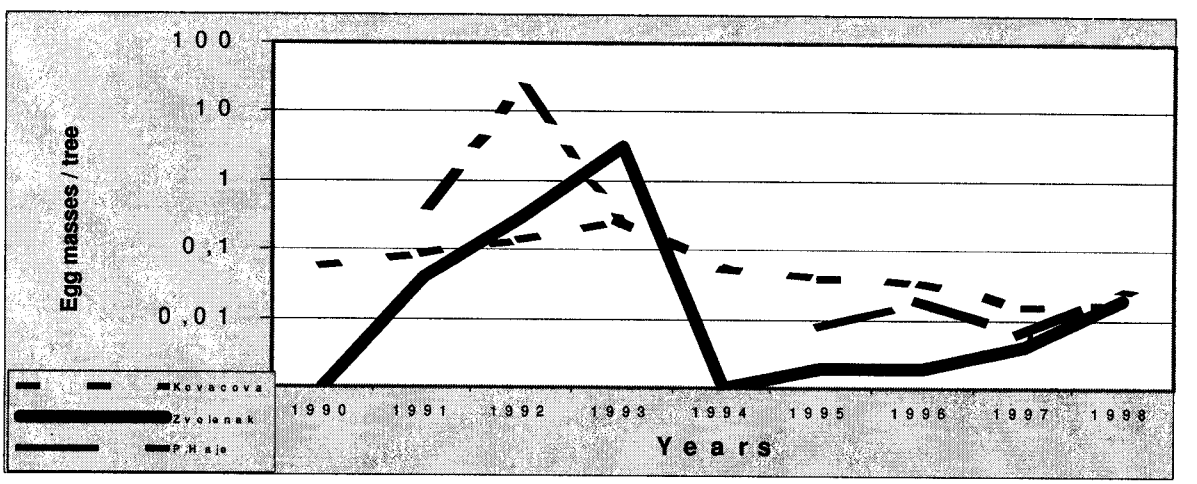

Figure 2. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Kovacova, Zvolenak, and Parovske Haje plots.

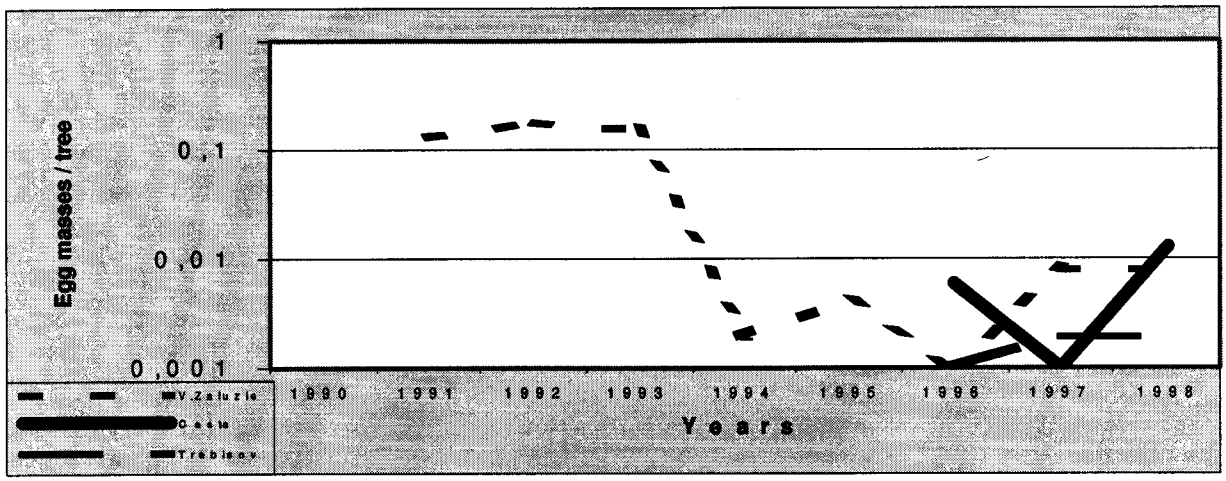

Figure 3. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Velke Zaluzie, Casta, and Trebisov plots.

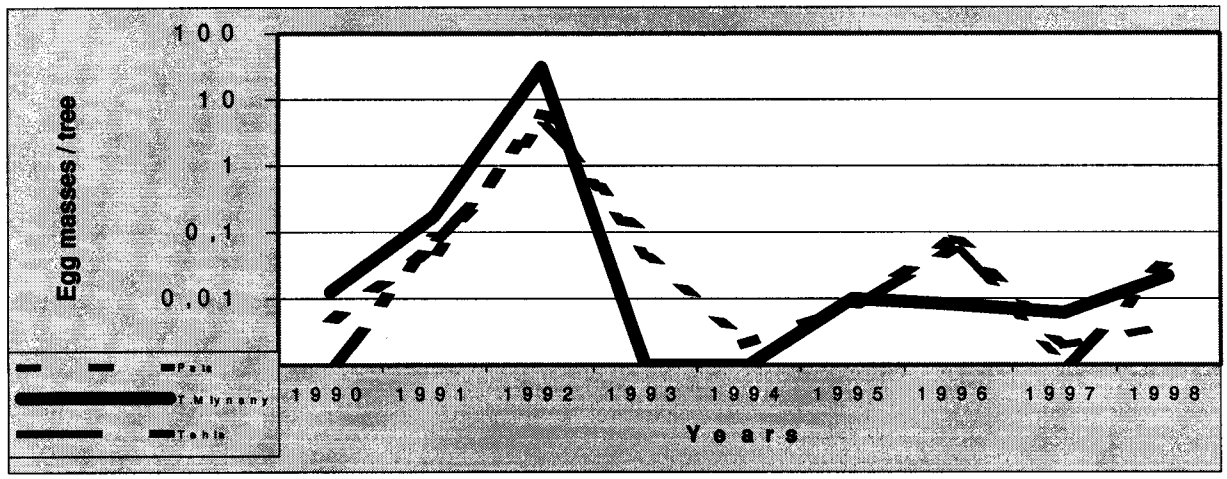

Figure 4. Gypsy moth population density (egg masses/tree) from 1990 to 1998 in the Pata, Tesarske Mlynany, and Tehla plots.

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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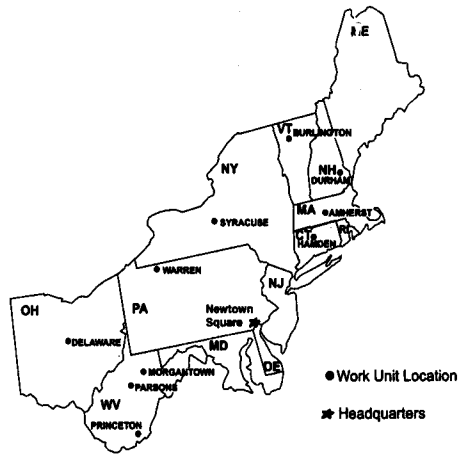
This publication contains 18 research papers about the population ecology and management of forest insect defoliators. These papers were presented at a joint meeting of working parties S7.03.06, "Integrated Management of Forest Defoliating Insects," and S7.03.07, "Population Dynamics of Forest Insects," of the International Union of Forestry Research Organizations (IUFRO). The meeting was held August 15-19, 1999, in Victoria, British Columbia, Canada.

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



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