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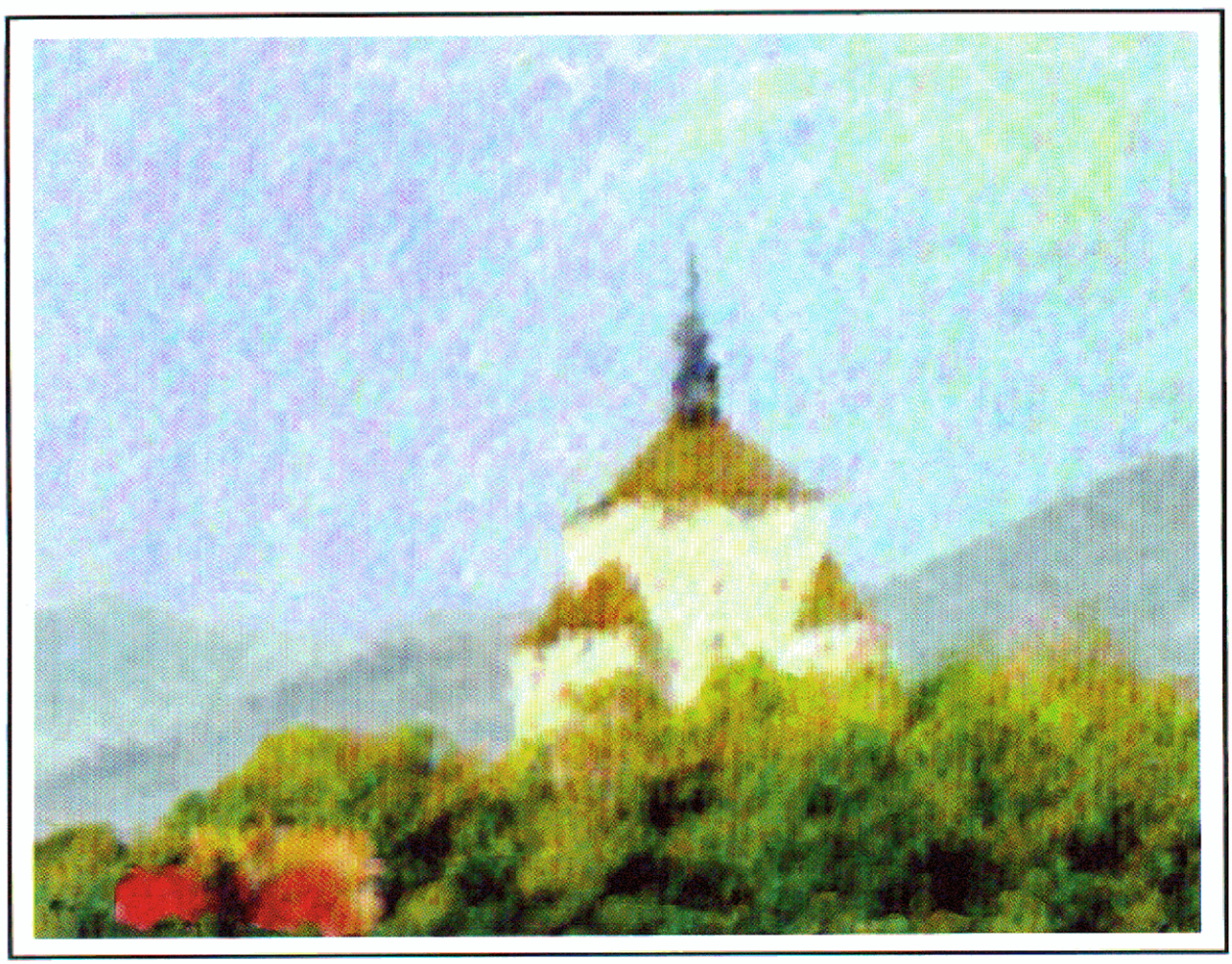
Proceedings

Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects

Edited by:

M.L. McManus
A.M. Liebhold

Banská Štiavnica, Slovak Republic
August 18-23, 1996



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Edited by:

M.L. McManus
USDA Forest Service, Northeastern Research Station, 51 Mill Pond Rd., Hamden, CT 06514-1703, USA

A.M. Liebhold
USDA Forest Service, Northeastern Research Station, 180 Canfield St. Morgantown, WV 26505, USA

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PREFACE

These proceedings result from a conference held at the Forestry School Hostel, Banská Štiavnica, Slovak Republic, on August 18-23, 1996. The meeting, held under the guidelines of the International Union of Forestry Research Organizations, was sponsored by two IUFRO Working Parties: S7.03-06 (Integrated Management of Forest Defoliating Insects) and S7.03.07 (Population Dynamics of Forest Insects).

It was the intent of the organizers to enhance the participation and involvement by scientists from central and eastern European countries who had been under-represented historically at many IUFRO Working Party meetings. This conference was attended by more than 80 scientist from 21 countries, indicating that we were extremely successful in enhancing the IUFRO goal of promoting international cooperation in forestry by providing a forum for the exchange of knowledge and experience in a broad field of forestry research. The enthusiasm and fellowship that was generated by all participants at this conference will long be remembered.

Acknowledgements

The editors wish to express their gratitude to Julius Novotný, who took primary responsibility for local arrangements, housing, field trips, and entertainment. Dr. Novotný, his staff, and the staff of the Forestry School Hostel put considerable effort into planning this meeting and their contributions made this conference a valuable and memorable experience for all participants.

We also are grateful to the IUFRO Special Program for Developing Countries (SPDC) for providing travel funds to several of the participants, and to Abbott Laboratories for their financial support of this conference.

We also thank Cyanamid Slovensko, Uniroyal Chemical Slovensko, Agrolinz Slovensko, and Zeneca Slovakia for their sponsorship of the conference.

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IUFRO and the Entomology Research Group, a Success Story

H. SCHMUTZENHOFER

IUFRO, Seckendorff-Gudent-Weg 8, 1131 Vienna, Austria

ABSTRACT The development of forest entomology in the International Union of Forest Research Organizations (IUFRO) is outlined in detail. The research subject was incorporated into IUFRO as early as 1929. After World War II, entomology research was dealt with in two Working Groups in what was then Section 24. In 1971, a reorganization of IUFRO was adopted and entomology found a home mainly within the Subject Group S2.07 in Division 2. During the following period of 25 years, the Subject Group contained up to 11 Working Parties covering major topics of entomological research. A restructuring in 1995 placed entomology into the newly established Division number 7 as Research Group 03, which currently incorporates nine Working Parties. The names of units and officers throughout this period of development are provided.

FOREST ENTOMOLOGY HAS a long tradition in IUFRO. The topic was placed on an agenda for the first time at the Congress held in Stockholm, Sweden, in 1929. A special working unit was established and was active at the Congress and during the period that followed.

After World War II, forest entomology and forest protection became increasingly important. As a consequence of vast clearcuttings and periods of drought, serious outbreaks of harmful insects threatened the forests and the economies that were still weak and just beginning to recover. Forest protection and forest entomology were, of course, called upon to offer remedies and an immediate and complete control of such pests through the use of modern pesticides.

The structure of IUFRO at that time was such that it was subdivided into so-called Sections. Entomology was placed in Section 24 - Forest Protection. The subjects of research included: damage to the forest caused by viruses, fungi, insects, and other animals, anthropogenic and inorganic influences, and prevention and control.

In Section 24, there were six active Working Groups, two of which were entomological in nature. There was the Working Group on International Cooperation in Forest Insect Research, which was chaired by Ron Stark of the United States. He was the driving force behind worldwide cooperation among scientists and the mentor of a spirit that continued to prevail later in the Subject Group (SG) "Entomology". The second was the Working Group on Population Dynamics. This was chaired by G.C. Varley of the United Kingdom, and its secretary, W. Baltensweiler of Switzerland, later became one of the most prominent people in the Subject Group.

At the IUFRO World Congress held in 1971 in Gainesville, Florida, under President Jemison, IUFRO was completely restructured. The sections dealing with five major subjects were abolished and six Divisions were established. Entomology became a Subject Group within Division 2, Forest Plants and Forest Protection, and was given the structural number S2.07-00. This subject group eventually contained a total of 11 Working Parties, the last

Pages 1-6 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

being S2.07-11, Integrated Management of Defoliating Insects, with M. McManus of the United States as Coordinator.

Development After the Reorganization of 1971

1972 - 1976. In 1972, the new structure of IUFRO was in force and the Subject Group Entomology, S2.07-00, had Ron Stark as Subject Group Leader (SL). His Deputy was H. Pschorn-Walcher of Austria, who was working at that time for the CCBC in Delemont, Switzerland. Six Working Parties were initiated during the period leading up to the 1976 IUFRO World Congress in Oslo:

S2.07-01, Cone and Seed Insects, A. Bakke (Norway) and A. Hedlin (Canada) as co-chairs
S2.07-02, Integrated Control of *Hypsipyla* Species, R. Gara (United States) and P. Grijpma (Netherlands)
S2.07-03, Integrated Control of *Hylobius* spp., H.H. Eidmann (Switzerland) and H.A. Thomas (United States) later replaced by J. Nord (United States)
S2.07-04, Integrated Control of *Thaumatopoea* spp., J. Halparin (Israel)
S2.07-05, Integrated Control of *Dendroctonus* spp., W. Cole (United States) and J.P. Vité (Germany)
S2.07-06, Population Dynamics of Forest Insects, G. Varley (United Kingdom) and W. Baltensweiler (Switzerland)

The most noteworthy accomplishments during that time were from S2.07-02, the *Hypsipyla* meeting in Turrialba, Costa Rica, and in April 1975, the Second FAO/IUFRO World Consultation on Forest Diseases and Insects in New Delhi, India, where many Division 2 representatives made significant contributions. Unfortunately, the *Thaumatopoea* group did not succeed and was cancelled after a brief revival in 1978.

The 16th IUFRO World Congress in Oslo was also a major highlight of that period; A. Isaev (Soviet Union) won a Scientific Achievement Award, interesting papers were presented, long lasting friendships were established, and the Subject Group was enlarged.

1977 - 1981. S2.07-07, Pine Insects in the Tropics, co-chaired by H. Schmutzenhofer (Switzerland) and A. Yamane (Japan), joined the already existing six units. Important and interesting changes in offices also took place. New Deputies were designated in the Subject Group: A. Bakke (Norway) and F. Kobayashi (Japan).

- 01, H.O. Yates III (United States) was named Chairman and D. Singh (Malaysia) became co-chair
- 02, G. Budovsky (Czechoslovakia) was designated as the new co-chair
- 05, L. Safranyk (Canada) was named chair and P. Carle (France) became co-chair
- 06, A.A. Berryman (United States) was designated new chair

As far as activities were concerned, all working units organized meetings during the inter-congress period, and some units held several meetings! The Cone and Seed Insect Group (01) became very active and developed a very individual life, while the mainly "cooperating groups" 05 and 06, the bark beetle and the population dynamic units, celebrated meetings in Zuoz, Switzerland (1978), in Sandpoint, Idaho (1979), in Dornoch, Scotland (1980), and in Irkutsk, Siberia (1981). Many stories and memories were generated from these meetings. There were many outstanding publications - the proceedings enriched the quality of the Grey Literature that still exists as the standard literature in Forest Entomology.

China became involved in IUFRO for the first time at the World Congress in Kyoto, Japan (1982), and Chinese Entomology provided us with many interesting contributions. Participants still remember the Pine sawyer, *Monochamus* sp. -Nematode story, and many of us will not forget the farewell party of the Entomology SG, and our Japanese hosts, the Forest Entomologists Association of Japan.

1982 - 1986. S2.07-08, Forest Gall Midges, Je Ho Ko (Korea), chair, and D.M. Benjamin (United States), as co-chairs, entered the SG; meanwhile, S2.07-02 and 04 were cancelled. Notable changes in offices occurred again as officers relinquished their duties after holding office for two periods. The change of units' names and similar "tricks" sometimes helped to avoid the loss of IUFRO-activists and therefore some officers managed to come in again "by the back door" to extend their participation.

New Officers:

- 00: Baltensweiler as Leader with Isaev (Soviet Union), Kobayashi (Japan), and McFadden (United States) as deputies
- 01: A. Roques (France) joined as a co-chair
- 03: Insects Affecting Reforestation, a new name for the unit, H.H. Eidmann (Switzerland) in the chair and J. McLean (Canada) joined as co-chair
- 05: A. Bakke (Norway) reintegrated himself as a co-chair
- 06: J. Stoakley (United Kingdom) became co-chair
- 07: Y. Katerere (Zimbabwe), J. Selander (Finland), and R. Stark (United States) joined me as co-chairmen.

During this period, some extra effort was needed to schedule productive meetings. The first business meeting of the SG was scheduled for 1983 in Banff, Alberta, Canada. Our twin working units S2.07-05 and 06, the bark beetle and population dynamics groups, held their next traditional meeting there. The Cone and Seed Insect Group (01) met in Athens, Georgia, that same year. In 1984, this group also participated in the Spruce Budworm Symposium, the joint meeting with CANUSA, at Bangor, Maine, USA, which was an all Subject Group meeting; the gall midges unit (08) also participated at this meeting.

All units held meetings during this period. S2.07-05 and 06 met in Göttingen, with Bombosch (Germany) as the host. Unit 03 met in Sweden, 07 in Curitiba, Brazil, and 08 in Korea. Most of the working units participated in the Ljubljana Congress, 1986, in addition to the programme of the Subject Group.

1987 - 1990. S2.07-09, Diseases and Insects in Nurseries, J.R. Sutherland (Canada) and B. Brown (Australia)

S2.07-10, Forest Protection in Northeast Asia, K. Kanamitsu (Japan), Y.J. La (Korea), M.J. Lee, G.R. Xiao (China). The WP was established in 1989.

Changes in other working units also occurred:

- 00: McFadden (United States) leader, and deputies Isaev (Soviet Union), J.Schoenherr (Germany), and Yo Tho Pong (Malaysia)
- 01: A. Roques (France) leader and G. DeBarr (United States) co-chair
- 03: R.J. Alfaro (Canada), chair and B. Langström (Sweden) co-chair
- 05: T.L. Payne (United States) chair and H. Saarenmaa (Finland), co-chair
- 06: F. Hain (United States), chair, and P. Grijpma (Netherlands), then N. Mills (United Kingdom), as co-chair

- 07: name change: Protection of Forests in the Tropics, Schmutzenhofer (Austria) initially and later K.S.S. Nair (India) as chair persons and deputies, Ch. Hutacharern (Thailand), M.O.Akanbi (Nigeria), and J.H. Pedrosa Macedo (Brazil) as co-chairs
- 08: Y.N. Baranchikov (Soviet Union) succeeded the late J.H. Ko as chairperson

There were many achievements during this period, including contributions to meetings and papers at the World Entomology Congress in Vancouver. Again, all working units had successful meetings. Significant proceedings were published as a result of the Lymantriid conference held in New Haven, Connecticut, USA, in 1988, and from the meetings in Abakan, Siberia, in August 1989. A stimulating session titled, "Does Chaos Exist in Ecological Systems?", was held at the 19th IUFRO World Congress, Montreal, Canada, in 1990.

At the SG business meeting in Montreal, a discussion ensued on the need for a Working Party devoted to problems with defoliating insects; however, an agreement for the establishment of a new Working Party was not realized.

Forest Entomology in IUFRO in the Nineties

3.1 - 1991 - 1995. The latest amendment to the Subject Group was in 1992 when unit number 11 was added. S2.07-11, Integrated Management of Forest Defoliating Insects; M. McManus (United States) became chairperson, and B. Glowacka (Poland) and A. Yamane (Japan) (his second working party chair) serve as co-chairs.

Several rather significant changes in officers occurred during this time.

- 00: Y. Baranchikov (Soviet Union) and later K.S.S. Nair (India) and Yo Tho Pong became Deputy Leaders; however, Yo Tho Pong, a SAA winner, died during this period.
-01: G. DeBarr replaced A. Roques (France) and M. Skrzypczynska (Poland) became co-chair
-06: H. Bogenschütz (Germany) replaced N. Mills (United States) as co-chair
-07: Pedrosa Macedo (Brazil) resigned as co-chair

Activities in Forest Entomology also occurred outside of SG S2-07.

W. Mattson (United States), S2.05-00, Genetic Resistance to Insects and Diseases, tried to re-introduce insect related Working Parties, and thus, reorganization took place and the following new units were created:

S2.05-00, Physiology and Genetics of Tree/Phytophage Interactions, new name
S2.05-08, Resistance to Insects, chair vacant, co-chair P. Niemela (Finland)
S2.05-10, Phytophage Adaptations to Plant Resistance Mechanisms. A reactivation also took place.
S2.06.08, World Directory of Forest Pathologists and Entomologists, D. Skilling (United States)

Finally, a reorganization of Division 2 was planned and put into place by IUFRO's IC at the recent Congress in Tampere, Finland, 1995. Since January 1996, a new structure exists.

Important meetings and activities that occurred during this period include the following:

06: Zakopane, Poland, 1991
05/06: Maui, Hawaii, 1994
IUFRO World Congress, Tampere, Finland, 1995
Entomology World Congress, Beijing, China, 1992

3.2 - 1996: New Structure in Force. General changes have been introduced. The designations for Subject Groups (SG) and Project Groups (PG) have been eliminated and replaced by the term Research Group. Research groups, of course, continue to be subdivided into Working Parties. Entomology was placed into the newly designated Division 7, Forest Health, which contains four Research Groups.

The numbering system has been changed, and the many titles have been reduced. We now have only a Coordinator (C) and Deputy Coordinators (DC) to oversee all structural units, and have eliminated the former titles of Leader, Deputy Leader, Chair, and Co-chair. There are four main topic areas under the newly created Division 7, Forest Health:

7.01.00 - Physiology and Genetics of Tree/Phytophage Interactions, W. Mattson (United States), Coordinator, and F. Kieutier (France), Deputy coordinator

7.02.00 - Pathology, C. Tomiczek (Austria), Coordinator, K. Rykowski (Poland) and J. Sutherland (Canada), Deputy coordinators

7.03.00 - Entomology, R. Alfaro (Canada), Coordinator, Y. Baranchikov (Russian Federation) and K.S.S. Nair (India), Deputy coordinators

7.04.00 - Impacts of Air Pollution on Forest Ecosystems, M. Tesche (Germany), Coordinator, Y. Morikawa (Japan) and F. Scholz (Germany), Deputy coordinators

There are nine Working Parties of interest within the topic of entomology (7.03.00), which are listed numerically:

7.03.01 - Cone and Seed Insects, G. DeBarr (United States), Coordinator, and M. Skrzypczynska (Poland), J. Turgeon (Canada) and S.K. Yue (China), Deputy coordinators

7.03.02 - Gall-forming Insects, H. Roininen (Finland), Coordinator

7.03.03 - Insects Affecting Reforestation, K. Day (United Kingdom), Coordinator, and S.M. Salom (United States), Deputy coordinator

7.03.04 - Diseases and Insects in Forest Nurseries, R. Perrin (France), Coordinator

7.03.05 - Integrated Control of Scolytid Bark Beetles, J.C. Gregoire (Belgium), Coordinator, and F.M. Stephen (United States), Deputy coordinator

7.03.06 - Integrated Management of Forest Defoliating Insects, M. McManus (United States), Coordinator, and B. Glowacka (Poland) and N. Kamata (Japan), Deputy coordinators

7.03.07 - Population Dynamics of Forest Insects, A. Liebhold (United States), Coordinator, and H.F. Evans (United Kingdom), Deputy coordinator

7.03.08 - Forest Protection in Northeast Asia, K. Furuta (Japan), Coordinator, and Chang Jie Chen (China), Ming Jen Lee (China-Taipei), and Chang Keun Yi (Korea), Deputy coordinators

7.03.09 - Protection of Forests in the Tropics, Ch. Hutacharern (Thailand), Coordinator, and Marguedas Gamboa (Costa Rica), J.R. Cobbinah (Ghana), and V.V. Sudheendrakumar (India), Deputy coordinators

We all hope that the working units will develop excellently and that the spirit of support and cooperation will emerge again to facilitate successful work within and between the units, and among our representative duty stations. We also hope that funding will be adequate so that we can continue to plan and organize Working Party meetings that are so vital to our organization. To enhance communication, the IUFRO Executive Board has created a "Net" Task Force to develop expanded access to the World Wide Web. You can find IUFRO on the Internet under URL>**http://IUFRO.boku.ac.at** where you can find

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Oak Decline in Central Europe: A Synopsis of Hypotheses

ERWIN FÜHRER

Institute of Forest Entomology, Forest Pathology & Forest Protection, University of Agricultural Sciences, Vienna Hasenauerstrasse 38, A-1190 Wien, Austria

ABSTRACT A brief overview is provided about the occurrence of oak decline in Central Europe during the past three decades, its development in space and time, the tree species affected, and the symptoms that have been recorded in different countries. Emphasis is placed on the critical discussion of several concepts and hypotheses about 'forest decline' in general and on 'oak decline' in particular, and on the importance of insects and fungi in the decline process. Excessive impairment of the water balance and metabolic disorders in oaks, attributed to climatic extremes, anthropogenic site deterioration, insect defoliation, and fungal infection, is frequently overcome by the trees, or results in mortality. The latter occurs either due to the impact of xylophagous insects and root pathogens, or by the physiological collapse of the tree. Despite the simplicity of this common scheme, the pathological processes involve numerous variations due to local site conditions and the locally involved stressors. Thus, 'oak decline' is considered a complex of different diseases, their ecosystem complexity requires better understanding.

A FEW OAK species (*Quercus robur, Q. petraea, and Q. cerris)*, being significant components of natural hardwood forests in Central European lowlands, represent an economically important basis of forestry in certain parts of Europe. In the past two decades, oak forests have been affected seriously by decline phenomena over wide areas of Central Europe. Foresters are extremely worried about the situation and seek predictive explanations from scientists who, in turn, are making efforts to understand the decline phenomena and their causes. However, the so-called oak decline turned out to be rich of facets. Therefore, scientific investigations resulted in distinct and diverging causal hypotheses, resulting in a confusing picture about the origin of pathologies observed in oak forests.

The general discussion of oak decline cannot be separated from the broader issue of forest decline and environmental perturbations such as air pollution and climate change. Additionally, pests and diseases appear to be involved in the dieback of oaks, though their importance in the causal chain is not thoroughly understood. However, as members of the ecosystem their impact on the health of oaks would also be influenced by the impact of external physical and chemical factors.

From the beginning, some questions stood in the forefront: Is the oak decline observed a novel phenomenon, or does it, at least, contain new pathogenic components? Can the oak decline syndrome in Central Europe be defined as a causally homogenous pathology? Can forest management be used to overcome the impact of oak decline and, if so, which techniques are most promising? Answers to these questions can be provided only after the pathological processes, which lead to disease symptoms and dieback, are sufficiently understood. A synoptic view of oak decline in Europe may be found in publications by Führer (1987), Hämmerli and Stadler (1989), Luisi et al. (1993), and Wulf and Kehr (1996).

Pages 7-24 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

In addition, Schlag (1994) discusses oak decline from a phytopathological point of view. In this paper I have tried to summarize the essential facts and theories about oak decline and to elucidate the contributions of insects to this phenomena.

Oak Decline in Space and Time

Oak forests in eastern Europe were affected several times during the 20th century by regional episodes of dieback (Marcu 1966). In the most recent period of the phenomenon, the first reports originated from the same region: 1967 in western Russia, 1971 in Romania. The affected area spread to central and western Europe during the second half of the seventies and early eighties, when first observations were reported from most adjacent countries (Hämmerli and Stadler 1989). The temporal sequence of reports about oak decline suggests a geographic extension from the continental over the sub-Mediterranean zone to the zone of maritime climate. On the British Isles, oak decline was first reported in 1989 (Fig. 1). Igmandy (1987) reported that the decline of *Q. petraea* in Hungary began in 1978 in the colline northeast and extended within three years to the west of the country, finally reaching the eastern regions of Austria in 1984. This pattern of spread somehow resembled that of epidemic diseases and suggested that pathogenic agents could be involved in the phenomenon of oak decline.

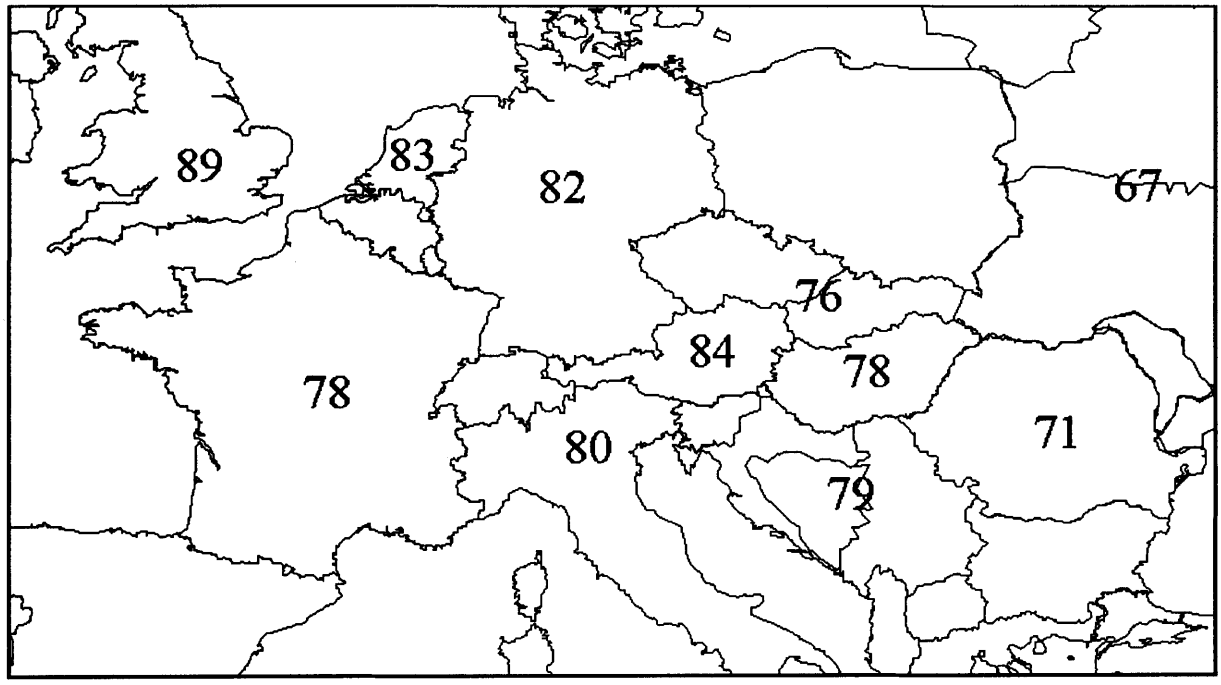


Figure 1. Years when recent oak decline phenomena were first recorded in individual European countries (Hämmerli and Stadler 1989).

It is noteworthy that since the beginning of the recent period of oak decline (Fig. 1), oak forests in most countries have not fully recovered. Although extensive tree mortality was limited to rather small areas, the condition of oak forests has not yet stabilized. In the countries of Central Europe, where oak forests play a major role in forestry, the impact of

decline is considered even worse than that which occurs in coniferous forests (Rösel and Reuther 1995, Wulf and Kehr 1996). This conclusion is drawn from the results of crown transparency assessments, which revealed a continuous deterioration in oak, in contrast to conifer species, which demonstrated a recovery at least regionally (Huber 1992, 1994). It must be mentioned, however, that conifer forests (*Picea abies, Pinus silvestris)* in certain parts of Central Europe have been fatally affected by 'conventional' agents, i.e., windthrow and epidemics of well-known pest species such as bark beetles and defoliators (Führer 1996, Majunke et al. 1996, Wulf and Berendes 1996). Unfortunately, it appears that such facts are not clearly reflected by the forest health assessment procedures that are commonly utilized.

Tree Species Affected

Due to their dominant representation in Central European hardwood forests, *Quercus robur* and *Q. petraea* are the species most affected by the decline syndrome. These same species are reported to have suffered from dieback during former periods of oak decline in southeastern Europe (Marcu 1966). Leontovyc and Capek (1987) listed nine oak species indigenous to Slovakia, based on their relative susceptibility to the syndrome of decline. *Quercus robur, Q. petraea* along with *Q. polycarpa* and *Q. dalechampii* were ranked among the susceptible species. However, one must question the specificity of the indicators of susceptibility and the definition of the stress impact such that a comparison could be made among the different oak species.

When analyzing the causative mechanisms involving in the oak decline syndrome, the tree species concerned must be considered individually. Because of their ecophysiological specificity, each species is subjected to specific ecological limitations. This is expressed in the diverging distributional patterns and eco-geographical ranges of the individual oak species. *Quercus robur*, for example, is more susceptible to drought but less susceptible to winter cold than is *Q. petraea.* Therefore, *Q. robur* prefers humid soils in warm lowland sites and is widely distributed to the continental East, while *Q. petraea* prefers drier colline sites, but is not common in regions that experience severe winters (Mayer 1977). Thus, it is not surprising that, when both species are present in a region, 'oak decline' often affects only one or the other species (Landmann 1992, Ackermann and Hartmann 1992). Careful consideration of the ecophysiological specificity of individual tree species is a first important step towards gaining a better understanding of the oak decline phenomenon.

In contrast to the decline phenomenon in conifers, where the severity of symptoms usually is related to the advanced age of the trees, the syndrome in oaks has been recorded from all age classes, thus de-emphasizing the age-related trend of disease. This characteristic of oak decline is especially discouraging to foresters because it negates a potential solution to the problem, which would be to reduce the rotation period. From the pathologist's perspective, the age-independent sensitivity of oaks could indicate either that conifers differ significantly in their pathophysiological responses, or that different causal factors are involved in oak and conifer decline phenomena. Innes (1993), after considering this and other peculiarities of the patterns of the oak decline syndrome suggests that basic differences exist between conifer and oak decline in Europe.

Symptomatology in Oak Decline

The list of symptoms reported in the literature in connection with oak decline is long and complex. Macrosymptoms include: crown transparency, yellowing, excessive twig abscission, dieback of branches and the whole crown, epicormic sprouts on branches and trunk. Less obvious are the following symptoms: undersized leaves, reduced shoot length, necrotic or dead foliage, dead twigs and buds, anomalous ramification, bark fissures and necroses, slime flux, reduced radial increment, sapwood discoloration, root necroses, damaged mychorrhiza, fungus infections in different organs, several kinds of insect infestation, nutrient imbalances, biochemical stress indications, etc.

Despite this long list, only a few selected symptoms are usually visible in individual cases, and these may differ from one site to another or from time to time, suggesting that different types of diseases may be involved. Most of the individual symptoms can be interpreted as being inter-connected, and may reflect sequential phases of physiological decline or recovery. They are, in part, unspecific manifestations of physiological stress acting upon the trees, or they may be directly or indirectly related to the impact of specific pest organisms. But uncertainty still remains about the origin of some of the symptoms. This is particularly the case concerning the allocation of individual symptoms to distinct positions in the causative chain of stressing influences: what is a primary effect, and what is secondary? This question also is relevant to our understanding of the causes of tree mortality.

Tree mortality is not a common feature of oak decline in Central Europe and information about mortality is incomplete because foresters usually cut the diseased trees before they die in order to prevent deterioration in timber quality. Hence, actual impacts on mortality may be greater than those recorded from monitoring sites. In controlled sites that were significantly affected by oak decline, tree mortality in peak years varied considerably: in Bavaria < 1% (Huber 1992, 1994), in Lower-Austria < 2% (Schopf and Mitterböck 1991), in Saxony ca 10% (Kontzog 1996), in Hungary > 22% (Igmandy 1987). These data are in contrast to the high rates of trees affected by oak decline, which frequently ranges from 70 to 90%. Thus, an apparently high proportion of affected trees recovers or at least survives in a weakened condition. The mortality of trees associated with the oak decline syndrome obviously depends on site specific conditions.

Hypotheses for the Causes of Oak Decline

Manion and Lachance (1992) edited a collection of essays that addressed concepts of forest decline. Although they did not directly focus on oak decline, their principles can be examined relative to their applicability to the oak decline syndrome in Central Europe. It can be demonstrated readily that most of the suggested concepts are partially appropriate to the phenomenon of oak decline, but none fully fit the diverse overall pattern of symptoms.

As a general assumption, the syndrome, although diverse in many details, is the result of synergies between sequentially or simultaneously acting influences on the trees. These influences can be classified as 'predisposing', 'contributing', and 'inciting' factors, respectively (Manion 1981). Careful examination is required to identify the real position of the individual influences in the causative constellation, however, and some factors could prove to be functionally unimportant.

A hypothesis for explanation of a *Q. petraea* dieback in Slovakia and Hungary was based on an epidemic concept analogous to the North American oak wilt disease (Leontovyc and Capek 1987, Igmandy 1987). A 'tracheomycosis', caused by fungi of the genus *Ceratocystis* and transmitted by insects (*Scolytus intricatus* Ratz., *Agrilus* spp. etc.), was considered to be the main causative factor responsible for tree mortality. This mechanism could neither be observed with European species of *Ceratocystis* in oak in other countries, nor did careful searches for a possible introduction of *C. fagacearum* reveal positive results. So far this 'epidemic concept' remained unconfirmed.

There is no clear evidence that air pollution is involved as the causative agent in oak decline. The role of air pollutants in the oak decline syndrome is frequently discussed. Excess nitrogen (agriculture-born ammonium) input and ozone impact is assumed to represent a risk potential causing predisposition for or synergism with natural stressors (Krapfenbauer 1987, Rösel and Reuther 1995, Hartmann 1996). Their relative significance in comparison with other stressors, though rated differently by different authors, is considered generally to be rather low.

Referring to the book of Manion and Lachance (1992), the 'cohort senescence theory' of Mueller-Dombois deserves consideration as a possible model to explain oak decline.

Several authors report that disease was more severe and mortality higher in trees that were over 60 years of age, however, they also emphasize that age classes below 60 years appear also to be affected (Wulf and Kehr 1969). This trend for predisposition of trees to be age- related can be regarded as a manifestation of senescence. Similarly, it has been suggested that coppice-derived trees suffer more from the syndrome than seedling-derived trees (Marcu 1987). This may correspond to the demographic aspect of predisposition and susceptibility as stated in the Mueller-Dombois theory, but it does not explain the anomaly of the present condition of oak forests.

Auclair et al. (1992) emphasize the importance of climatic perturbations in triggering forest dieback. Frost damage, which leads to xylem embolism, in combination with periods of drought, is regarded as the driving force leading to crown dieback in hardwoods. There is consensus among most European researchers that climatic factors are strongly involved in causing the oak decline syndrome. The occurrence of drought periods preceding the start of or enhancing the progress of the decline process is mentioned in many reports (Donaubauer 1987, Marcu 1987, Leontovyc and Capek 1987, Eisenhauer 1990, Gonschorrek 1995, Innes 1993). Extreme frost events that occurred after relatively warm winter periods were repeatedly recorded in the years preceding the manifestation of the oak decline syndrome, suggesting that cold damage has an inciting effect on the syndrome (Marcu and Tomiczek 1989, Rösel and Reuther 1995, Hartmann 1996). Even if the 'climatic perturbation hypothesis' seems to provide a plausible explanation of oak decline in Central Europe, many questions remain unanswered. Hartmann (1996) concludes that site condition and defoliation by insects are more important than climatic stresses, and, indeed, the role of organisms and of site is not considered sufficiently in the discussed hypothesis.

The 'host-stress-saprogen model' proposed by Houston (1992) requires that host trees are affected by stress factors, such as climatic perturbations (Auclair et al. 1992) or biotically caused defoliation in order for pathogens to successfully infect the root system. This model is based on the generally accepted theory of stress-induced predisposition of trees to pathogen/pest attack. The organisms considered as being mainly involved in the decline

process are 'secondary' agents that are situated near the end of the causative chain. In Houston's examples, oaks seriously affected by the decline syndrome were often infected by species of *Armillaria*. However, the pathological role of these infections often remains dubious because the taxonomic identity of the species of *Armillaria*, which possess different pathogenicities, usually was not ascertained. In his study in Austria, Halmschlager (1997) mainly isolated the saprophytic *A. gallica,* but in certain cases only the pathogenic *A. ostoyae*, from the roots of diseased oaks. He concluded that in sites where *A. ostoyae* is present, this fungus might play a significant role in the physical decline of oaks. In Germany secondary root infections caused by certain species of *Phytophthora* are regarded to be more important than those caused by *Armillaria* (Hartmann 1996). In view of the fact that the potential of pathogenicity in the observed fungi is not completely clear, it seems justified to consider even the pathogenic species as 'secondary' rather than as among the 'primary' pathogenic agents, thus requiring a stress-born predisposition of the host tree. Under this assumption, the host-stress-saprogen model from the pathologist's view could be partially, i.e., in certain cases, applicable to oak decline in Central Europe.

In connection with the host-stress-saprogen model the xylophagous insects also must be considered. In the literature, importance is attached to only a few species, which are well known to be associated with the stressed condition of the host tree and that cause lethal impairments of the tree's conductive system. In Slovakia and Hungary, *Scolytus intricatus* Ratz. (Coleoptera, Scolytidae) was the dominant species (Patocka 1985, Szontagh 1987). Much attention was paid to this insect in connection with the 'tracheomycosis model', in which a vector-function was ascribed to the bark beetle. However, in other countries *S. intricatus* seemed to be irregularly associated with oak mortality, and occurred only occasionally. Large-scale inventories of symptoms in oaks affected by the decline syndrome in Austria revealed that *S. intricatus* was found infrequently, except in specific sites (Schopf and Mitterböck 1991, Schopf 1992). Representatives of the genus *Agrilus* (Coleoptera, Buprestidae) are mentioned in reports from most Central European countries. *Agrilus angustulus* Ill. was found to play a dominant role in the mortality of younger age classes of *Q. robur* that occurred locally in Hungary and Slovakia (Szontagh 1987). In Austria it was the dominant species among the Buprestidae that were found in diseased oaks, but without obvious significance in the causative chain of the decline syndrome (Schopf 1992). A completely different situation is described from Germany (Hartmann 1996), where *A. biguttatus* F. is considered to play a key role in oak dieback and mortality. Among the cambiophage insect groups, the Cerambycidae are inconspicuous. *Xylotrechus antilope* Schonh. is mentioned by Szontagh (1987) as being economically important in Hungary because it damages timber by excavating sites for pupation. In Austria, where this insect proved to be the dominant Cerambycid species found in dying oaks, the chronology of attack suggested that *X. antilope* was actively involved in tree mortality (Schopf 1992).

Wood boring insects usually occurred not earlier than in advanced phases of the dieback of whole trees or portions of them (Schopf 1992, Hartmann 1996). While these insects were mainly recorded from dead wood, their initial attacks oftentimes occurred when the trees were still alive. *Xyleborus monographus* F. (Col., Scolytidae) and *Xiphydria longicollis* Geoffr. (Hym., Xiphydriidae) are representatives of this group. Although their contribution to the physiological decline is rather improbable, the loss of value in wood caused by these insects is significant.

In summary, xylophagous insects proved to participate frequently in the final phase of the causative chain that leads to mortality of oaks. The involved species varied regionally or locally, probably according to the eco-geographic situation or individual site and stand condition. The incidence of their infestation may also depend on additional circumstances that contribute to the actual level of population density, such as the frequency of forest hygiene and control measures. Due to the ecological characteristics of the relevant species, it seems correct to classify them principally as 'secondary' pests, thus fitting in the host-stress-saprogen model, that is characteristic for certain species of fungi. Within limitations they seem to be able to substitute for one another, however, this does not mean that they are ecophysiologically and pathologically equivalent in their host tree - xylophage/parasite associations. Furthermore, there is no evidence that xylophages or phytopathogenic fungi of the types considered would be indispensable components that exhibit a killing function in the dieback phenomenon. The dominance of truly saprophytic/saprophagous species and the complete absence of potentially pathogenic species, can be interpreted as an indication that the dead tree had succumbed physiologically from abiotic influences. The 'host-stress-saprogen' model would not be applicable in such cases where biotic incitement of the pathological mechanism is lacking.

Further Involvement of Biotic Agents

When using this rough classification to describe the causative chain of oak dieback, many pests and pathogens behave as "primary" disease agents rather than as secondary agents. Defoliators and mildew fungi apparently act independently of the physiological condition of the host trees. By destroying 'only' foliage and buds, which are renewable organs of the tree, they are considered to be incapable of killing trees outright. Nevertheless, their outbreaks, which lead to a loss of photosynthetic capability, and induce an energy-consuming second flush of foliage in oaks, represent an important stressor, which severely predisposes trees to attack by other detrimental influences. This is the simplified, essential conclusion drawn from the reports in which defoliator outbreaks are thought to contribute to the oak decline phenomenon. Springfeeding species belonging to several families of Lepidoptera (Lymantriidae: *Lymantria dispar* L., *Euproctis chrysorrhoea* L.; Geometridae: *Operophthera brumata* L., *Erannis defoliaria* Cl., *Colotois pennaria* L.; Tortricidae: *Tortrix viridana* L., *Archips xylosteana* L., etc.) cause episodes of defoliation in all countries considered here (Marcu 1987, Szontagh 1987, Donaubauer 1987, Hartmann 1996). Sometimes their outbreaks take place temporally in alternate years or even simultaneously, this way causing more or less continuous periods of defoliation over consecutive years. Trees affected by repeated defoliation are highly susceptible to abiotic stressors such as drought and strong frost. Coincidence of spring defoliation with epidemic mildew (*Microsphaera alphitoides* Griff. and Maubl.) infection of the regenerated foliage in late summer may be fatal for the trees (Lobinger and Skatulla 1996).

The statements concerning the role of defoliators need some qualifications. Although defoliation by insects is considered to be one of the most important components among predisposing stresses in Germany (Hartmann 1996), there is evidence that oak decline phenomena frequently occur in absence of severe insect defoliation (Donaubauer 1987, Schopf and Mitterböck 1991, Schopf 1992a). Marcu (1987), and Varga (1987) list insect

defoliation as only one of the possible factors responsible for the initiation of decline phenomena. Therefore, defoliation by insects should not be regarded generally as the initiating factor in oak decline. Another point deserves critical examination that is the chronology of insect outbreaks and other stress episodes in relation to when decline symptoms appear. Coincidence in time may provoke confusion in the interpretation of symptoms on the one hand; on the other, a site-related or climatically caused delay of recovery after defoliation may conceal a causative connection. Finally, there is the question, concerning how far insect defoliation and subsequent decline phenomena coincided locally over time. Small local outbreaks of defoliators are frequently overlooked. In the past, delineation of defoliated areas usually was not sufficient to reconstruct the differential pattern of infestation intensity in a region of interest. Similarly, the decline phenomena show locally differentiated patterns of intensity. Unfortunately, therefore, the availability of reliable data has not been adequate for us to reconstruct the pattern of these events on past epidemics.

Besides the xylophagous insects and the defoliators, a third group of rather inconspicuous pest insects is frequently found at high densities in oak stands associated with the decline syndrome: sapsuckers, gallmakers and shootminers. Varga (1987) mentions that serious infestation of *Kermes quercus* L. (Homoptera, Kermesidae) occurred in chronically devitalized stands of *Q. robur* in Hungary. From Austria, Schopf and Mitterböck (1991), Schopf (1992a), Gotsmy and Schopf (1992) mention *Asterolecanium variolosum* Ratz. (Homoptera, Asterolecaniidae) and *Mytilococcus ulmi* L. (Homoptera, Diaspididae), but in much higher densities, *Iassus lanio* L. (Homoptera, Cicadellidae) and *Harpocera thoracica* Fall. (Heteroptera, Miridae) are associated with oak stands that exhibit decline symptoms. In contrast to the Coccoidea, which affect the host tree only by their sap sucking habits, all of *I. lanio* and *H. thoracica* developmental stages feed on young tissues of buds, flowers and growing shoots and, additionally, injure the host plant by ovipositing into the base of young buds. In heavily infested trees, the density of egg-pockets of Hemiptera exceeded 2.2 per young shoot on average; the intensity of feeding damage on shoots and leaves was correspondingly high. These insects attained outbreak levels only in a portion of the sites investigated, and they appeared to prefer healthy oaks rather than obviously weakened trees. Another insect that attacks oaks and is easily overlooked is *Andricus quercusradicis* F. (Hymenoptera, Cynipidae), which builds its tiny galls inside the young shoots and in the bases of leaf stalks, thus causing the death of infested shoots Schopf and Mitterböck (1991). In contrast to the Hemipterans, *A. quercusradicis* was at outbreak densities in nearly all investigated sites, showing a slight preference for trees affected by the decline syndrome. In extreme cases, over 80% of the young shoots per tree were infested with galls. In the same study, authors report the occurrence of outbreaks of the oak shoot moth, *Stenolechia gemmella* L. (Lepidoptera, Gelechiidae) in certain sites in Austria. The larva, which mines the young shoots, causes considerable damage to the terminals of branches.

It is difficult to evaluate the importance of this complex of insects to the syndrome of oak decline. Our knowledge about the geographical distribution and dynamics of these species is poor because they are rather inconspicuous animals and are frequently overlooked. Very scarce records, with the exception of Austria, come from Hungary (Varga 1987 concerning *K. quercus*; Szontagh pers. comm. concerning *A. quercusradicis* after reinspection of diseased trees) and Slovakia (Patocka 1980 concerning *S. gemmella*). Possibly, the importance of these species was limited to the pannonian climatic region. Very

little is known about the host-plant relationships, population dynamics and epidemiology of these insects. Thus, it is difficult to judge whether they are involved in the initiation of tree decline or whether they benefit from it. The contemporaneous occurrence of outbreaks in numerous isolated sites suggests that the different species had directly or indirectly responded to a region-wide factor, probably weather. In their pathological function they clearly contribute to the disturbance of photosynthetic efficiency, and to the expression of visually recognizable symptoms, which include bushy shape of branches, necroses and malformation of leaves, and possibly pathological twig abscission (Schopf et al. 1991). It would be speculative to suggest that these species might be transmitters of hitherto undiscovered or functionally unidentified pathogens, such as viruses or MLOs (Nienhaus 1987, Ahrens and Seemüller 1994).

Synopsis

Recalling the fact that decline phenomena are the manifestation of ecosystemic processes, and that oak forest ecosystems in Central Europe are very diverse, we should not expect that the manifestation of oak decline should be uniform. The circumstances under which oak trees show symptoms of decline or dieback, or eventually die are likewise diverse. The genesis and course of pathological processes differ from case to case, regardless of whether the final result is recovery or death of trees. Although many different factors are considered to be involved in the causality, their negative effects seem to be based on a few ecophysiological disfunctions present in the trees. These problems can be triggered by abiotic influences or by organisms, or by both factors in combination. In summation, sets of impairing influences are acting on the trees, which are mainly interconnected to causative chains according to the predisposition-incitement principle. The diversity of stressor sets is derived from the variable combinations of static and dynamic environmental traits to which trees are exposed.

Static traits are represented by the properties that are characteristic of individual sites, which consist of mosaics of different edaphic, hydrologic, and nutritional conditions on both a small and large scale. Hartmann (1996) emphasized the importance of site conditions with respect to the effects of drought or extreme wetness. The type of climate can also be regarded as a static condition, characterized by the average amplitudes of climatic extremes, and determining the adaptedness of the oak population, the type and outbreak behavior of potential pest populations, etc. This pattern of static traits is understood to be a basic pattern of qualitatively and gradually different predisposing conditions that are being acted upon by a variety of dynamic stress factors. Under the influence of a differentiated pattern of dynamic stressors, this may produce a heterogenous pattern of tree stress and, consequently, a heterogenous pattern of tree response. The local configuration of predisposing conditions and the likelihood of interactions with stress-enhancing dynamic influences will collectively determine the local risk of damage. Dynamic variables include the episodic meteorological extremes, populations of potentially harmful organisms, and, even if not environmental, the changing vulnerability of the target, the oaks. Crucial to the pathological process is the spatial and temporal occurrence of ecophysiologically risky static and dynamic influences.

The basic physiological properties of the trees that seem to be affected adversely in every variant of oak decline syndromes, are the carbon budget and the water balance. There

are numerous ways and mechanisms by which these functions can be reversibly or irreversibly disturbed. Disturbance that results from water stress (alone) is usually reversible, whereas that caused by cambio-xylophagous insects is generally irreversible. Different factors and agents can cause uniform effects, and can operate mutually or self-enhancing on the progressively stressed tree.

The impact of stressors can directly or indirectly affect adversely the photosynthetic apparatus in the leaves and the water and nutrient absorbing apparatus in the roots. The impact on one (e.g., leaves) can cause negative effects on the other (e.g., fine roots), and is mediated by the intact conductive system in the trunk and branches. Critical conditions in the foliage and/or roots also can be provoked by functional disturbances of the conductive system. A simplified diagrammatic representation of their interactions is provided in Figure 2.

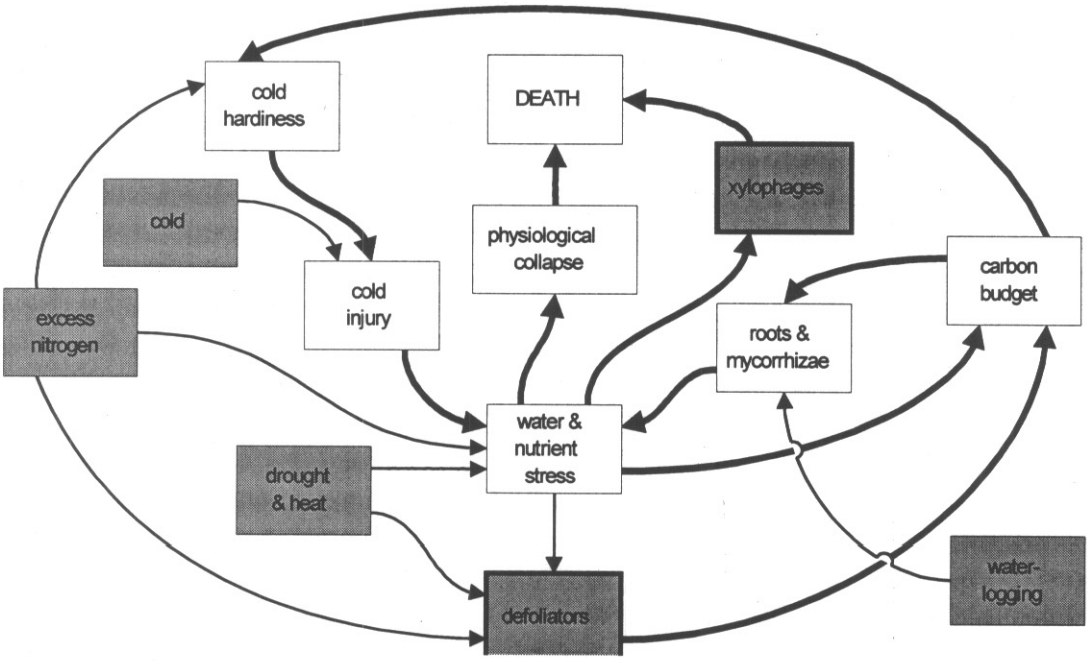


Figure 2. Oak decline: eco-physiological decline cycle, indicating essential effects of environmental factors on the tree, and showing the positions and contributions of defoliating and xylophagous insects, respectively, in the decline process.

As demonstrated in Figure 3, the carbon budget can be negatively affected by defoliation and, alternately, by water and/or nutrient-stress, which causes a reduction of photosynthesis, and which, in itself, can be induced by physical and chemical influences of the environment. Water and/or nutrient-stress also can arise due to the insufficient function of the root-mychorrhizae system, which is, in turn, a consequence of the affected carbon budget; therefore, this results in a self-enhancing, destructive cycle. Another feedback of water and/or nutrient-stress caused by disturbance of the carbon budget is a reduction of cold hardiness. Thus, under episodes of extreme cold, embolisms occur in the xylem, which adversely affect

the ability of vessels to transport water (Tyree and Sperry 1989). The severity and duration of impact of the individual or combined influences determine the fate of the affected tree. Survival and recovery are possible if the stress does not exceed a critical intensity and duration and, additionally, if the tree is spared the successful attack by aggressive xylophagous insects or root pathogens. Excessive stress impact results in the physiological collapse of the tree and finally in its demise. In this case the associations of xylophages and fungi will be characterized by the non-aggressive, saprophilic life habits of the participating species.

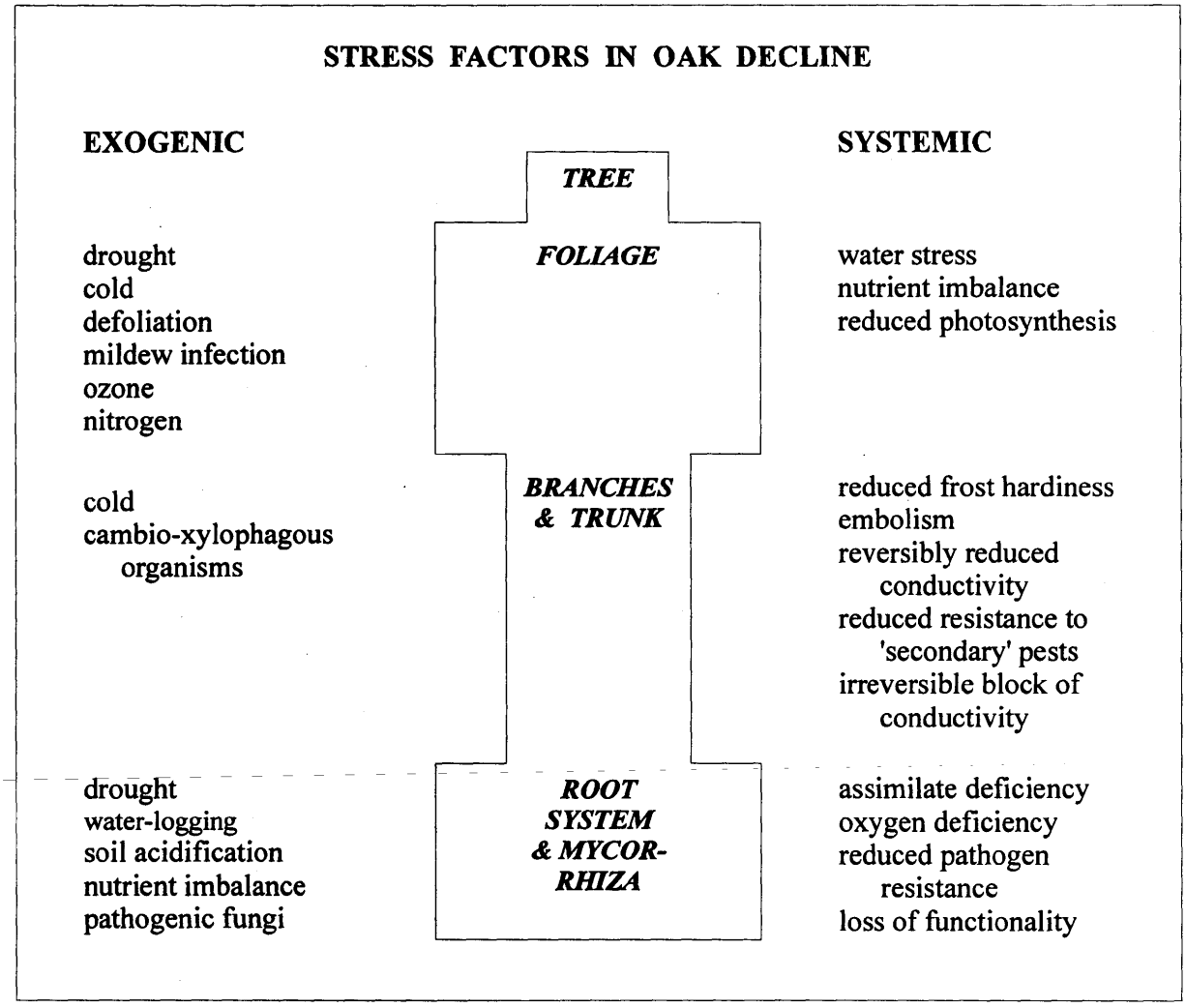


Figure 3. List of exogenic and systemic stress factors relevant for the genesis of oak decline phenomena, arranged by their main points of attack in the tree.

Figure 3 indicates that very different exogenic and endogenic mechanisms that are functionally interchangeable can adversely affect the sensitive target 'carbon budget' of the tree. But, there is an additional point where environmental conditions influence these functional cycles, the root-mychorrhizal system, where vulnerability is very high. The normal function of the root-mychorrizal system can be disrupted by deprivation of assimilates, or by

the direct impact of abiotic stressors such as extreme drought or anaerobic conditions caused by excessive soil moisture. It has been suggested that advanced soil acidification causes damage to fine roots of oaks (Hartmann 1996). Root mortality under the influence of continuous oxygen deficiency in heavy, water-saturated soils is reported frequently as a dieback of oaks (Varga 1987, Prpic and Raus 1987, Hartmann 1996). The coincidence of these soil conditions with defoliation prevents the rapid transpiration of surplus water, thus prolonging adverse conditions for the root systems. Weakened or damaged roots are more susceptible to aggressive pathogens that may be present (Halmschlager 1997). Infections by pathogens that are initiated in such situations, then cause persistent disruption in the function of the root system, increases the susceptibility of the tree to other stress agents.

The roles of pest organisms in the pathological pathway and the nature of their pathophysiological effects on the tree are relatively clear. However, the circumstances under which these organisms reach outbreak status are not well documented. The action of defoliators as well as that of the relevant 'secondary' organisms can be crucial at either the beginning or the end of the disease process. In contrast to stresses caused by meteorological factors, the origin of which is external to the ecosystem, pest organisms are basic components of the system itself. Their biological organization is different from that of green plants, and the temporal patterns of their life cycles differ considerably from that of their hosts, the oak trees. Due to their obvious and significant role in the oak decline syndrome, pest organisms and their dynamics deserve particular consideration within the context of ecosystemic disturbances (Führer 1997).

In order to clarify the role of defoliators in the context of oak decline, the following facts should be considered: The geographical distribution of the relevant defoliator species indicates that they are omnipresent in all regions where oak decline occurs in Central Europe. Nevertheless, and considering the large number of individual oak stands in their region, outbreaks of the different defoliator species and local populations show neither strong synchrony nor local or regional homogeneity. This cannot be solely because of differences in the coincidence of bud burst. The opinion that outbreaks of oak defoliators are only dependent on the synchrony between bud burst and egg hatch is a misjudgment of the situation with insects (Innes 1993). The highly diverse pattern of fluctuation caused by the occurrence, delay, extension or suppression of mass outbreaks, is the result of the successful regulation of insect abundance in multitrophic systems. In addition to the influence of environmental factors on the food-chain members, the host plant interaction among herbivores, the interspecific competition between herbivores, and the herbivore - natural enemy interactions, and the complicated structure of the natural enemy complexes themselves, are relevant variables in this regulation process (Führer 1997). Better knowledge of significant details would improve our ability to predict the spatial pattern of defoliator outbreaks, and in this way predict better the onset of oak decline.

As with the defoliators, the 'secondary' pest organisms, i.e., cambio-xylophagous insects and root pathogens, demonstrate a high diversity of participation and local representation in oak stands affected by the decline syndrome (Szontagh 1987, Schopf 1992, Hartmann 1996). Although no basic limitations of geographical distribution seem to exclude them from individual oak forest sites in Central Europe, their outbreak behavior may be influenced by site conditions, which directly affect the pest species or indirectly provide favorable or unfavorable habitat for the pest population. Distribution and abundance of

specific organisms depends also on the availability of suitable food substrate in the form of weakened of dying branches, trunks and roots. Thus, forest management practices on individual sites may strongly influence the populations of these 'secondary' pest species. Another important consideration is the physiological potential of the individual cambio-xylophage and pathogen species to successfully attack the host tree. The species/populations observed in connection with oak dieback no doubt exhibit considerable variation in their relative aggressiveness. This is a critical factor related to their significance in the causative chain of dieback because progressively stressed trees are considered to have gradually and qualitatively different susceptibility to attack by these organisms. In this context it appears noteworthy that the host tree selection by cambio- and xylophagous insects does not necessarily correspond with the categories of crown transparency. Schopf (1992) reports cases where trees that appeared to be healthy during summer did not survive until next spring because of severe infestation by 'secondary' pests, while other trees on the same site, which looked to be mortally ill in summer, remained uninfested and survived to the following year. We lack knowledge on the host tree relationships and population dynamics of cambio-xylophagous insects. Therefore, we depend mainly on assumptions when we try to interpret the epidemic patterns that are observed and to evaluate the significance of individual species to the syndrome of oak decline. Because of their potentially crucial role in oak decline, it would be highly desirable if we could predict their patterns of abundance.

As previously stated, site conditions in many respects play a decisive role in the behavior of pest organisms. Hence, alterations of site conditions can influence the risk of injurious effects caused by abiotic and biotic agents. Characteristics of sites that are frequently exposed to anthropogenic alteration are hydrology, availability of nutrients, and soil acidity. Due to the outstanding significance of drought stress among the factors involved in oak decline, site hydrology was the subject of attention in relevant investigations. The prevailing opinion was that gradual manifestation of the oak decline syndrome often was related to site hydrology, which, under the influence of region-wide weather extremes, causes periods of excessive drought or excessive wetness. Such effects, which happen even in natural situations (Hartmann 1996), can be expected to occur even more frequently when manmade changes in the hydrology of oak forest sites may exceed the adaptive capacity of the existing oak stands. Changes in site hydrology, which increase the probability of both excessive drought and wetness, usually occur when human interventions into the landscape water regime cause either a drop of groundwater level (Hager et al. 1992), or the increased likelihood of long-term flooding of the sites (Prpic and Raus 1987). Increasing demands for water, attributed to changes in land use (river regulations, drainage of wet lands, irrigation of agricultural land, settlement of industrial centers, extensive urbanization, etc.) has taken place in all Central European countries during the past decades. Since forested land in Central Europe, particularly where oaks are dominant, is entangled spatially with human settlements, agricultural land and industries, significant adverse ecological effects may result from human-related activities. This is especially true in the case of water regimes, which may sustain alterations that are irreversible. Many authors such as Donaubauer (1987), Marcu (1987), Varga (1987), and Schume (1992) suggest that manmade changes to site hydrology contribute significantly to the oak decline phenomenon by increasing the predisposition of trees on these sites to climatically induced stresses.

Persistent deterioration of site hydrology (similar to permanent latent loads of photooxidants, nitrogen, etc.) probably exposes oaks to a permanent latent stress, even during periods of moderate climate. Considering the self-intensifying mechanisms of the stress response, and the additive or synergistic effects of accompanying stress factors, one should expect that such affected forests will become extremely sensitive to an episodic impact of an additional stressor. Because of this high predisposition to stress, the incitement of visible disease symptoms may occur in response to a very minor environmental event. Hartmann (1996), for example, regards the aggravating influence of episodes of severe late-winter frost during the period 1985-1987, on oak forests that had previously been stressed by defoliation, for the synchronized initiation of oak dieback in Germany. Initiation of the visible decline process caused by a similar mechanism may have occurred elsewhere and earlier, without preceding defoliation (Donaubauer 1987, Marcu and Tomiczek 1989). The effect of climatic perturbations, which doubtlessly are essentially involved in the past/present period of oak decline, are more significant now than in the past because oak forests are more predisposed to stress. This increased susceptibility has anthropogenic origin, which lies mainly, but not exclusively, outside the responsibility of forestry.

Concerning the causative climatic effects, oak decline phenomena cannot be explained by global climate change, nor can they be used as possible indicators of global climate change. In past centuries, the climate in Central Europe has changed periodically between more continental and more maritime phases. These changes were also reflected by changes in plant health and pest problems in both agriculture and forestry (Auer et al. 1994, Pschorn-Walcher 1954), which may provoke more easily the coincidence of different stress impacts during the continental phases. Hence, the oak decline syndrome seems to be related less to the hypothetical global change of climate, but much more to the declining health of oak forest ecosystems combined with the well-documented fluctuation of climate in Europe.

Conclusion

'Oak decline' is not a disease, but rather a process driven by several 'diseases' involving site factors, environmental factors, pests and pathogens. Due to differences in local conditions, the constellations of participating stressors, their individual weights and the duration of their impact can vary between sites, resulting in qualitatively and quantitatively different loads and patterns of stress. The local response of oak stands, i.e., the manifestation of disease, or so-called 'oak decline syndrome' is correspondingly variable and depends on which tree species are involved. In this respect 'oak decline' does not differ fundamentally from the general term 'forest decline' (Führer 1991). Its separation in time of occurrence from other recent 'tree declines' may be due to different spatial patterns and regional dynamics of climatic stress in Central Europe during the past three decades. After all, oaks are growing in regions that are climatically different to those where Norway spruce and white fir are found. Therefore one should not expect that the impact of climatic stress must occur simultaneously in both areas. In addition, differences in the susceptibility of tree species (conifers, hardwoods), and of their speed of response and recovery, also may have contributed to the chronological separation of 'oak decline'.

In spite of the basic similarity with other 'tree declines', there seem to be striking differences in the dominant causative factors that are involved. While nutrient deficiencies

and imbalances, combined with soil degradation and air pollution, play a major role in the initiation of decline phenomena of conifers, water stress and outbreaks of defoliators, combined with frost damage, seem to be the primary initiators of oak decline. In view of this divergent array of causative factors, the different pathological characteristics of tree diseases, and the different nature of the hosts, we must first distinguish between diseases of conifers on one hand, and of oaks on the other. Focusing on oak decline phenomena only, the lack of uniformity in the array of factors and their pathological performance, does not justify that we consider oak decline as one 'complex disease' but as a 'complex of diseases' in the sense of Kandler (1992). The term 'disease' in this context implies the involvement of more than one causative agent, i.e., the combination of predisposing and inciting factors, thus describes better a 'complex' phenomenon.

Each variant of oak disease is based on impairment of the water balance and a metabolic disorder of the tree, particularly of the carbon budget. The ways in which this occurs differ from place to place, depending, in part, on the local site conditions. The nature, intensity and duration of the participating stress factors, together with the degree of predisposition, determines the dimension of the pathological response of the tree. The constellation of 'primary' stressors (climate, defoliators, pollutants etc.) and their stress-enhancing coincidence in time may be accidental, as is the occurrence of aggressive 'secondary' pest organisms. Here again the diversifying effects of site and stand properties must be emphasized. It should be noted that every involved causative complex follows its special laws: climatic extremes and man-made flooding of sites are neither inter-related nor related to the impact of pollutants; ecophysiology of trees exhibits endogenously induced patterns and dynamics that differ in part among tree species; outbreaks of defoliating insects are determined by specific rules of population dynamics, which differ from those of cambio-xylophagous insects and of root pathogens; additionally, dynamics of site conditions and oak stand quality are highly dependent on human actions. Hopefully, this enumeration has demonstrated that in order to interpret oak decline phenomena and to explanation their genesis, many disciplines must be studied. Furthermore, in order to understand what is common and what is specific to the individual cases of oak disease, every group of causative factors must be given special consideration. This applies, in particular, to all further attempts to conduct research and apply forest practices to counteract the progression of oak dieback in Central Europe. The need for such attempts appears to be very urgent, because the state of the art is based much more on assumptions than on well founded scientific knowledge.

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Gypsy Moths, Mice and Acorns

J.S. ELKINTON[1], W.M. HEALY[2], J.P. BUONACCORSI[3], G. BOETTNER[1], H.R. SMITH[4] AND A.M. LIEBHOLD[5]

[1]Dept. of Entomology, University of Massachusetts, Amherst, MA 01003 USA
[2]Northeastern Research Station, USDA Forest Service, University of Massachusetts, Amherst, MA 01003 USA
[3]Dept. of Mathematics and Statistics, University of Massachusetts, Amherst, MA 01003 USA
[4]Northeastern Research Station, USDA Forest Service, 51 Mill Pond Rd., Hamden, CT 06514 USA
[5]Northeastern Research Station, USDA Forest Service, 180 Canfield St., Morgantown, WV 26505 USA

ABSTRACT Low density populations of gypsy moth, *Lymantria dispar*, a major defoliator of deciduous forests throughout the northern hemisphere, were studied over a 10-year period in Massachusetts. Increases in density were associated with declines in density of the white-footed mouse, *Peromyscus leucopus*, a principal predator. Furthermore, changes in density of *P. leucopus* populations were closely associated with mast crops of acorns, a dominant winter food source. The previously demonstrated effects of weather, such as late spring frosts, on acorn crops and the synchrony of such crops over regions of at least 1000 km^2 may explain the synchronous fluctuation of gypsy moth and white-footed mice evident in our data and the regional onset of gypsy moth outbreaks.

THE GYPSY MOTH is a major defoliator of hardwood trees throughout the northern hemisphere. Throughout its range, populations of gypsy moth occasionally erupt into outbreak phase. In 1868, it was accidentally introduced into northeastern North America, where outbreaks tend to be synchronized (Liebhold and Elkinton 1989a). Analyses have shown that the natural dispersal of gypsy moths (mainly by windborne transport of first instars) is too slow to explain the synchrony of population trends across a region (Liebhold and McManus 1991).

Gypsy moth populations in most regions remain at low density during long intervals between outbreaks. Undoubtedly, the most important question in gypsy moth population dynamics is: what factors maintain such populations at low density and why do they fail to act in certain years, allowing populations to grow into outbreak phase? Based on a series of studies conducted in low density and outbreak populations of gypsy moth and building upon the earlier hypotheses of Bess et al. (1947), Campbell and Sloan (1977, 1978) concluded that low density populations are maintained primarily by small mammal predation. In particular, they argued that the white-footed mouse (*Peromyscus leucopus*) was the main source of mortality and one that acted as a stabilizing agent on gypsy moth at low density. According to their theory, in most years predation by *P. leucopus* is sufficient to keep gypsy moth populations from expanding. Occasionally, however, gypsy moth populations rise above a hypothetical threshold above which such predators consume a declining proportion of the gypsy moth population and the densities grow exponentially into outbreak phase. This threshold exists because all predators are limited in the amount of food an individual can consume (i.e., the functional response is asymptotic); generalist territorial predators such as

Pages 25-33 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

P. leucopus have extremely limited numerical responses, meaning that their density is unlikely to be affected by changes in gypsy moth density. Campbell and Sloan (1977, 1978) did not speculate as to why gypsy moth populations sometimes rise above this threshold, but the reasons could involve either changes in gypsy moth fecundity or early instar survival, or else the threshold itself could change due to declines in *P. leucopus* density or changes in other factors affecting mouse predation on late instar gypsy moth.

Because of the difficulty of sampling low density populations, Campbell and Sloan (1977, 1978) based their conclusions on quite limited data. Although many researchers have addressed various questions pertaining to gypsy moth biology, few subsequent studies have attempted to quantify the impact of predators on changes in gypsy moth density across one or more generations.

Campbell and Sloan (1977) attempted to prove the importance of small mammal and avian predation by trapping and removing small mammals from several sites and by wrapping burlap and poultry netting around the stems of trees to protect larvae from predaceous birds on other sites. The results indicated an increase in egg mass counts in plots with either treatment compared to control plots. They concluded that both avian and small mammal predators were important. We find their conclusion regarding small mammal predation fairly convincing but not their conclusion regarding avian predation. The differences between counts in the bird protected plot vs. control plots was small. Furthermore, several studies have shown that burlap bands may provide good resting locations for gypsy moth larvae where they are protected from small mammal predators.

Here we report the results of a long-term study wherein we showed that the density of gypsy moths in low density populations is linked to that of their principal predator, the white-footed mouse. Mouse densities in turn are determined by acorn crops, which constitute their major source of food during winter months. Details of this study are given in Elkinton et al. (1996).

Materials and Methods

Our studies were conducted in western Massachusetts on eight forest stands defined by a predominance of northern red oak, *Quercus rubra* L., a favored host of gypsy moth. The mean distance between stands was 8 km (range 1-21 km), a distance sufficient that no stands were directly linked by dispersal of either gypsy moths (Liebhold and McManus 1991) or white-footed mice (Batzli 1977).

Yearly estimates of the densities of mice, gypsy moths and acorn production were made on three 1-ha plots within each stand. Estimates of gypsy moth density were obtained from counts of egg masses within five 15-m diameter circles in each plot (Kolodny-Hirsch 1986). Mice were captured in Sherman live traps set on a 7 X 7 m grid in each plot with 15-m intervals between traps. The mice were marked with metal ear tags (Hansen and Batzli 1978) and densities were estimated with capture-recapture techniques (White et al. 1982). Beginning in the autumn of 1989, we counted acorns falling into 40 0.5 m^2 funnel traps positioned at random in each 1-ha plot in each stand. An index of predator impact on gypsy moths was obtained by measuring the daily rate of consumption of 300 gypsy moth pupae over 3-day intervals in each plot in July from 1986-1990 (Fig. 1). The pupae were placed in the forest litter where most naturally occurring pupae are found (Campbell et al. 1975) and were attached in groups of 12 to burlap-covered boards (Smith 1989).

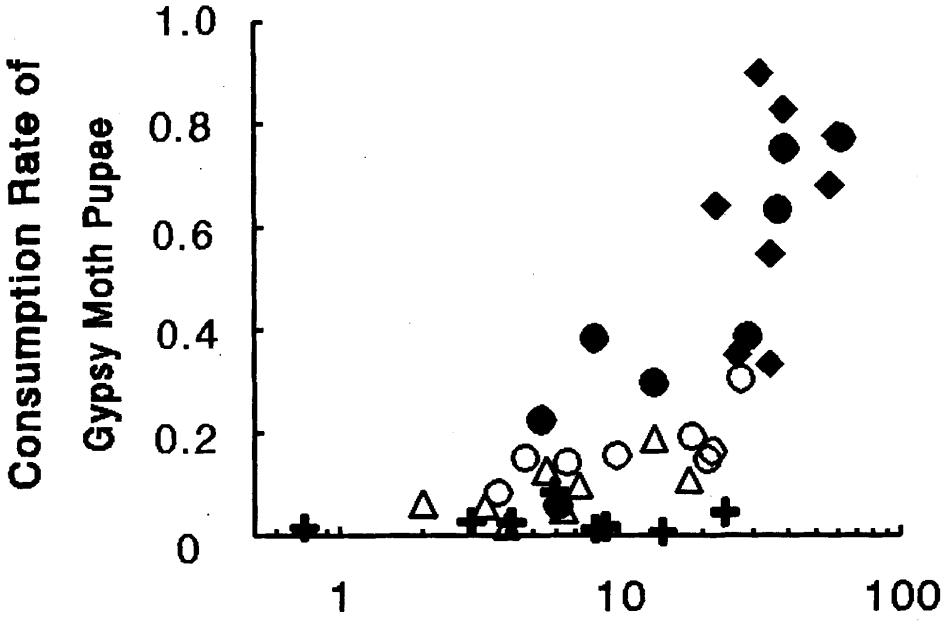


Figure 1. Daily proportion of 300 gypsy moth pupae deployed on each plot that were consumed by all predators versus density of white-footed mice. Symbols indicate different years. Reproduced from Elkinton et al. (1996) with permission from *Ecology*.

To assess the effects of mice on gypsy moths, we fit, using least squares regression, the model:

$$\text{Log}(N_{t+1,s}) \approx \alpha_s + \beta_s \text{Log}(N_{ts}) + \gamma_s \text{Log}(M_{ts}) + \varepsilon_{ts} \quad (1)$$

where N_{ts} and M_{ts} represent the density of mice in year t and stand s, and ε_{ts} is the error term. This yielded parameter estimates α_s, β_s, γ_s and residuals r_{ts} but temporal and spatial correlations in the error term would invalidate any estimates of standard errors or hypothesis testing based on standard least-squares procedures. Instead, we used a bootstrap procedure (Efron and Tibshirani 1993) similar in spirit to the density dependence tests proposed by Dennis and Taper (1994). Details are given in Elkinton et al. (1996).

The same analytic procedure was used to test for a significant link between mouse densities and previous years' acorn crops. Here the model was:

$$\text{Log}(M_{t+1,s}) \approx \phi_s + \chi_s \text{Log}(M_{ts}) + (\psi + \omega \text{Log}(M_{ts}))\text{Log}(A_{ts}) + \delta_{ts} \quad (2)$$

where A_{ts} is the estimated density of acorns falling per ha in year t and stand s, and δ_{ts} is the error term. The model includes an interaction term, the addition of which significantly improved the fit of the model ($F = 3.78$, $P = .028$).

Results and Discussion

Over the 10-year period, gypsy moths fluctuated between 0 and 100 egg masses ha^{-1} (Fig. 2A). These are densities characteristic of non-outbreak populations, an order of magnitude lower than those which cause noticeable defoliation (Gansner et al. 1985). Increases in gypsy moth density occurred in years when densities of white-footed mice were low (Fig. 2). This trend was statistically significant ($F= 3.48$, $P = 0.022$) as determined by a test for no mice effects (that is H_0: $\gamma_S = 0$, $s = 1$ to 8). Consumption rates of gypsy moth pupae by all predators were positively correlated with mouse densities providing further support for the impact of mice on gypsy moths.

Mid-summer mouse densities declined or remained at low levels when acorn production was low the previous autumn and increased or remained at high levels following large acorn crops (Fig. 2 B,C). A test for no acorn effect ($\psi=0$, and $\omega=0$) in model (2) was rejected at $P<0.001$, $F= 47.24$. At high densities, populations of mice are constrained by other factors (Vessey 1987) and will not increase further despite heavy acorn crops. This fact explains the significant interaction term. Acorns constitute a major over-wintering food source for white-footed mice (Hansen and Batzli 1978). Our data provide the first clear link between densities of white-footed mice and acorn production. The determinants of acorn production are complex, involving both genetic and weather-related factors (Olson and Boyce 1971), but acorn crops tend to be synchronized over large areas (Wentworth et al. 1992). These findings provide a possible explanation for regional synchrony of gypsy moth outbreaks reported in previous studies (Liebhold and Elkinton 1989a, Liebhold and McManus 1991).

These results support the conclusions of earlier research on gypsy moth population dynamics which indicated that changes in density of non-outbreak populations were determined by survival during late instars (Campbell 1967) and that the dominant source of mortality during this period was predation by the white-footed mouse (Campbell and Sloan 1977).

Despite the significant effects, mouse densities explain only a part of the overall variation in the change in gypsy moth numbers (Fig. 2A). Some of the unexplained variation is due to measurement error, especially in our estimates of egg masses per ha at the lowest densities. Additional variation is undoubtedly caused by other sources of gypsy moth mortality, including other predators, parasitoids and disease. In particular, in 1989, the first recorded epizootic of the fungal pathogen *Entomophaga maimaiga* decimated gypsy moth throughout the northeastern United States (Hajek et al. 1990). Despite larval mortality from *E. maimaiga* ranging from 60 - 90% on our plots (Hajek et al. 1990), we saw little consistent change in gypsy moth egg mass density (Fig 2A). We believe this occurred because densities of white-footed mice across the region were low in 1989. In subsequent years, *E. maimaiga* caused substantially lower mortality on our plots.

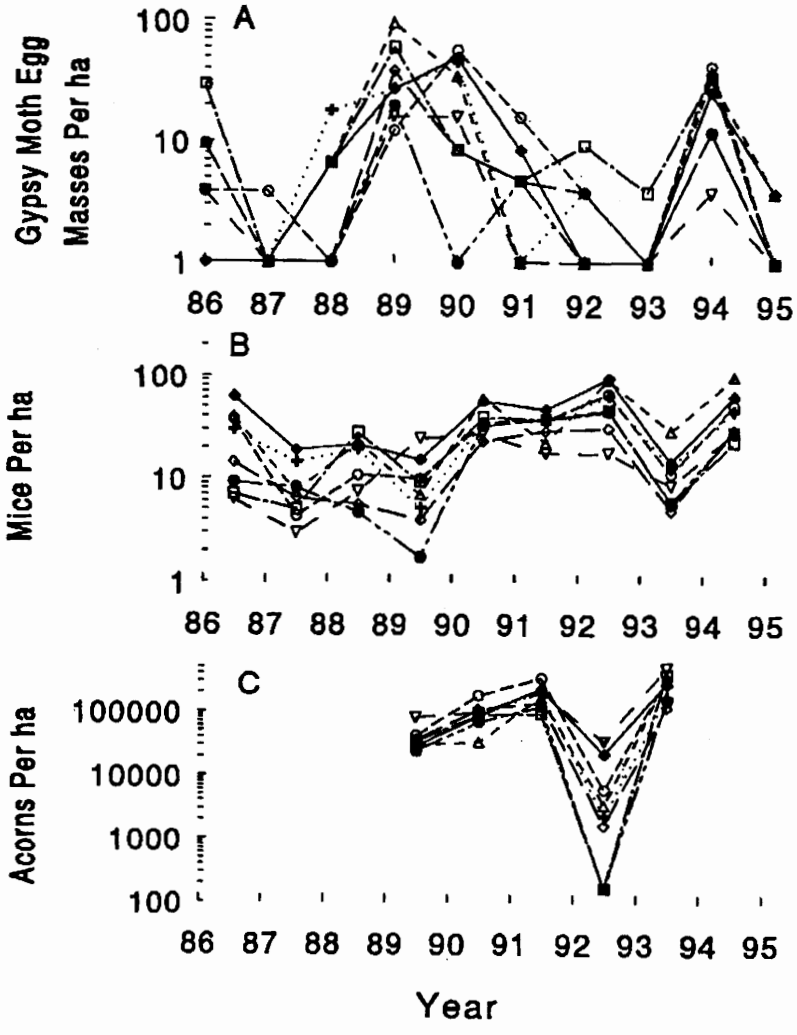


Figure 2. Yearly estimates from each of 8 stands of A) gypsy moth egg masses per ha as determined prior to hatch in each year, B) white-footed mice per ha and C) sound acorns per ha from each stand beginning in 1989. Reproduced from Elkinton et al. (1996) with permission from *Ecology*.

Changes in population densities of mice and gypsy moth, and in acorn production, were all partially synchronized between stands across the study region (Fig. 2). Quantitatively, we can express synchrony as the pairwise spatial correlation in density between stands after removing the effects of local dynamics, as described by Hanski and Woiwood (1993). The mean correlations were 0.75 (range: 0.42 to 0.96) for gypsy moth egg masses, 0.23 (range: -0.34 to 0.98) for white-footed mice and 0.77 (range: 0.34 to 1.00) for acorns.

Our findings are compatible with the general synoptic model for outbreak insects proposed by Southwood and Comins (1976) in which low density populations are maintained by generalist predators, whose densities are not determined by their prey. A version of this idea specific to gypsy moths was proposed by Campbell (1975). A key feature of such systems is a threshold density of the prey above which the generalist consumes a declining

fraction of the population, which thereupon expands exponentially to outbreak phase. We propose that the threshold density is determined by variation in the density of *P. leucopus*, which is thus a major possible cause of gypsy moth outbreaks.

The synoptic model contrasts with previous descriptions of the dynamics of gypsy moth populations in Yugoslavia, which appear to be regulated by parasitoids (Sisojevic 1975, Montgomery and Wallner 1988) and exhibit delayed density dependence as determined by time series analysis (Turchin 1990). In North America, 10 species of specialist and generalist parasitoids have been introduced and established, but their role in gypsy moth population dynamics is ambiguous. Several studies have shown that parasitoids can decimate experimentally created populations of gypsy moth with a marked spatially density-dependent parasitism (Liebhold and Elkinton 1989b, Gould et al. 1990). However, most studies of natural populations in North America have indicated little or no evidence for direct or delayed density-dependent parasitism and that rates of parasitism are much lower at all gypsy moth densities (Liebhold and Elkinton 1989b, Williams et al. 1992) than those reported for European populations (Sisojevic 1975, Montgomery and Wallner 1988).

The link we have established between gypsy moths and mice, both of which are autocorrelated systems (density in any year is a function of density in previous years), complicates the interpretation of findings of significant direct and delayed density dependence (Turchin 1990). Tests of direct density dependence for gypsy moths entail fitting model (1) without the term involving mice, the effect of which is incorporated into the error term. The resulting autocorrelated error may lead to spurious positive tests for density dependence (Solow 1990). Such autocorrelated errors will also result in findings of significant delayed density dependence (Royama 1992 Williams and Liebhold 1995) using the time series analyses of Turchin (1990). Thus, findings of significant delayed density dependence does not necessarily imply the action of agents such as specialist parasitoids whose densities lag behind that of their hosts by one or more generations. The relative importance and density dependence of specific agents such as mice or parasitoids can only be revealed by experimental manipulation (Liebhold and Elkinton 1989b, Gould et al. 1990), coupled with long-term studies of natural populations in which mortality caused by these agents in each life stage is quantified.

Our results suggest that acorn crops may be the ultimate cause of gypsy moth outbreaks. The determinants of acorn production are complex, involving both genetics and weather-related factors (Olson and Boyce 1971). Each oak species appears to have a tendency to produce large acorn crops at certain intervals, but weather effects are superimposed on these inherent tendencies and explain much of the yearly variation in acorn crop size (Sork et al. 1993). In our research area, and indeed over much of the northeastern United States, red oak is by far the most abundant oak species. Good and poor acorn crops have been reported for relatively large areas (Downs and McQuilkin 1944, Goodrum et al. 1977, Christisen and Kearby 1984, Wentworth et al. 1992). Good mast years result from exceptional production from one species, or coincident fair to good production among several species. Poor production by one species is often offset by good production from another (Beck 1977, Christisen and Kearby 1984). Although complete mast failures are considered rare, synchronous poor production among species has been reported frequently within stands (Rogers et al. 1990, Sork et al. 1993), and occasionally over large areas (Uhlig and Wilson 1952, Wentworth et al. 1992). Weather effects, such as those of late spring frosts, on acorn

crops (Goodrum et al. 1971), and the synchrony of such crops over regions of at least 1000 km^2 (Christisen and Kearby 1984), may explain the synchronous fluctuation of gypsy moth and white-footed mice evident in our data. These findings may thus explain the regional synchrony of gypsy moth outbreaks reported in previous studies (Liebhold and Elkinton 1989a, Liebhold and McManus 1991) and the regional onset of gypsy moth outbreaks.

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Periodic Outbreaks of the Beech Caterpillar, *Quadricalcarifera punctatella*, and its Population Dynamics: the Role of Insect Pathogens

NAOTO KAMATA

Laboratory of Ecology, Faculty of Science, Kanazawa University Kakuma, Kanazawa, Ishikawa 920-1192, Japan

ABSTRACT The beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lepidoptera: Notodontidae), often causes serious defoliation in beech forests in Japan. Outbreaks have tended to occur synchronously among different areas with an interval of 8-11 years. The population dynamics of this insect showed cycles both in outbreak and non-outbreak areas. Because such cycles are believed to be caused by one or more factors that are delayed density-dependent, several organic and inorganic factors that might influence the population dynamics of this insect were investigated to see if they had these characteristics. The infectious disease, *Cordyceps militaris* Link (Clavicipitalis: Clavicipitaceae), was considered to be the most plausible factor for generating cycles of the beech caterpillar population because it acted as a density-dependent manner with a time-lag both in outbreak and non-outbreak areas.

THE SIEBOLD'S BEECH, *Fagus crenata* Blume, is frequently a predominant tree species in climax forests in the cool temperate zone in Japan. The beech caterpillar (*Quadricalcarifera punctatella*) is a monophagous lepidopteran insect which sometimes defoliates the beech forests completely. Outbreaks have occurred synchronously in different areas at intervals of 8-11 years (Liebhold et al. 1996).

The moth populations exhibit 8-11 year cycles, widely synchronizing both in outbreak and non-outbreak areas (Kamata and Igarashi 1995b). Since theoretical studies have shown that 8-11 generations are due to one or more mortality factors that are time-delayed and density-dependent (May et al. 1974, Berryman 1987), several organic and inorganic factors that might influence the population dynamics of the beech caterpillar were investigated from the viewpoint of whether they acted in such a fashion.

The delayed induced resistance (DIR) of beech trees was observed for three years following severe defoliation (Kamata et al. 1996b). Nitrogen decreased and tannins increased in the foliage on the trees, and the performance (survival and fecundity) of caterpillars on this foliage was low. However, the DIR of beech trees does not seem to be an essential factor causing the beech caterpillar cycles, because no DIR occurred in areas where conspicuous defoliation was not observed, although strong DIR occurred on these beech trees when they were artificially defoliated (Kamata et al. 1996a).

The bird community was surprisingly stable despite great changes in the caterpillar density (Kamata et al. 1997). The percentage of the beech caterpillar population preyed on by birds decreased when the caterpillar density became high (Holling's type III) because little change in the density of predatory birds was observed (i.e., the numerical response was

Pages 34-46 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

trivial), although a functional response was clearly recognized: during outbreaks, beech caterpillars accounted for 75% of the diet of predatory birds. Bird predation was not effective when the caterpillar density was high, so the insects could continue to increase once they exceeded a certain population density threshold.

A coleopteran predator, *Calosoma maximowiczi* Morawiz (Coleoptera: Carabidae), increased during the outbreaks and acted as a density-dependent mortality factor (Kamata and Igarashi 1995a). The agile flying capability and high reproductive potential of this hunter enabled it to show a rapid numerical response to the caterpillar increase. However, this predator-prey interaction cannot generate cycles because its density dependence had no time delay: the beetle decreased rapidly in the following year when the beech caterpillar decreased. Furthermore, a numerical response was not observed in places where caterpillar densities were low.

Infectious disease, especially *Cordyceps militaris*, is considered the most plausible factor responsible for the main cycles of the beech caterpillar. This paper provides evidence that insect diseases act as delayed density-dependent mortality factors, both in outbreak and non-outbreak areas.

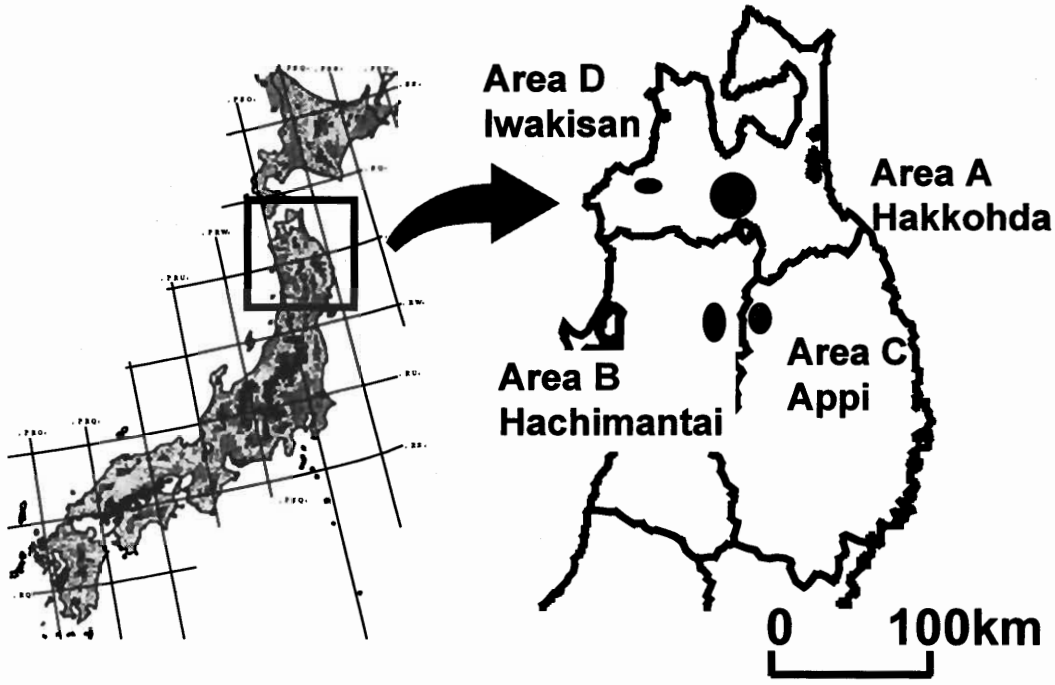


Figure 1. Four study areas in northern Japan, all located in natural deciduous broad-leaved forests mainly occupied by Siebold's beech, *Fagus crenata*.

Materials and Methods

Study Sites. Studies were conducted in four disjunct beech forests in northern Japan (Fig. 1). Variations in natural enemy populations and host plant properties associated with population dynamics of *Q. punctatella* were investigated in three out of the four forests (areas A, B and C). In area A (Hakkohda), an outbreak occurred during our study. In area B (Hachimantai), there were records of past outbreaks but an outbreak did not occur during our

study. In area C (Appi), no outbreaks have been recorded. The *Q. punctatella* population reached outbreak levels and almost all of the beech trees were defoliated in area D (Iwakisan) in 1994, although the population dynamics of *Q. punctatella* had not previously been investigated there. Various numbers of plots were established in each of the four areas for the purpose of sampling. Areas A and B had seven plots (A-1...A-7; B1...B7), area C had 4 plots (C-1...C-4), and area D had 2 plots (D-1 and D-2). Each plot was approximately 0.25 ha.

Caterpillar densities (last instar) in three areas (A-C) changed in a similar manner (Fig. 2). Larval densities increased from 1986 to 1990 in all areas and reached outbreak levels in some plots of area A in 1989 and 1990. A synchronous population decrease was observed in 1991 and was speculated to have been induced by a long and intense rainy season (Kamata and Igarashi 1994a, Kamata and Igarashi 1995b). In areas B and C, the density began to decrease without conspicuous defoliation.

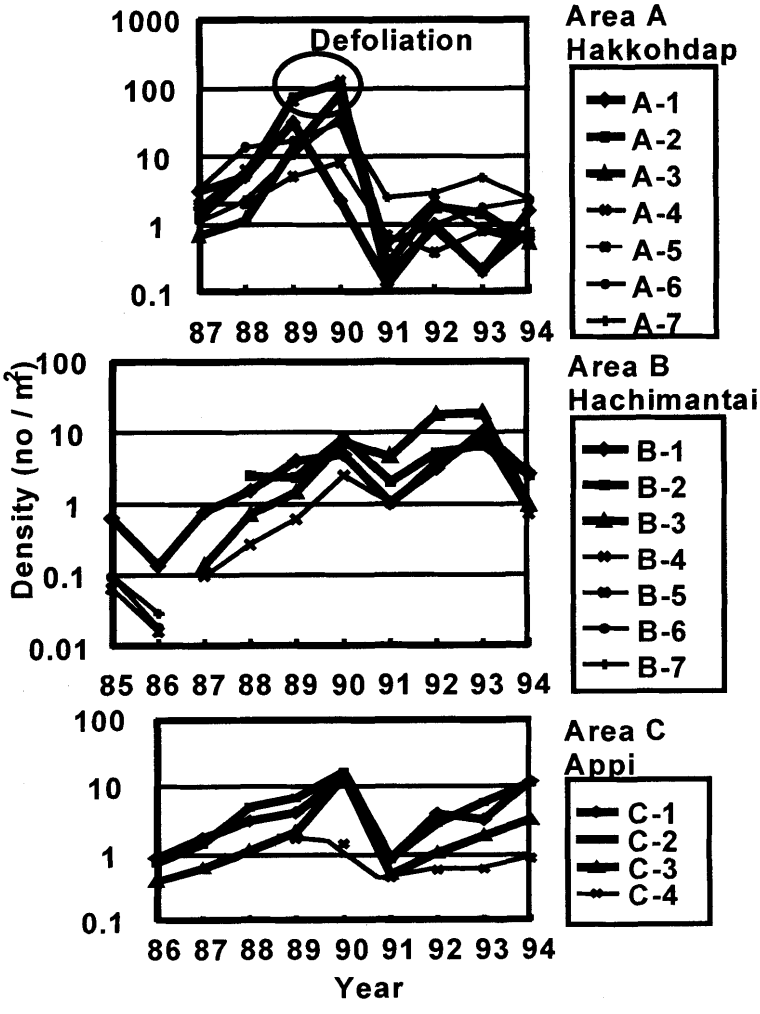


Figure 2. Final instar density of the beech caterpillar, *Quadricalcarifera punctatella* in each study plot of three disjunct beech forests.

In 1994 at site D, larval densities reached outbreak levels, resulting in severe defoliation. The defoliated areas estimated from aerial photographs were ca. 20 ha ranging from 670 m to 860 m above sea level (Kamata and Igarashi 1994b). *Q. punctatella* were collected at elevations of 760 m (D-1) and 710 m (D-2). Plot D-1 was at the epicenter where the larval density was highest and the defoliation was first discovered, and D-2 was located at the outskirts of the severely defoliated area.

Table 1. Sampling schedule of *Q. punctatella* during outbreak periods in site D (Iwakisan) in 1994

Date	Site	Developmental Stage
Aug. 1	Epi-Center (D-1)	Final Instar, Mature Larva
	Outskirts (D-2)	Final Instar, Mature Larva
Aug. 7	Outskirts (D-2)	Mature Larva
Aug. 26	Epi-Center (D-1)	Pupa
	Outskirts (D-2)	Pupa

Parasites During Outbreaks

The final stadium larvae, mature larvae, and pupae were collected during the outbreak period (Table 1). Beech trees were mostly defoliated in D-1 on August 1, but many beech leaves were left on the trees at D-2. However, most beech trees in D-2 were also defoliated on August 7. No larvae were found on August 27. The final stadium larvae were individually placed in plastic cups (5 cm in height, 10 cm in diameter) and fed fresh beech foliage daily. The mature larvae and pupae were placed in similar plastic cups containing moist Kimwipe® tissue paper and kept in the dark because they pupate in the soil. Individuals that died were kept in a plastic cup with moist tissue paper and checked weekly to determine the mortality factor. The mortality factor was identified by emerged parasitoids, a corremium or a fruiting body of the entomogenous fungus formed on the cadaver, or by conidiogenous structures.

The survivorship and importance of each mortality factor were analyzed from life table assembled for each collecting site.

Aerial Infection of Larvae by Entomopathogenic Fungi. In 1993, branches with an egg mass of *Q. punctatella* were covered with a netted enclosure to protect them from predators and parasitoids in areas A, B, and C. At that time in area A (in the third year after the outbreak), the population was in the decreasing phase. The area B population was at its peak but the density was not high enough to cause conspicuous defoliation. The area C population was in the increasing phase. The enclosures were checked at least once every week; the number of larvae was counted and dead individuals were returned to the laboratory where they were checked for the presence of infectious diseases. Larvae were occasionally shifted from one branch to another so that food was always plentiful and starvation did not limit larval survivorship. Survivorship and mortality caused by fungal diseases were compared among experimental groups.

Infections of Entomopathogenic Fungi in the Soil. This experiment was conducted from 1992 to 1995 at each of the four study plots in area B (B1...B4), where the

larval density increased until 1993 and then decreased. Although the peak was in 1993, no conspicuous defoliation was observed in that year.

Five litter samples from each of the four study plots were placed in plastic cups and returned to the laboratory, and five laboratory-reared pupae were buried in each litter sample as described by Sato et al. (1994). These cups were incubated at 25°C, since Ogawa et al. (1983) reported that *C. militaris* had maximal growth at this temperature. Moisture was supplied to the litter from time to time to prevent desication. These pupae were checked weekly for six months, and if a pupa died, the cause of mortality was determined as described above.

Pupae were buried in the field litter inside a PVC pipe to avoid predation as described by Kamata et al. (1997). The top of the pipe was covered with a wire net. Five pipes were set in each study plot and five laboratory-reared pupae were buried in each pipe in mid-August. The total number of buried pupae was 25 (5 x 5) at each plot in each year. These pupae were returned to the laboratory in mid-May of the following year. They were placed in individual plastic cups containing moist tissue paper, kept in the dark, and checked weekly.

Table 2. Life table of *Q. punctatella* collected at the final instar stage from the outskirts of defoliated area D-2

stage *x*	*lx*	*lx*(%)	*dxF*	*dx*	*dx*(%)	*qx*(%)
final instar	275	100.0%	sub total	124	45.1%	45.1%
		entomopathogenic fungi				
			Paecilomyces farinosus	11	4.0%	4.0%
			Beauveria bassiana	21	7.6%	7.6%
		wasp parasitoid				
			Eulophus larvarum	1	0.4%	0.4%
		tachinid fly parasitoids				
			Pales pavida	2	0.7%	0.7%
			unidentified fly	2	0.7%	0.7%
		unidentified disease		87	31.6%	31.6%
mature larva	151	54.9%	sub total	117	42.5%	77.5%
		entomopathogenic fungi				
			Paecilomyces farinosus	11	4.0%	7.3%
		tachinid fly parasitoids				
			Pales pavida	54	19.6%	35.8%
			Eutachina japonica	1	0.4%	0.7%
			unidentified fly	11	4.0%	7.3%
		failure to pupate		4	1.5%	2.6%
		unidentified disease		36	13.1%	23.8%
pupa	34	12.4%	sub total	14	5.1%	41.2%
		entomopathogenic fungi				
			Paecilomyces farinosus	2	0.7%	5.9%
			Cordyceps militalis	10	3.6%	29.4%
		unidentified disease		2	0.7%	5.9%
adult	20	7.3%				

Results

Parasites During Outbreaks. Forty-five percent of the final stadium larvae collected from the outskirts of the defoliated area in area D (plot D-2) on August 1 died before maturing (Table 2). Most of the cadavers (70.1%) did not have entomopathogenic fungi, viruses or parasitoids. However, one species of bacteria with weak pathogenicity was found in most of the checked larvae (K. Miyamoto, personal communication); their deaths were attributed to "unidentified disease" because only a small number of these cadavers were checked. The most common identified mortality factor before maturing was the entomopathogenic fungus, *Beauveria bassiana*; 21 individuals died from this infectious disease (qx = 7.6 %). The second largest cause of mortality was another entomopathogenic fungus, *Paecilomyces farinosus* (qx = 4.0 %). Tachinid fly parasitoids were the largest mortality factor during the mature larval stage (qx = 43.8 %). Of these, *Pales pavida* caused the largest mortality (qx = 35.8 %). *Paecilomyces farinosus* was the second largest mortality factor (qx = 7.3 %), except for the "unidentified disease" (qx = 23.8%). Only 34 individuals out of 275 pupated (lx = 12.4 %), but ten died from *C. militaris* (qx = 29.4 %) and two from *P. farinosus* (qx = 5.9 %) during the pupal stage. The deaths of two individuals were attributed to unidentified disease. Twenty adults emerged (lx = 7.3 %). There have been several reports that infectious diseases, especially *C. militaris*, caused large mortalities during the pupal stage of *Q. punctatella* in the soil (Igarashi 1975, Igarashi and Suzuki 1980, Yanbe and Igarashi 1983). The results shown here indicate that parasites, including larval-attacking parasitoids, caused considerable mortality during the population outbreaks.

Table 3. Percentage mortality (dx) of *Q. punctatella* collected during population outbreaks

Collecting Stage	Final Instar Before Maturing		Mature Larva		
Collecting Date	Aug.1	Aug.1	Aug.1	Aug.1	Aug.7
Site	Epi-Ctr D-1	OS D-2	Epi-Ctr D-1	OS D-2	OS D-2
Mortality Factor					
Entomopathogenic fungi					
Beauveria bassiana	1.7	7.6	4.8	1.5	2.9
Paecilomyces farinosus	3.3	8.7	7.3	7.0	4.3
Cordyceps militaris	1.2	3.6	4.0	10.3	7.2
Wasp parasitoid					
Eulophus larvarum	0.2	0.4			
Tachinid fly parasitoids					
Pales pavida	5.3	20.3	23.4	20.6	27.5
Eutachina japonica		0.4	16.9	18.0	17.3
P. pavida + *E. japonica*			4.8	4.4	2.9
unidentified fly 1.0	4.0		8.0	3.3	10.1
N.I.	86.6	46.9	27.4	5.1	21.6
Total dx	99.3	91.9	96.6	70.2	93.8

OS: Outskirts; N.I.: Not Identified

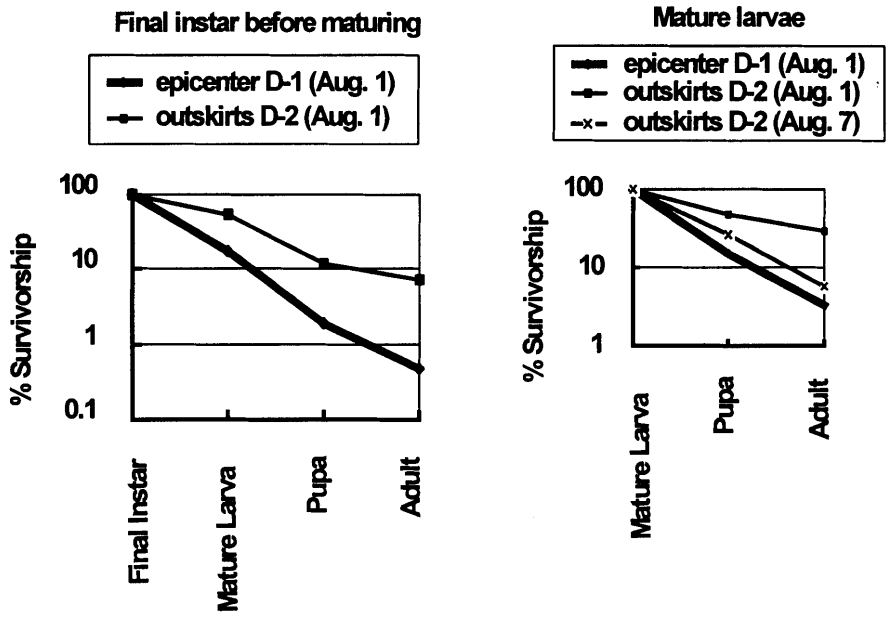


Figure 3. Survivorship curves of *Quadricalcarifera punctatella* collected during population outbreaks in Area D (Iwakisan) in 1994.

Mortality and body size were compared among these groups collected at different developmental stages, from different plots, and on different dates. There was a clear tendency for the survival rate to be high in groups collected (1) at earlier dates when they were collected at the same stage from the same location, (2) at the later developmental stages when collected from the same location on the same date, and (3) at the outskirts when collected at the same stage on the same date (Fig. 3). The mortality caused by unidentified disease varied greatly, being lower in the groups with high survival rate than in the groups with low survival rate (Table 3). Conversely, the mortality caused by fungal diseases was high in high survival groups. A similar tendency was found with body size. The weight of *Q. punctatella* pupae was larger in groups collected at earlier dates, in older developmental stages, and in locations farther from the epicenter (Table 4). These results indicate that high mortality and small body size were caused by a food shortage and/or density effects because there was a clear tendency for groups that had experienced a food shortage from the younger developmental stages to become smaller and suffer greater mortality.

Table 4. Mean weight of *Q. punctatella* pupa (in mg) collected during population outbreaks in site D (Iwakisan) in 1994

Date	Site	Collected Stage	Mean	SE	(n)	Mean	SE	(n)
Aug. 1	Epi-Center (D-1)	Final Instar Before Maturing	302	102	(6)	367	24	(2)
Aug. 1	Outskirts (D-2)	Final Instar Before Maturing	340	57	(23)	391	46	(11)
Aug. 1	Epi-Center (D-1)	Mature Larva	412	67	(12)	450	39	(6)
Aug. 1	Outskirts (D-2)	Mature Larva	320	41	(12)	370	34	(7)
Aug. 26	Epi-Center (D-1)	Pupa				394		(1)
Aug. 26	Outskirts (D-2)	Pupa	401	52	(23)	439	57	(16)

Aerial Infection of Larvae by Entomopathogenic Fungi. The survival rate was highest at area C where the field population was in the increasing phase and lowest at area A in the decreasing phase three years after the outbreak (Fig. 4). A delayed induced response of beech trees was the main factor causing the great mortality at area A (Kamata et al. 1996b). The mortality caused by fungal disease was lowest in area C but highest in area B (Fig. 5). This shows that infectious disease still caused high mortality in area A where the *Q. punctatella* density decreased after the population outbreak in 1990. These results indicate that infectious disease and delayed induced response of the beech trees operate as delayed density-dependent mortality factors which continue for at least three years after severe defoliation.

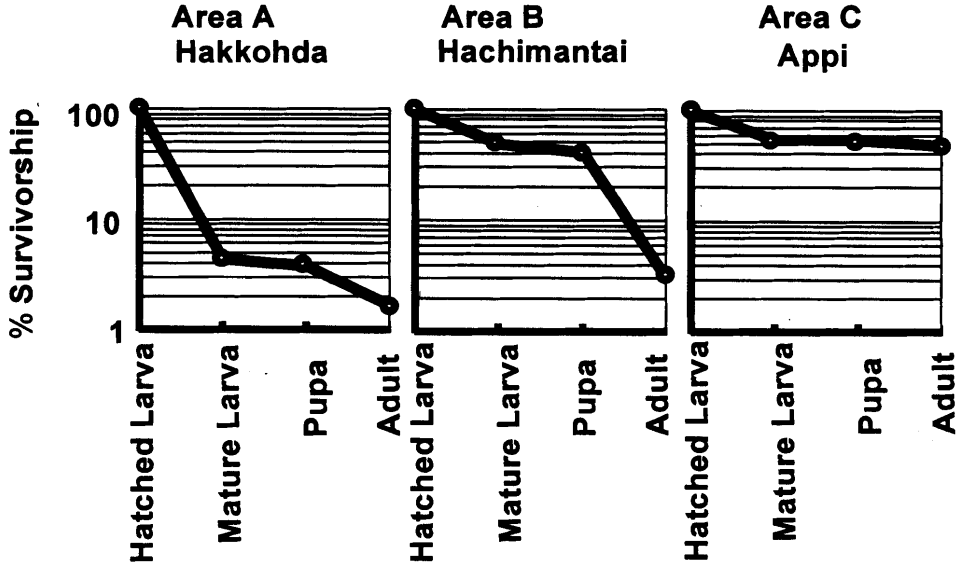


Figure 4. Survivorship curves of *Quadricalcarifera punctatella* reared in netted enclosures in three disjunct beech forests. Survivorship curves are shown for a year of decreasing population in site A, for a peak generation year in site B, and for a year of increasing population in site C.

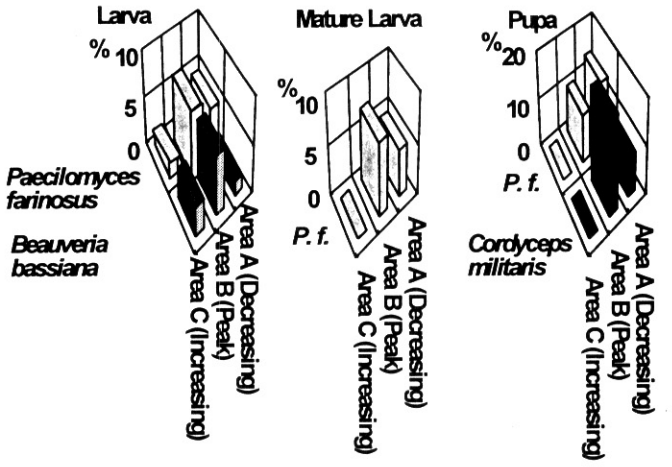


Figure 5. Aerial infection by fungal diseases of *Quadricalcarifera punctatella* larvae reared inside netted enclosures in three disjunct beech forests. Percentage mortality in each developmental stage is shown for each entomopathogenic fungus.

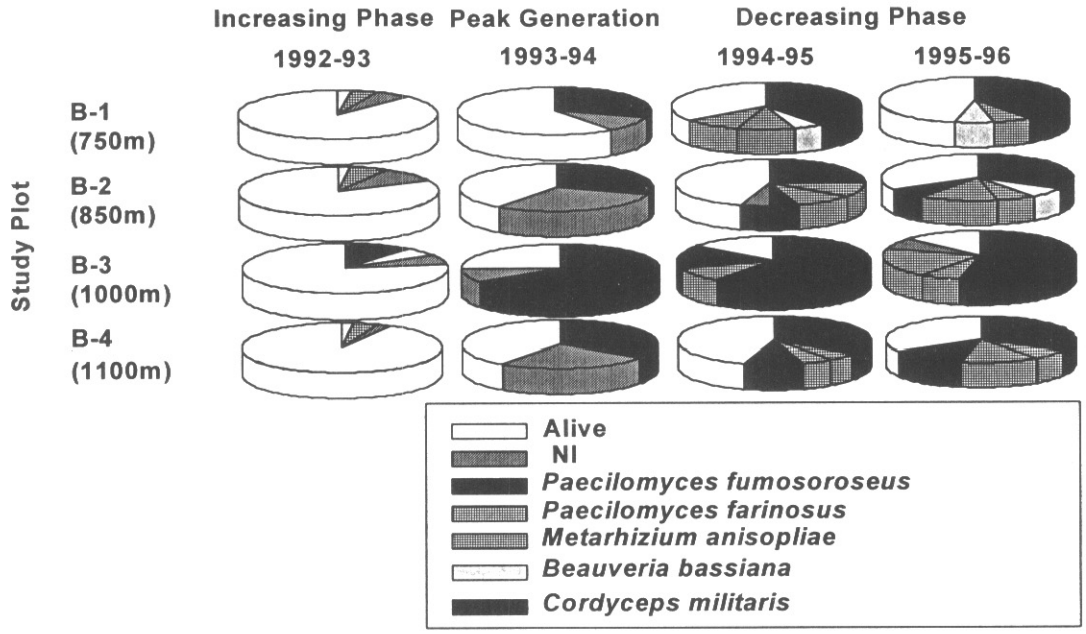


Figure 6. Annual changes in mortality caused by infectious disease when *Quadricalcarifera punctatella* pupae were buried in soil samples placed in plastic cups. Numbers in parentheses are elevations above sea level.

Infections of Entomopathogenic Fungi in the Soil. Five entomopathogenic fungi (*C. militaris*, *Beauveria bassiana*, *Metarhizium anisopliae*, *Paecilomyces fumosoroseus*, and *P. farinosus*) were identified as the mortality agents of pupae of *Q. punctatella* in the soil, with *C. militaris* being the most prevalent. In the year preceding the peak generation, the

survival rate was high (Fig. 6). More than 75% of individuals survived in 1992. *C. militaris* was found only in B-3 where the field population density of *Q. punctatella* was highest among the four study plots (B-1 ..B-4), but the percentage mortality caused by the fungus was low. In the year of the peak generation (1993), the survival rate decreased greatly: the percentage survival was highest in B-1 where *Q. punctatella* density was lowest, but the survival rate was smaller than 25% in B-3 where the field density was highest. More than 70% of the pupae were infected with *C. militaris* in B-3. Many fruit bodies of *C. militaris* were found on dead pupae in B-3 and its density in 1993 was estimated at 2.5 /m². Infection by *C. militaris* occurred in all the study plots. *P. farinosus* caused the second largest mortality during that peak year. In 1994, when the larval density decreased greatly, these entomopathogenic fungi still caused high mortality. Mortality caused by *C. militaris* was almost the same as that in 1993. *C. militaris* and *P. farinosus* still caused high mortality in 1995 two years after the peak generation.

From the viewpoint of temporal density-dependence, these fungal diseases acted as time-delayed density-dependent mortality factors, and *C. militaris* was the most effective among them. The mortality caused by *C. militaris* also showed spatial density-dependence: the mortality was highest in B-3 where the field population density was highest and lowest in B-1 with the lowest caterpillar density.

C. militaris caused higher mortality to *Q. punctatella* pupae when the pupae had been buried in field soil (Fig. 7). This shows that these pathogens caused high mortality in non-outbreak areas because almost all experimentally introduced insects were killed by the fungi during the peak generation. More than 70% of the insects were killed by *C. militaris* in the two years after the peak. Thus, these fungal diseases caused time-delayed density-dependent mortality in the soil of non-outbreak areas

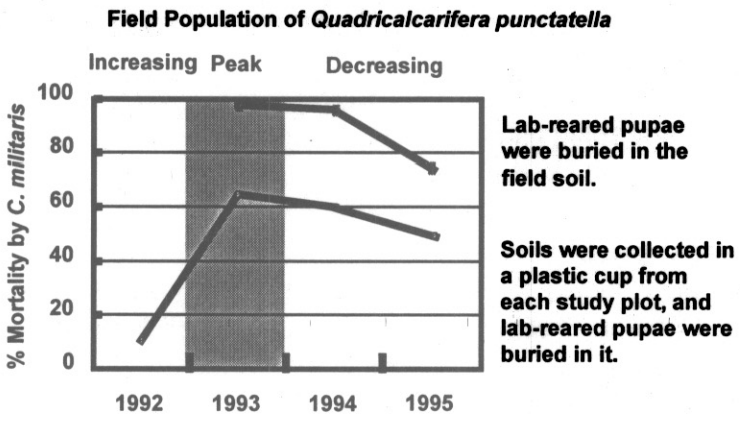


Figure 7. Annual changes in mortality caused by *Cordyceps militaris* when *Quadricalcarifera punctatella* pupae were buried in the soil of plot B-3.

Discussion

These insect pathogens seem to be the most plausible factors generating the main cycles of *Q. punctatella* because they acted as time-delayed density-dependent mortality factors both in outbreak and non-outbreak areas.

There have been several reports that *C. militaris* had appeared the year following *Q. punctatella* outbreaks (Igarashi 1975, Igarashi and Suzuki 1980, Igarashi 1982, Yanbe and Igarashi 1983), so it has been speculated that this entomopathogenic fungus is a main factor in terminating the beech caterpillar outbreaks (Igarashi 1982, Yanbe and Igarashi 1983). The present experiment in which field larvae were reared in the laboratory proved that parasites, including tachinid fly parasitoids, played important roles in terminating these insect outbreaks. Unidentified diseases and tachinid fly parasitoids caused higher mortality; and fungal diseases caused lower mortality in groups collected at a later date, in younger developing stages, and in places nearer the epicenter.

However, these results do not necessarily indicate that the fungal diseases are less important than bacteria and/or tachinid fly parasitoids, because the greatest mortality (> 99%) was caused by these fungal diseases when lab-reared insects (pupae) were artificially introduced to the soils of severely defoliated beech forests (Kamata et al. unpublished), suggesting that fungal disease could have given the caterpillar outbreaks a finishing blow even if the other mortality factors had not been so effective. Bacteria and tachinid flies attack *Q. punctatella* at earlier stages than do fungal diseases, and bacteria and tachinid flies possibly had a stronger spatial density-dependence than did the fungal diseases; the bacteria and tachinid flies became effective only when the caterpillar density became extremely high. May (1974) and Royama (1992) showed that most insect cycles were caused by endogenous population processes and that weather anomalies only synchronize oscillations of disjunct populations by causing deviations from intrinsic population processes. Liebhold et al. (1996) speculated that the cyclic behavior of the beech caterpillar was caused by endogenous population processes, such as numerical interactions with natural enemy populations or host trees. The results of this study generally support the hypothesis that infectious disease generates *Q. punctatella* cycles. The synchrony of oscillations of disjunct populations is probably caused by a synchrony of weather conditions (Moran 1953, Wellington 1957, Martinat 1987, Kamata and Igarashi 1995b).

The next question is why these entomopathogenic fungi have a time lag in their density-dependence. These fungi can live in the ground as soil fungi (Watanabe 1994). If the fungi increase more intensively within the insects than in the soil, and if this continues until the time of the next generation of the host, the host-parasite system will possess a time-lag. However, the time-lag depends mainly on the fruiting bodies or coremia of the fungi because these organs scatter their spores to the air in the summer following the infections of the insects by the fungi: *C. militaris* scatters ascospores from its fruit bodies in July-August, and *P. farinosus* and *P. fumosoroseus* scatter their conidia from their coremia in June-September. These spores directly infect *Q. punctatella* larvae on trees (Sato et al. 1997) and also enhance the density of fungi in the soil (Kamata et al. 1997).

Acknowledgement

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Regarding the Outbreak of *Zeiraphera rufimitrana* H.S. on Silver Fir in Romania

VASILE MIHALCIUC AND MIHAELA BUJILÃ

The Forestry Research and Management Institute- Station of Brasov, Romania

ABSTRACT The last outbreak of *Zeiraphera rufimitrana* H.S. on silver fir in Romania took place during the period 1989-1994 in the curved zone of the Oriental Carpathians and affected fir forests from the Regional Districts Covasna, Buzău, Vrancea, Harghita, and Bacău.

FROM 1989-94 an outbreak of *Zeiraphera rufimitrana* occurred in the carpathian region of Romania. The primary focus of the outbreak occurred on the perimeter of the Ranger Districts Sânmartin (Harghita), Bretcu (Covasna) and Gura Teghii (Buzău). The research that is presented here summarizes the development of an outbreak that occurred during this period and the damages associated with it. We also discuss the abiotic and biotic factors that are implicated in the dynamics of *Z. rufimitrana*.

Drought conditions (barreling index = 21-24) existed for several years prior to the outbreak and these conditions were very favorable for increasing populations of *Z. rufimitrana*. The study established that the highest mortality caused by biotic factors (parasites, predators, disease) occurred in the egg stage (20-75%); mortality caused by biotic factors in the larval and pupal stages was less than 20%.

Evolution of the Outbreak

Studies of past outbreaks of *Zeiraphera rufimitrana* (1959-1963) within the Ranger Districts of Sinaia, Brasov and Anina, as well as the most recent outbreak (1992-1994) within the Range District Sănmartin, Bretcu and Gura Teghii, emphasize that the highest density in the outbreak occurs in a relatively short interval of 5 years or less.

At Băile Tusnad (Table 1), visible defoliation appeared in the spring of 1989, followed by an increase in both the average percentage of defoliation and the frequency of defoliated shoots until 1991 when maximum values occurred. A decrease in both these measurements, which are measures of damage intensity, occurred in 1992.

In 1993 the defoliation was very minimal and analysis of shoots was not needed. Based on these data, we estimate that the outbreak in this area lasted 4-5 years, 3 years for population build-up and 1-2 years for decline.

Pages 47-52 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Table 1. Estimation of damage to silver fir shoots caused by defoliation by *Zeiraphera rufimitrana* H.S., Băile Tusnad - Ranger district Sănmartin

Year	Number of shoots analyzed	Number of shoots defoliated	Defoliated shoots frequency %	Defoliation (%)	Defoliation intensity (%)
1989	1095	401	37.5	45.5	17.1
1990	2020	1055	52.2	60.5	31.6
1991	2965	1790	60.4	75.9	45.9
1992	4190	910	21.7	59.9	13.0

Field observations also indicate that on sites where silver fir grows best, the gradation ends faster and *Z. rufimitrana* populations reach much higher densities than in other areas at the periphery of the primary focal areas. The outbreaks are prolonged in stands located on north slopes, at altitudes over 1,000 m, and on valley floors, places where chronic populations occur.

Natural Factors Involved in the Outbreak

Abiotic Factors. The fir red-headed caterpillar is adapted to a continental climate so it is less sensitive to temperature variations that occur during the winter and in the spring. If high variation in temperature occurs in the spring and there is a delay in opening of the foliaceus buds, and if there are no male flowers to feed upon, larvae can survive for possibly one week and then will die of starvation. If the foliaceus buds open at the last moment, the larvae will survive but their development will be prolonged.

In the branch samples from Băile Tusnad that we analyzed during May 1993, we found first stage larvae that were drowned in resin. This mortality was caused by the abundance of resin in the foliaceus buds which occurs during periods of high humidity, when sap flow is active. Also, in years with high variation in temperature during the month of May, when the appearance of larvae is delayed on shaded branches, the larvae are forced to feed on needles from growing foliaceus-shoots that are high in resin and they may drown.

Usually, unfavorable climatic factors cannot stop the outbreak from progressing, but they can play an important part in the release phase of the outbreak. With regard to this assertion we provide some information on the climatic factors that preceded the outbreak on the Bretcu Ranger district area.

Climatic factors that occurred prior to and during the outbreak of 1989-1994. The following climatic factors were recorded at the Targu Secuiesc Meteorological Station during the period 1982-1993: mean annual temperatures (°C) (Fig. 1), annual rainfall (mm) and the general average rainfall provided by "Clima RSR, vol. II," (Fig. 2), and the annual barreling index (Fig. 3).

Before the start of the gradation in 1989, below average mean temperatures occurred in 4 of 8 years (1982, 1985, 1987, 1988). Mean rainfall was below the general average value in 6 of 8 years during this period (Fig. 2). The more arid climate reflected in the calculation of the barreling index, which was below the critical value of 30 in 6 of 8 years, thus indicating drought conditions.

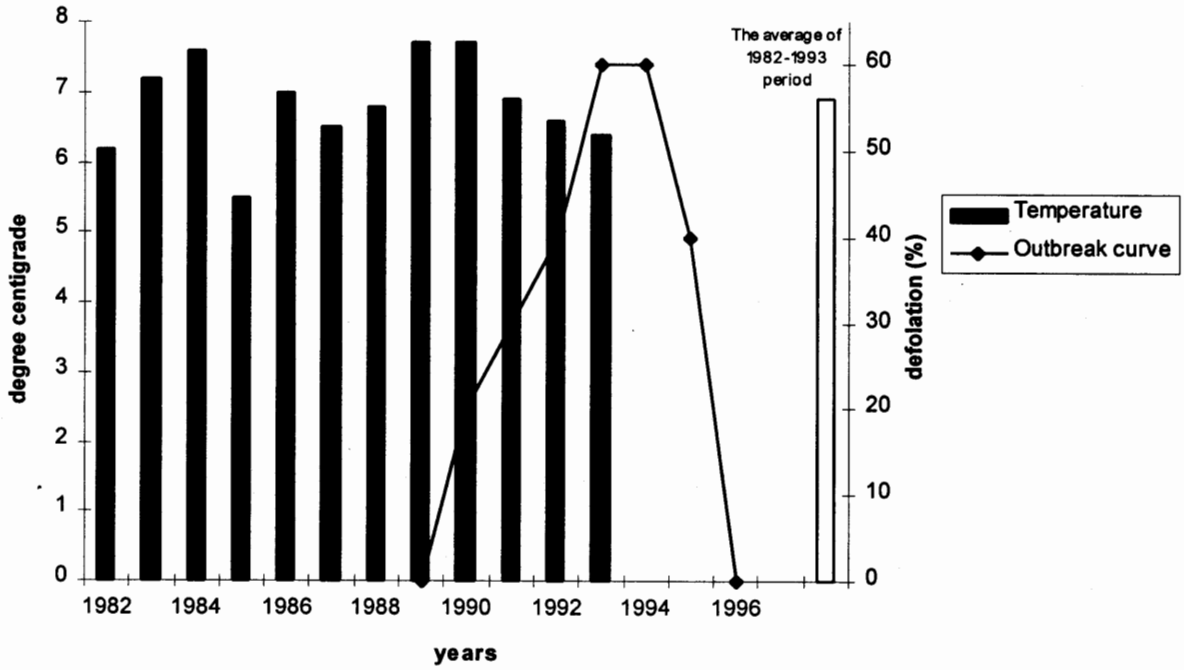


Figure 1. Average yearly temperature (degrees Centigrade).

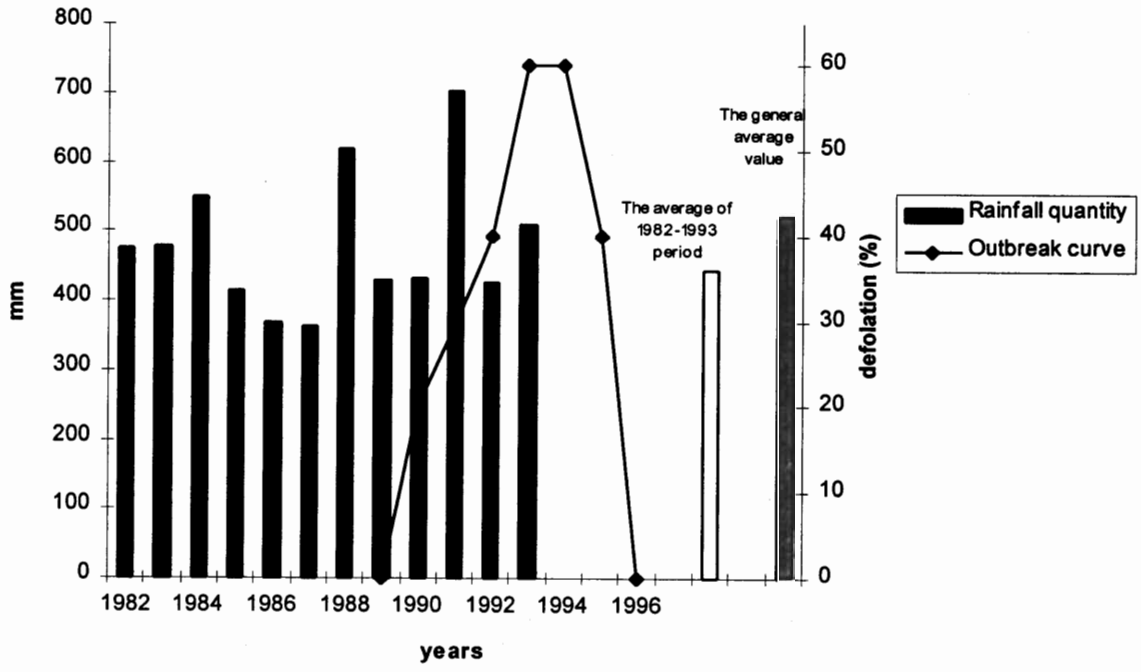


Figure 2. Annual rainfall (mm).

In 1990, the incipient phase of the outbreak, the mean annual temperature, was higher than that recorded for any other year during the period (7.7°C compared with 6.8°C). Precipitation was below average and the barreling index was significantly low (24.4).

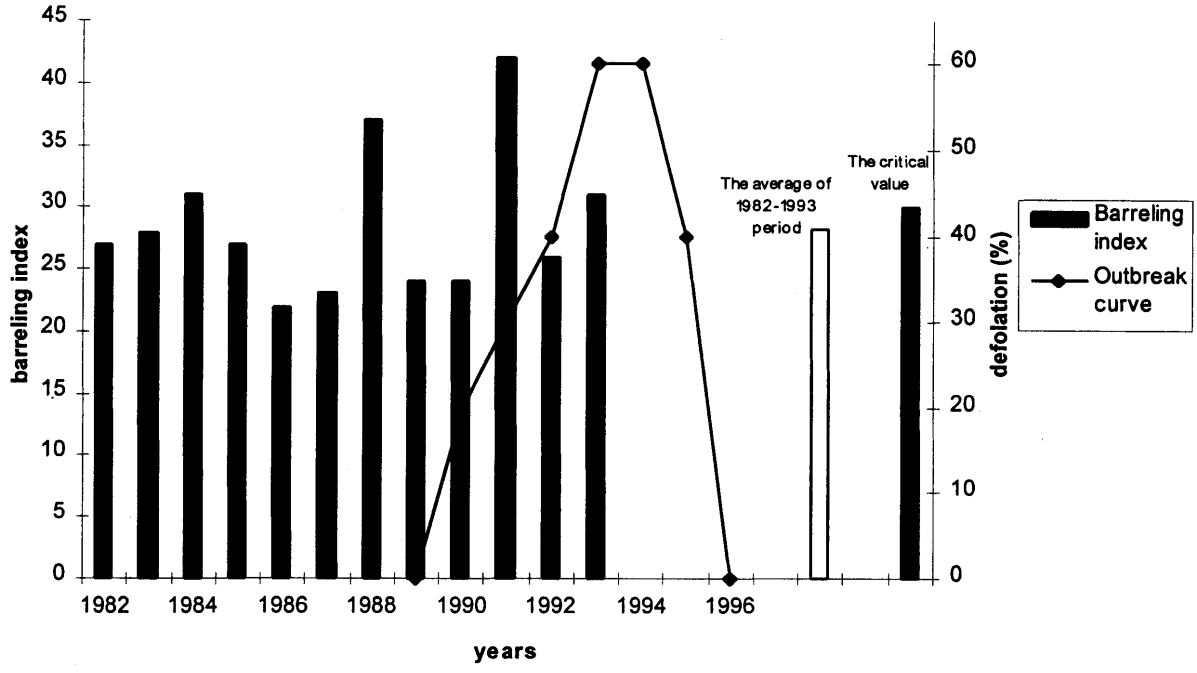


Figure 3. Barreling index.

Climatic conditions during the numeric growth phase of the outbreak (1991-1992) were variable. In 1991, the mean annual temperature was near the average for the period, however, precipitation was much above the general average (701.3 mm/m^2 compared with 517.0 mm/m^2). This resulted in a barreling index of 41.5, which is well above the critical value of 30. However in 1992, the barreling index was again below the critical value (26).

In 1993, the first year of the eruption phase of the gradation, the mean annual temperature was lower than the average for the period (6.4°C vs 6.8°C). Annual precipitation was higher than for the period average, but lower that the general average. The barreling index was 31.8 above the average value for the period, but under the general average.

In conclusion, although the average barreling index (a measure of drought stress) for the period 1982-1993 was only slightly below the critical value of 30 (Fig. 3), the extremely low values that occurred in 4 of the 8 years (1986, 1987, 1989, 1990) were important in the release phase of the outbreak.

Biotic Factors. Biotic factors which are important causes of mortality in the various life stages of *Z. rufimitrana* include parasites, predators, and pathogens. During our research, conducted in areas where gradations occurred, we established that the highest mortality was recorded in the egg stage. Most of the eggs were parasitized by *Trichogramma* sp., and were distinct from the rest of the eggs because they are black in color. Other eggs were destroyed by predators, which included hemipterans, and some of the eggs were unfertilized.

In the Băile Tusnad area, there were distinct differences in the level of egg mortality during gradation phases. In the winter of 1991/1992, just prior to the eruption phase of the outbreak (1993), egg mortality was estimated at 20-30%. However, at the same location, egg mortality was 51% in 1992 and 55% in 1993. At Bretcu Ranger District, egg mortality was 57.3% in the winter of 1993/1994 and 60% in the spring. Egg mortality of 56-60% was measured also in the Gura Teghii Ranger district during the same year.

Estimates of the natural mortality of *Z. rufimitrana* caterpillars were obtained by collecting larvae in the field and rearing them in the laboratory. By collecting infested branches from Băile Tusnad during May-June 1991, we determined that natural mortality was 2-3% for the first two larval stages and 10-20% for the last stage larvae. Mortality of the mature caterpillars was caused by pathogenic organisms (10%), parasites (5%) and predators (2-3%). Analysis of the biological material reared in the laboratory from the Bretcu Ranger District during May-June 1994 indicated that natural mortality in the larvae stages was less than 10%.

A bilateral cooperation with the International Institute of Biological Control (IIBC), Delemont, Switzerland, was initiated to determine the species and abundance of parasitoids that attack the late stage larvae of *Z. rufimitrana*. Twelve thousand larvae were collected and reared from Băile Tusnad (1992) resulting in the recovery of parasitoids from the families Braconidae, Ichneumonidae, and Tachinidae. A list of species and rates of parasitism are provided in Table 2.

In the summer of 1993, 694 pupae were collected from Băile Tusnad and Bretcu and held for emergence of parasitoids. Only 30 parasitoids (0.04%) emerged between 30 July and 9 August, and the most frequent species recovered was an ichneumonid, *Tycherus osculator* (Thunberg).

Table 2. Percentage parasitism of *Zeiraphera rufimitrana* larvae collected at Băile Tusnad in 1992 and reared at the IIBC European Station, Delémont, Switzerland

Date No. larvae reared Main instar	June 3-4, 1992 6,923 L4	June 9-10, 1992 4,755 L5
Braconidae		
Dolichogenidea lineipes (Wesmael)	7.4	3.4
Macrocentrus marginator (Nees)	0.7	7.0
Ichneumonidae		
Campopleginae[a]	0.4	2.5
Lissonota sp.	0.4	0.1
Mesochorus sp.[b]	*	*
Metopiinae	--	2.2
Others	0.1	2.2
Tachinidae		
Undetermined	*	

[a]Campopleginae included, by order of importance, an undetermined diapausing species, *Tranosema nigridens* (Thomson), *Campoplex interruptusI* Horstmann, *C. rufinator* Aubert, *C. satanator* Aubert, and *Sinophorus* sp.

[b]Hyperparasitoid

*Less than 0.1% parasitism

Acknowledgements

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Towards the Use of Pine Sawfly Pheromones in Forest Protection: Evaluation of a Behavioral Antagonist for Mating Disruption of *Neodiprion sertifer*

OLLE ANDERBRANT[1], HANS-ERIK HÖGBERG[2], ERIK HEDENSTRÖM[2] AND JAN LÖFQVIST[3]

[1]Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
[2]Department of Chemistry and Process Technology, Mid Sweden University, S-851 70 Sundsvall, Sweden
[3]Department of Plant Protection Sciences, Swedish University of Agricultural Sciences, Box 44, S-230 53 Alnarp, Sweden

ABSTRACT Pine sawflies of the family Diprionidae use sex pheromones for mate location. These odors can potentially be used in forestry for detection, population monitoring or suppression of harmful populations. The European pine sawfly, *Neodiprion sertifer*, uses the acetate or propionate of (2*S*, 3*S*, 7*S*)-dimethyl-pentadecan-2-ol (diprionol) as its pheromone, whereas the (2*S*, 3*R*, 7*R*)-isomer acts as an antagonist in most of the species' distribution range. Three small-scale attempts to use the antagonistic isomer for disturbance of the mate location system (mating disruption) are presented. The isomer was released alone or in combination with the pheromone isomer from dispensers 10 m apart in plots ranging from 0.5 to 4.5 ha in size depending on the experiments. The catches in pheromone traps inside and outside the treated plots were used for evaluation, together with the sex ratio of the following generation. Comparison with earlier studies showed that the antagonistic (2*S*, 3*R*, 7*R*)-isomer is less efficient for mating disruption than the attractive (2*S*, 3*S*, 7*S*)-isomer. A combination of the two isomers, containing 10% of the (2*S*, 3*R*, 7*R*)-isomer, was not more efficient than using the attractive isomer alone. Finally, a project, "Pine Sawfly Pheromones for Sustainable Management of European Forests," supported by the European Commission, is presented.

SEVERAL SPECIES OF the sawfly family Diprionidae, conifer or pine sawflies, are notorious pests of pines, because the larvae feed on needles and can consume a large proportion of the foliage (Smith 1993). Suppression of outbreaks is usually accomplished using aerial application of insecticides. Because these sawflies use chemical communication (pheromones) for mate finding (Anderbrant 1993), it may be possible to exploit their pheromone system for monitoring population densities or population suppression. Although the chemical structure of the first pine sawfly pheromone was determined 20 years ago (Jewett et al. 1976), attempts to develop application methods did not begin until recently (Anderbrant et al. 1995a, b).

The European pine sawfly, *Neodiprion sertifer* (Geoffroy), occurs in large parts of Europe, Asia and eastern North America (Kolomiets et al. 1979). In some regions, it is the most important diprionid species. It hibernates in the egg stage; in northern areas, the eggs hatch in late spring and the larvae feed on needles until pupation, usually in July. After a short period as pupae, adults emerge from August to October. The female emits a sex pheromone to attract males, and after mating, she oviposits on the current year's needles.

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Unfertilized eggs develop into males and fertilized eggs develop into females. Unmated females can also lay eggs, which result in male offspring only.

The sex pheromone of *N. sertifer* is the acetate or propionate (both are behaviorally active) of the alcohol (2*S*, 3*S*, 7*S*)-3,7-dimethyl-2-pentadecanol (diprionol) (Kikukawa et al. 1983, Wassgren et al. 1992). Esters of another stereoisomer, (2*S*, 3*R*, 7*R*)-diprionol, act as behavioral antagonists, and by adding about 1 % or more to the attractive isomer, a nearly complete inhibition is obtained (Anderbrant et al. 1992b).

Earlier studies have described the first attempts to use the pheromone (2*S*, 3*S*, 7*S*)-diprionyl acetate for mating disruption of *N. sertifer* (Anderbrant et al. 1995a, b). By "saturating" the pine stand with synthetic pheromone, the male's ability to locate and reach the pheromone emitting females was expected to decrease to such an extent that matings would be rare. The result would be fewer females emerging the following year, which in turn would reduce the population size. Indeed, mating disruption occurred as recorded by reduction of catch in traps baited with synthetic pheromone (Anderbrant et al. 1995a, b), but no effects on the sex ratio or population density have been recorded to date (Anderbrant et al. 1995b).

Parallel to the work described above, a number of small field experiments were conducted with the behavioral antagonist as an agent for mating disruption. These studies will be described below. Possible future use of pine sawfly pheromones in forestry will be discussed at the end. An international and interdisciplinary project, PHERODIP, will also be presented. This project, supported by the European Community, has the goal of developing pheromone-based methods useful in forestry.

Materials and Methods

In the treated areas, dispensers with (2*S*, 3*R*, 7*R*)-diprionyl acetate were placed at about 2 m heights in a grid with 10 m spacing between dispensers. Dispensers consisted of 4 x 1 cm dental cotton rolls (Celluron® No. 2, Paul Hartmann, S.A., France). To monitor the mating disturbance, Lund-I pheromone sticky traps (Anderbrant et al. 1989) were placed inside the treated area. These traps were baited with (2*S*, 3*S*, 7*S*)-diprionyl acetate released from the same type of dispenser. Catches in these traps were compared with catches in similar traps placed in comparable untreated areas. The pure synthetic diprionyl acetate isomers were prepared according to Högberg et al. (1990).

Experiment 1 - 1988. This experiment was conducted in a young Scots pine, *Pinus sylvestris* L., plantation in the province Östergötland, Sweden, during 1988-1989. In early summer 1988, a large number of pine plantations were censused for larval *N. sertifer* using the method described in Anderbrant et al. (1995a). Two plantations that were similar in larval density, tree height (2 m) and tree density (3,500 per hectare) were selected for this experiment; one was for the treatment and the other was used for comparison. In the treated area, 64 dispensers were used to cover a 0.5-ha area, and in both the treated and untreated plantations, three pheromone traps were used. They were placed about 30 m from each other, forming a triangle.

In 1988, each disruption bait contained 150 μg of (2*S*, 3*R*, 7*R*)-diprionyl acetate in a *threo*-mixture, containing <0.02 % *erythro*-isomers. Two of the other three stereoisomers

present in this mixture, (2*R*, 3*S*, 7*S*)- and (2*R*, 3*S*, 7*R*)-, are both electrophysiologically and behaviorally inactive (Hansson et al. 1991, Anderbrant et al. 1992b), and the third, (2*S*, 3*R*, 7*S*)-, has a similar, but much weaker, effect compared to the (2*S*, 3*R*, 7*R*)-isomer. The dispensers were displayed on August 17, replaced on August 30 and removed on October 4. The estimated release of the (2*S*, 3*R*, 7*R*)-isomer was about 0.35 mg ha^{-1} d^{-1} (estimated from Anderbrant et al. 1992a).

The baits in the monitoring traps contained 600 mg of (2*S*, 3*S*, 7*S*)-diprionyl acetate. The stereoisomeric purity was >97.5 % (Anderbrant et al. 1992b and their "SSS 1988"). Traps were put out on August 17 and baits replaced on August 30 and September 16. The release rate per trap was about 30 μg d^{-1} (Anderbrant et al. 1992a). Sticky bottoms were replaced seven times during the trapping period, which was completed on October 4.

Experiment 1 - 1989. In 1989, larvae were censused in the same way as the previous year, and in addition, 30 larvae were collected from each site. The larvae were reared in ventilated cardboard boxes (Wassgren et al. 1992), fed fresh pine twigs and moistened until cocoon formation, at which time the sex was determined by cocoon size.

The same number of disruption dispensers was used as in the previous year. However, they were loaded with four times as much, i.e., 600 mg, of a mixture containing 87% (2*S*, 3*R*, 7*R*)-diprionyl acetate, 13% of the (2*S*, 3*R*, 7*S*)-isomer and 0.07% of the attractive (2*S*, 3*S*, 7*S*)-isomer. The remaining five inactive stereoisomers made up around 0.5%. The experiment began on August 2, and dispensers were replaced on August 19 and 30 and on September 14. The experiment was completed on October 4. The estimated release of the (2*S*, 3*R*, 7*R*)-isomer was about 3 mg ha^{-1} d^{-1} (Anderbrant et al. 1992a).

Instead of three monitoring traps per site, six traps were used: three were baited as the previous year with 600 mg (2*S*, 3*S*, 7*S*)-diprionyl acetate, and three were baited with 100 mg only. The stereoisomeric purity was >99%, (Anderbrant et al. 1992b and their "SSS 1989"). Baits and bottoms were replaced on the same days as mating disruption dispensers, and bottoms were exchanged even more frequently if necessary. The average release rate was around 30 μg d^{-1} from the strong traps and 5 μg d^{-1} from the weak traps. The intention was to make a census of the larval density as well as the sex ratio the following year (1990); however, due to a general crash of the population in the area, no larvae were found at the two sites.

Experiment 2 - 1990. This experiment was done in a large (>100 ha), 16-year-old lodgepole pine, *Pinus contorta* Douglas, plantation in the province of Värmland, Sweden. The treated area was 210 x 210 m, approximately 4.5 ha. In a different area within the same plantation, a mating disruption experiment with the attractive isomer was performed (Anderbrant et al. 1995b). Pheromone traps were placed at a 50-m distance along two lines through and outside the treated area (Fig. 1). To check whether the infestation level before treatment was similar inside and outside the treated area, the proportion of shoots consumed by the larvae was estimated using the method described by Anderbrant et al. (1995b).

Four hundred and eighty-four disruption dispensers were placed 10 m apart on August 5-7, and removed on October 13. Each dispenser was loaded with 2 mg of (2*S*, 3*R*, 7*R*)-diprionyl acetate from the same batch that was used in 1989 in Experiment 1, above. The average release rate was estimated at 3 mg/ha per day.

The pheromone traps were identical to the weak ones used in 1989, but bottoms and dispensers were only replaced once, on August 30. The average release rate was about 2.4 μg d^{-1}.

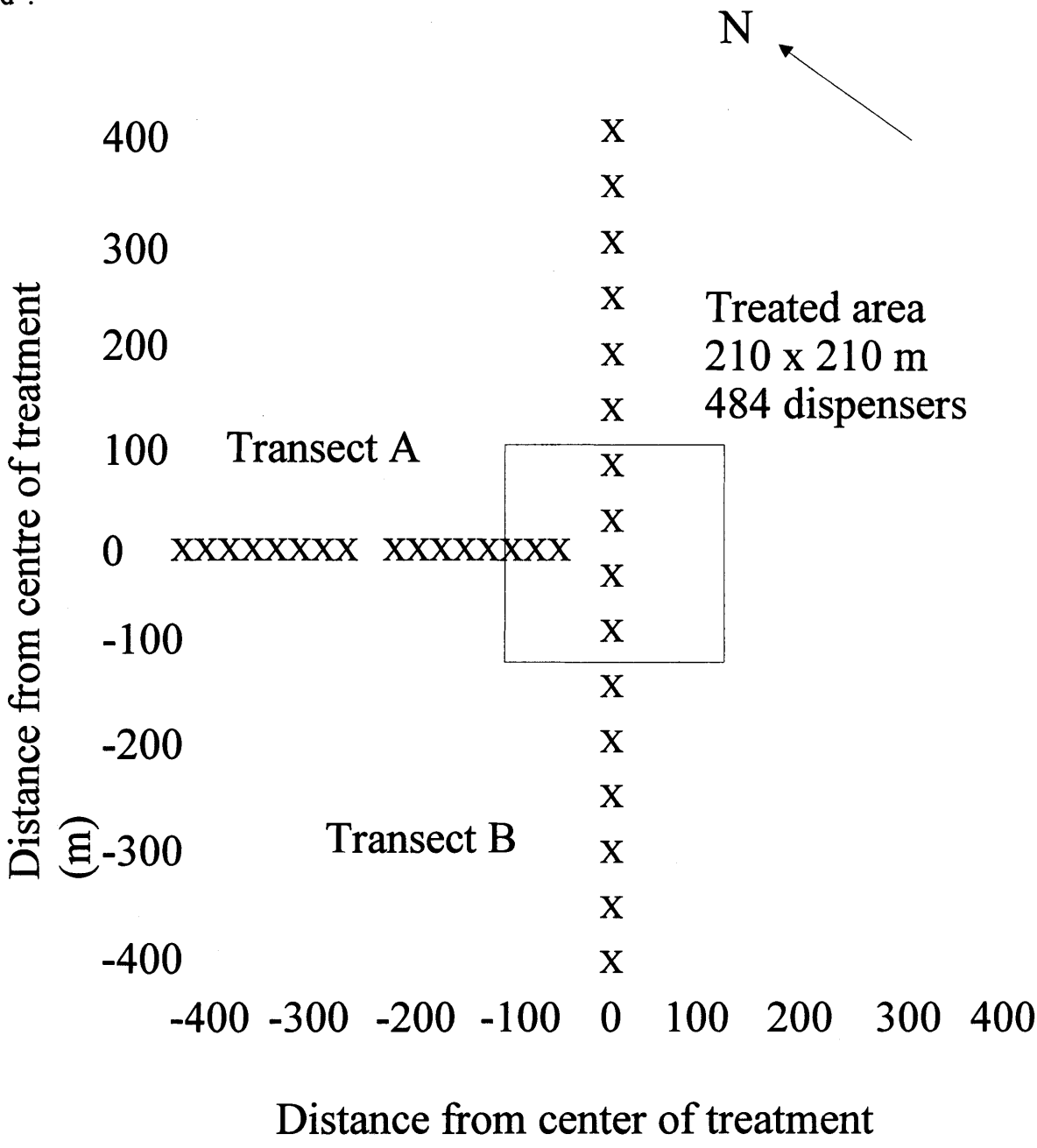


Figure 1. Outline of *N. sertifer* mating disruption Experiment 2 in 1990, showing the area treated with the behavioral antagonist (2*S*, 3*R*, 7*R*)-diprionyl acetate and the two lines with pheromone monitoring traps.

In early summer of the following year, 75 larvae were sampled inside the treated area to determine the sex ratio of the eggs laid during the treatment. Fifteen larvae were reared to pupation in each of five cardboard boxes, and the sex determined by cocoon size. As a

comparison, larvae collected outside the area treated with the attractant, 1 km away, were used.

Experiment 3 - 1994. This experiment was performed to test a possible synergistic mating disruption effect between the attractive and antagonistic isomers. It took place in young Scots pine plantations in the province Östergötland, Sweden. In 20, 1-hectare plots (one per plantation), the larval density was censused in June according to the procedure described in Anderbrant et al. (1995b). The plots were divided into three groups which were similar to each other with respect to tree height and density as well as larval density. Twelve plots were untreated, 4 plots were treated with the attractant only (*SSS*) and 4 plots were treated with a mixture of the attractant and antagonist (*SSS+SRR*). The same type and spacing of disruption dispensers as in previous experiments were used.

The 100 disruption dispensers used per plot for *SSS*-treatment were each loaded with 1 mg (2*S*, 3*S*, 7*S*)-diprionyl acetate in an *erythro*-mixture (Hedenström and Högberg 1994). The dispensers in the *SSS+SRR*-treatment were loaded with the same as in *SSS* plus 0.1 mg of (2*S*, 3*R*, 7*R*)-diprionyl acetate in a *threo*-mixture (Experiment 1 - 1988, above). Treatments began on August 1 and ended on October 6. Three pheromone traps baited with 100 µg (2*S*, 3*S*, 7*S*)-diprionyl acetate were placed at approximately a 30-m distance in the center of each plot. Bottoms and baits were replaced on September 4.

Results

Experiment 1 - 1988 and 1989. Larval densities at the two experimental sites were very similar before the treatment began in 1988: 19 larvae/m^2 at the treated site and 22 larvae/m^2 at the untreated site. The three traps at the treated site caught a total of 1747 males during the entire season compared to 3444 at the untreated site, i.e. the catch at the treated site was 59% of that at the untreated site. This percentage varied between 41 and 69 for the different trapping periods, but without seasonal trends or dependence on time since renewal of baits.

The following year, the larval density had decreased to 10 larvae m^{-2} at the treated site and 11 larvae m^{-2} at the untreated site. Seven hundred and thirteen of the larvae collected at the untreated site formed cocoons, and 17% were males, compared to 29% of 660 cocoons at the treated site. These percentages were significantly different ($p<0.01$) based on binomial confidence limits (Rohlf and Sokal 1969). The three strong pheromone traps caught a total of 3,766 males at the untreated site, and 1,321 at the treated site (35% of the catch at the untreated site). The weak traps caught 1,902 and 401 males at the untreated and treated sites, respectively, i.e. the catch at the treated site was only 21% of that at the untreated site.

Experiment 2 - 1990. The background population level, as determined by census of consumed shoots, was similar inside and outside the treated area (Fig. 2). The traps along the lines caught from a few to more than 800 males, but no effect of the disruption treatment could be detected (Fig. 3). Between 153 and 750 cocoons were formed per rearing box, with a male proportion between 19 and 39%. The average was 30% males, which was similar to the 36% found for larvae collected outside the area treated with the attractant at about a 1-km distance (Anderbrant et al. 1995b).

Experiment 3 - 1994. The average larval density for the sites in the different groups was similar: 4.5 larvae per m^{-2} for the 12 untreated plots, 4.1 for the *SSS*-treated plots and 4.4

for the *SSS+SRR*-treated plots. The trap catch in the treated plots was very small, especially during the first trapping period (Fig. 4).

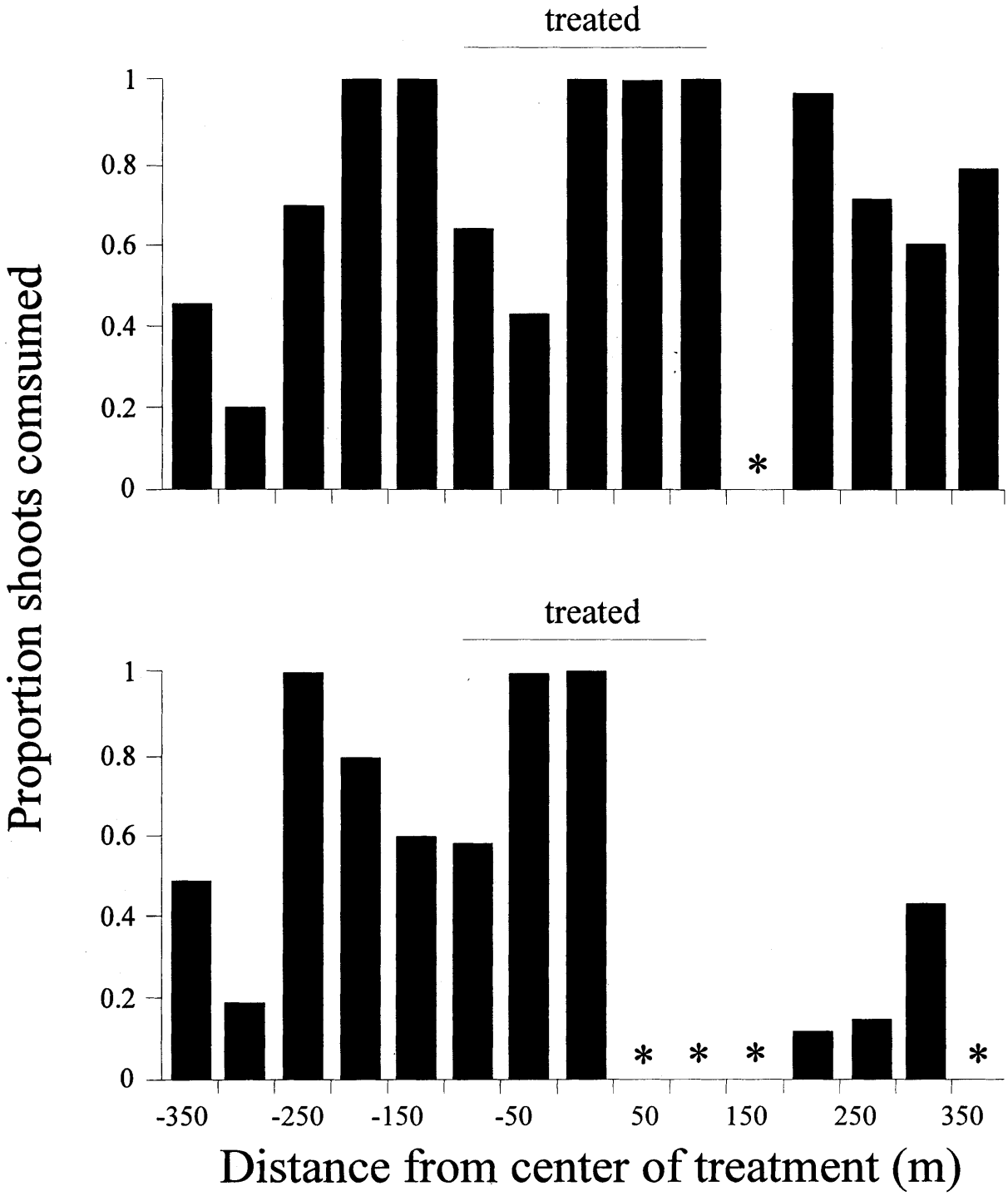


Figure 2. Damage caused by feeding *N. sertifer* larvae during 1990 along transects A (above) and B. An * indicates that no suitable tree for census of the damage was available.

Analysis of variance of log-transformed data showed that there was a significant effect ($p<0.001$) of both treatment and trapping period, and of their interaction. The latter was an effect of a decreased disruption effect over time. This resulted in a rise of the relative trap catch (trap catch in untreated areas = 100 %) from 1.7% to 10% in the *SSS*-treated plots and from 2.5% to 21% in the *SSS+SRR*-treated plots. The catch in the *SSS*-plots was lower than in the *SSS+SRR*-plots, but the difference was not significant during either of the trapping periods (Fig. 4).

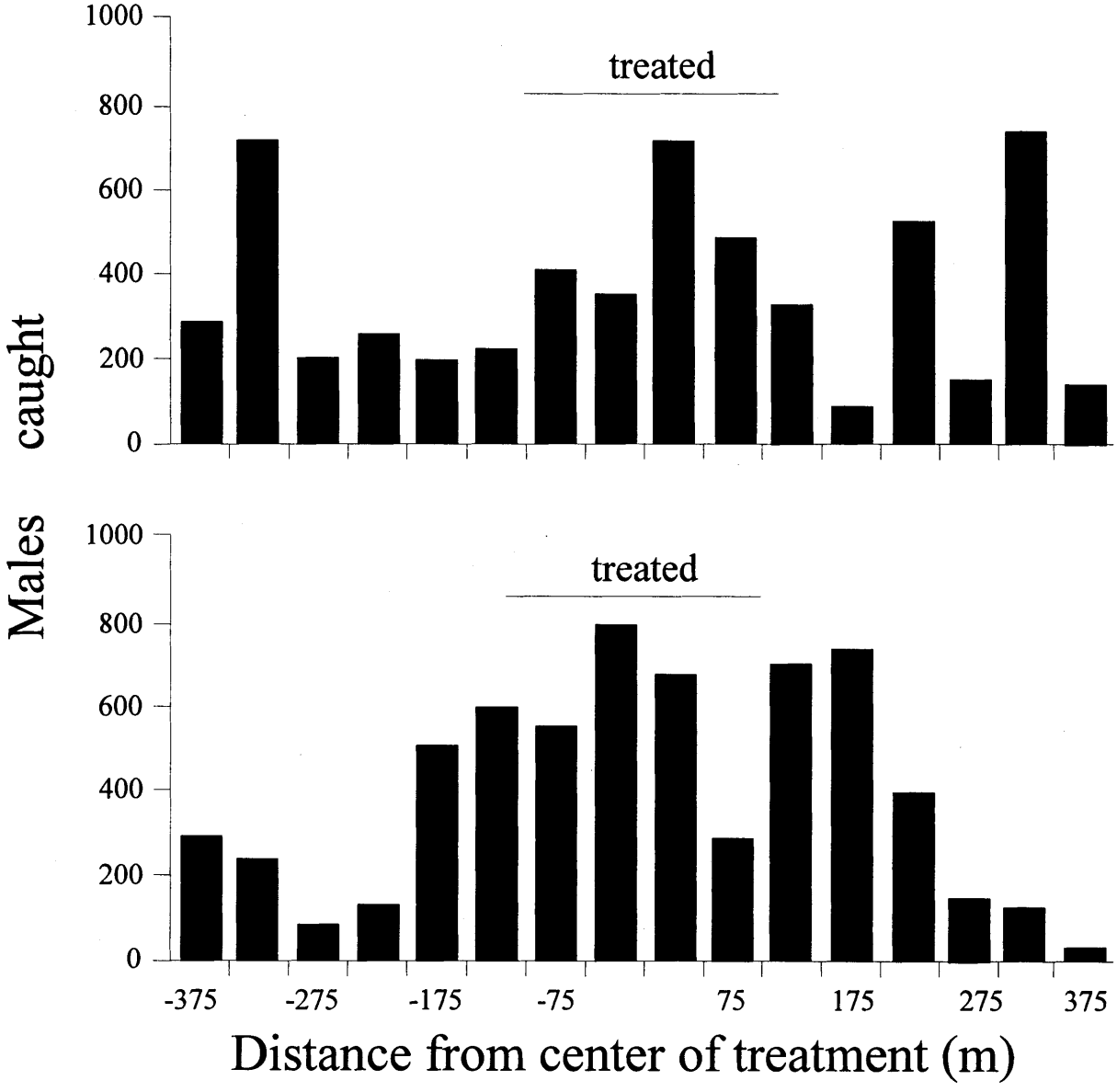


Figure 3. Catch of male *N. sertifer* in pheromone traps along transects A (above) and B.

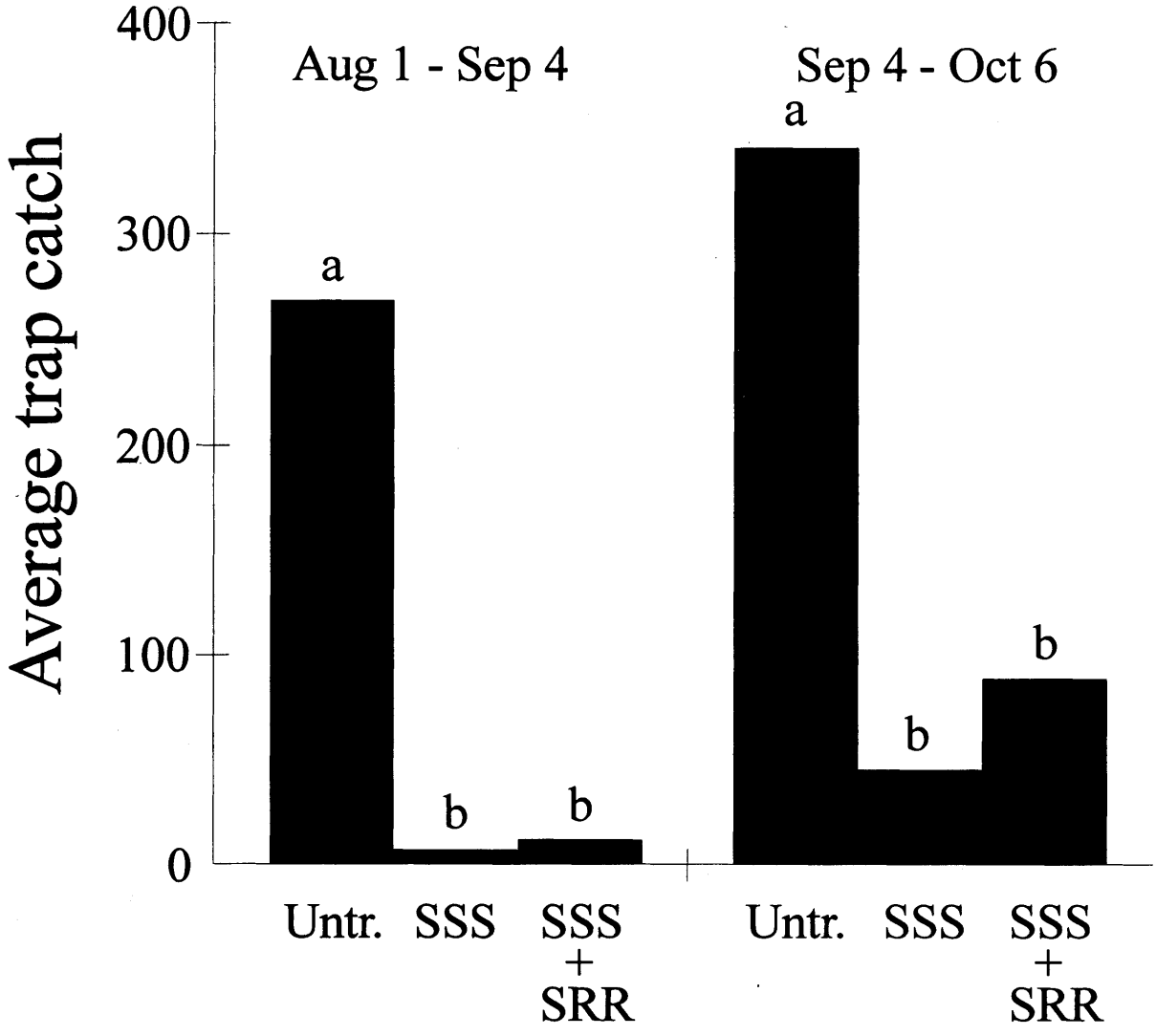


Figure 4. Average catch of male *N. sertifer* in pheromone traps placed in untreated plots (n=12), in plots treated with the attractive *SSS*-isomer (n=4), and in plots where 10% of the antagonistic *SRR*-isomer was added to the *SSS*-isomer (n=4). Within trapping periods, the same letter above bars indicates no significant difference (p>0.05, Tukey HSD-procedure).

Discussion

Experiments. The results of the first experiment indicated a slight effect on mate finding behavior. The trap catches were lower at the treated than at the untreated site both years, and by releasing about 10 times as much substance the second year, the trap catch in the treated plot decreased from 59% to 35%. In addition, the proportion of males was higher at the treated site after one year of treatment. Unfortunately, data on sex ratio from 1988 were not available, and thus the difference in 1989 may only reflect the natural variation between sites. The general population crash between 1989 and 1990 made a continuation of this experiment impossible.

In contrast to the first experiment, the second, performed over a larger area, did not reveal any effect of the antagonistic isomer on mating behavior. This is in sharp contrast to the effect of the attractant, which resulted in a trap catch reduction of nearly 100% (Anderbrant et al. 1995a,b). After this experiment, we concluded that the antagonistic (2*S*, 3*R*, 7*R*)-diprionyl acetate is less efficient for mating disruption than the attractive (2*S*, 3*S*, 7*S*)-isomer. The antagonist could possibly be used along the margins of areas treated with the *SSS*-isomer to reduce immigration of males. However, usually it is the migration of females, and especially of mated females, that causes problems in pheromone mating disruption applications.

The last experiment dealing with a 1:10 mixture of the antagonistic and attractive isomers did not increase the disruption effect compared to the pure attractant. Of course, there are an infinite number of ratios that can be tested, and it is still possible that other ratios could be effective, although it seems unlikely that the effect would be very large.

Future Use of Pine Sawfly Pheromones in Forestry. In addition to direct control of pest insects by mating disruption or mass trapping, pheromones may be used for detection and population monitoring:

1. Detection. As soon as the pheromone of a species is properly identified, traps can be used to determine presence/absence at certain places, e.g., along edges of the natural distribution or at harbors where import of wood and other forest products takes place. In addition, pheromone traps may be useful in scientific work and in censuses of biodiversity.

2. Population monitoring. The aim is to use the pheromone trap catch as an indicator of the population size or trend. Several problems have to be solved before the method is reliable. For instance, there has to be a reasonably good fit between the catch and actual population density. At an even more sophisticated level, one should be able to tell something not only about the present population density, but also about the expected population development. However, to reach this level it is important to know not only basic natural history and population dynamics, but also how the pheromone traps work, e.g., what is their sampling range, i.e. the area from which the trap catch is sampled during a certain period of time (Schlyter 1992 for a general discussion). It may also be essential to know the effects of weather and trap positioning (Jönsson and Anderbrant 1993, Simandl and Anderbrant 1995). Among the pine sawflies, several species exhibit complicated life cycles, with one or two generations per year, probably depending on a number of biotic and abiotic factors (Geri et al. 1995 and references therein), which also have to be considered when evaluating pheromone trap catches.

3. Control. As for other insect species that use sex pheromones, the use of mating disruption is most likely to be successful for suppression of diprionid pine sawfly populations. As a result of using this method, mating may, theoretically, be completely interrupted; if mass-trapping were used and even if 90% of the males were trapped, this method would fail because the remaining 10% may very well fertilize all the females. The main problem, as indicated above, with application of the mating disruption technique is the potential immigration of fertilized females from surrounding areas. Thus, to prove the effect of such a treatment, one may have to use either very isolated or very large areas.

The three areas mentioned above in which pine sawfly pheromones may be useful for forestry form the basis for a newly initiated international and interdisciplinary project supported by the European Community. The title of the project is "Pine Sawfly Pheromones

for Sustainable Management of European Forests," (PHERODIP). Eight institutes in six European countries are involved and the project runs from February 1996 to January 1999. The objective of PHERODIP is:

- To improve forest health, reduce economical losses caused by diprionid pine sawflies and decrease the use of insecticides against these insects by improving and applying knowledge about their pheromone communication.

Specific objectives are:

- To identify the sex pheromones of the species not yet studied from this perspective.
- To develop methods for detection, monitoring population densities and assessing the risk of outbreaks.
- To develop and evaluate sustainable and environmentally sound pheromone-based methods for suppressing outbreak populations.

Additional information about the project and the diprionid species involved can be found at the PHERODIP homepage at:
http://www.forst.uni-muenchen.de/WWW-Daten/ZOO/HEITLAND/PROJECTS/pherodip_intro_e.html

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Pheromone Monitoring of the Larch Bud Moth, *Zeiraphera diniana* Gn., in Poland

WOJCIECH R. GRODZKI

Forest Research Institute in Warsaw, Forest Management in Mountain Regions Section, ul. Fredry 39, 30-605 Kraków, Poland

ABSTRACT In 1977-83, a large outbreak of *Zeiraphera diniana* heavily damaged Norway spruce stands in the western part of the Sudety Mts. in Poland. Since that time, it has been recognized that a system of monitoring pest population levels was needed. In 1991, such a system was established in Polish mountains. In this paper, the organization of this system is presented and results of observations carried out from 1992-1995 are discussed in comparison with other methods of monitoring. Practical conclusions are given and possible sources of errors are indicated.

THE LARCH BUD moth (LBM), *Zeiraphera diniana* Gn. (Lepidoptera: Tortricidae), is a common insect pest in larch stands in the Alps, where outbreaks have been recorded since the beginning of the 19th century (Baltensweiler et al. 1977). The history of mass outbreaks on Norway spruce is shorter. Damage by the pest was first recorded in 1925-32 on 120,000 hectares on the Czech-German border (Pfeffer 1930); outbreaks in this region reoccurred in 1965-71 and 1979-85. Before 1977, the insect was not recorded as a pest in Poland, and it was only found by Zukowski (1960) in other locations during faunistic studies. However, in 1934, a local outbreak was recorded in close proximity to Poland, in the Czech portion of the Karkonosze Mts. (Martinek 1980). In 1977-83, the LBM attacked Norway spruce stands in part of the Sudety Mts. in Poland, covering 35.5 thousand hectares; isolated foci of the pest also caused local damage in Beskid Zywiecki in the western Carpathians (Capecki et al. 1989). The most severely damaged stands in the Sudety Mts. died in spite of pesticide applications. In the stands that survived, heavy defoliation resulted in reduced increment, and an outbreak of bark beetles completed the process of forest decline on nearly 15,000 hectares (Grodzki 1994a).

During the outbreak in the Sudety Mts., a method for predicting pest population levels was developed that involved counting eggs on branch samples: eggs were placed in growth chambers and emerging larvae were counted in late winter (Capecki et al. 1989). This method, which was difficult to use, needed to be replaced by a system of monitoring that was easier and gave more precise results.

Zeiraphera diniana has two forms related to host plants: the larch form lives on *Larix* sp. and the mountain pine form lives on *Pinus cembra* and *Picea abies*. The sex attractant of these forms is different; the form living on Norway spruce has a stronger response to E9-12Ac than that of the larch form (Vrkoc et al. 1979). This synthetic pheromone has been used for monitoring the LBM in Czechoslovakia and the Czech Republic from the beginning of the 1980's (Kalina and Skuhravy 1985) until the present (Liska 1993). Field trials using this attractant, conducted in Poland during the outbreak, gave variable and largely unsatisfactory results (Capecki et al. 1989, Kolk and Podgórski 1992).

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The concept of pheromone monitoring of the LBM was revisited in 1991 when a draft project was created; research observations began in 1992 in both the Carpathians and in the Sudety Mts. The goal of monitoring is to collect continuous data concerning LBM dispersion in Norway spruce forests, population density, and dynamics, and, on this basis, to predict the risk of LBM outbreak in Norway spruce stands.

Materials and Methods

Pheromone monitoring of the LBM in Poland is based on the Czech method described by Hochmut and Skuhravy (1983). As mentioned above, E-9-dodecenylacetate was used as the synthetic pheromone in a dosage of 50 mg per dispenser. Delta type glue traps (DELTASTOP ZG) with an attached pheromone dispenser (produced by Propher, Czech Republic) were placed in groups. One group was used for every 400-800 hectares of observed spruce stands. Each group contained three traps located 50 m apart in a line. Traps were affixed to tree branches with needles ca 2 m above ground level in places with good air circulation, and were exposed from July 10th to September 10th. After monitoring was completed, entire traps were sent to the Forest Research Institute in Kracow or to the Forest Protection Services office of the State Forest and analyzed to determine the number of captured insects.

The pheromone monitoring network was composed of 71 permanent points: 50 in the Sudety Mts. (a region of former LBM outbreak) and 21 in the Carpathians. Observation points were primarily located on permanent plots associated with biological monitoring in the State Forests with some additional points located outside these plots. Seven points were located on National Park land: three in the Carpathians and four in the Sudety Mts.. All monitoring points were located in Norway spruce stands with emphasis on locating plots at higher altitudes or in the former outbreak area where the occurrence of the LBM was expected (Grodzki 1994b).

In 1995, monitoring was conducted only in the Sudety Mts.. Polish glue traps (PL-2) containing the synthetic pheromone Rhyodor for attracting *Rhyacionia buoliana* Shiff. were used.

The interpretation of trap results was made using Czech prediction criteria: captures lower than 20 pest specimens per group of traps (observation point) indicated a normal population level, captures of 20-100 specimens per point indicated an elevated population level, and captures of 100-200 specimens per point indicated the possibility of visible damage occurring the following year (Hochmut and Skuhravy 1983). Verification of these results was made using a "classic" prediction method, i.e., by counting the number of larvae that emerged from branch samples reared in growth chambers. The first level of risk (+) was reached when 80 larvae emerged from one sample, the second level (++) when 130 larvae emerged, and the third level (+++) when more than 300 larvae emerged from the branch sample (Grodzki 1994b).

Table 1. General results of pheromone monitoring of *Z. diniana* in the Carpathians and the Sudety Mts. in Poland in 1992-1995

Year	Number of points	Number of missing points	Number of points with captures (specimens)			Max. number of specimens caught at a point
			20-100	100-200	>200	
CARPATHIANS						
1992	21	2	4	4	9	541
1993	21	2	9	2	1	209
1994	21	1	6	0	0	44
SUDETY MTS.						
1992	50	1	4	0	0	45
1993	50	2	7	0	0	73
1994	50	6	1	0	0	30
1995	50	4	2	0	0	69

Results

The results of pheromone monitoring varied in successive years, as shown in Table 1. In most cases, LBM captures were higher in the Carpathians than in the Sudety Mts., especially in 1992, when captures of more than 200 specimens were recorded on nine monitoring points in the Carpathians. In 1993 and 1994, captures in this region were lower, but results that indicated elevated population levels (>20 specimens) were obtained on 12 and 6 monitoring points, respectively. In the Sudety Mts., however, captures of 20-100 specimens were recorded on only one to seven monitoring points in successive years, even in the former LBM outbreak area, and no points had captures exceeding 100 specimens.

The spatial distribution of relatively higher captures partially corresponded with the range of the LBM outbreak from 1977-83 (Table 2), but the highest captures ($\geq$ 500 specimens) were recorded outside this area, in the eastern part of the Beskidy. In the region containing the local focus of the LBM (the Beskid Zywiecki), captures of more than 100 specimens were recorded on three points in 1992 and 1993. In 1994, 1 to 28 moths were caught per monitoring point. In the Sudety Mts., captures higher than 20 specimens were recorded only on monitoring points located in the former outbreak area (except for one point in the Eastern Sudety, that recorded 24 moths in 1993). However, the results varied from year to year, generally without visible continuation. There was only one point (Swieradow 375b), located in the Izerskie Mts. in the area most severely damaged during the outbreak, where captures higher than 20 specimens were recorded in 1992, 1994, and 1995.

Table 2. Results of pheromone monitoring of *Z. diniana* on sampling points with relatively higher captures in 1992-1995

Locality		Altitude	Captures by year: 1992	1993	1994	1995*
SUDETY MTS.						
WESTERN SUDETY						
Kamienna Góra	120 i	700	7	51	2	0
Kamienna Góra	231 h	700	0	25	0	0
Kamienna Góra	79 b	700	0	28	0	1
Kamienna Góra	138 a	600	2	79	0	1
Szklarska Por.	213 a	940	30		13	0
Sniezka	172 a	1000	27	13	4	0
Sniezka	158 c	700	17	23	0	0
Swieradów	375 b	1000	45	16	30	21
Swieradów	428 b	900	34	6	12	3
Karkonoski PN	69 j	1240	17	11	9	69
Karkonoski PN	201 i	1300	10	20	3	19
EASTERN SUDETY						
Ladek Zdr.	342 c	1200	8	24	0	0
CARPATHIANS						
BESKID ZYWIECKI						
Jelesnia	174 f	1150	80	31	1	**
Jelesnia	94 a	850	120	0	2	**
Ujsoly	17 a	1200	266	153	13	**
Wegierska G.	75 a	1300	350	209	28	**
BESKID SADECKI						
Kroscienko	15 b	1200	385	27	44	**
Kroscienko	251 d	700	491	46	20	**
TATRA						
Tatrzanski PN	237 a	1150	bp	43	27	**

* traps PL-2 with the attractant Rhyodor
** no traps in 1995

Verification of pheromone monitoring results was made on all points where more than 20 moths were caught. Egg masses on branch samples collected from trees on these selected points were reared in growth chambers every year from 1992 to 1995. There was no locality where elevated population levels predicted by pheromone monitoring were also predicted by the "classic" method; in addition, no larvae were observed feeding in tree crowns in these stands.

Discussion

The results obtained by pheromone monitoring are not easy to interpret. A comparison of the three methods used for monitoring LBM population levels, i.e., pheromone traps, growth chamber rearing, and observation of eventual damage made by larval feeding, indicates that there is no threat to observed stands from the pest. However, pheromone monitoring indicated higher densities of the LBM in several localities, whereas the real status of the population seemed to be near its normal level. In this situation, possible sources of error in the pheromone monitoring method need to be found and defined.

The first and most important source of error is the spectrum of species that responded to the attractant used and was caught by the traps. While analyzing the glue elements of the traps, moths were counted by observing their size and shape with no determination of species from genitalia. It is very possible that, among the moths captured, more species than *Z. diniana* were caught. Liska (1993), investigating the spectrum of species captured in traps baited with E9-12Ac in Norway spruce stands, found 24 species of moths representing 5 families; some showed a highly specific reaction to the synthetic pheromone used. Field trials conducted in Norway spruce and larch stands of the High Tatra also revealed that 21 moth species other than *Z. diniana* were captured using this attractant (Liska et al. 1990). In tests conducted by Kolk and Podgórski (1992) using the same attractant, *Rhyacionia buoliana* Shiff. was captured in significant quantities.

Significantly higher captures in 1992, especially in the Carpathians, could be related to the high cone crop recorded in mountain Norway spruce stands in Poland, even in weakened stands in the Sudety Mts. where no cone production has been observed since the LBM outbreak (Grodzki 1994c). It is possible that other species of *Tortricidae* developing in the cones were captured in the traps and not identified during analysis of glue elements. It is, however, interesting that captures in the Carpathians were always higher than in the Sudety Mts., where the occurrence of higher population levels was expected. The answer to this question may be determined by qualitative analysis of the traps this autumn.

Conclusions

1. The LBM monitoring system applied in Poland is useful and needs to be continued, but with some cautions.
2. The main objective of this monitoring system is to determine the spatial distribution of the LBM, but trap analysis needs to include the determination of all species captured.
3. Population density estimates of the LBM made in order to predict its threat need to be based not only on pheromone monitoring, but on growth chamber rearing results and observations of subsequent larval damage.
4. It is necessary to study the data patterns to predict the LBM threat and investigate its population dynamics.

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Monitoring Gypsy Moth (*Lymantria dispar* L.) Populations (Lep., Lymantriidae) in Slovakia using Pheromone Traps

MAREK TURCANI

Forest Research Institute, Lesnícka 11, 96923 Banská Štiavnica, Slovak Republic

ABSTRACT This paper presents the use of pheromone traps to monitor gypsy moth populations in Slovakia. This insect has been the most destructive defoliator in Slovakia since 1986. This study involved optimization of pheromone (attractant, trap and dispenser), determination of the minimum number of sample trees and pheromone trap sets required for statistical evaluation, long-term assessment of population densities and gypsy moth males captured by pheromone traps, and specification of relationships between population density and numbers of gypsy moth males captured by pheromone traps (by means of correlation analysis). Based on the results obtained, it is possible to use pheromone monitoring mainly during the latency and ascending phases. However, in some cases, results are not universal. A considerable part of the results may be influenced by inaccuracies, e.g., relatively low sample sizes due to physical feasibility limitations of the study and immigration of males. In the next outbreak cycle of the gypsy moth, the proposed system will be completed and used as a component of the integrated pest management of gypsy moth in Slovakia.

GYPSY MOTH IS the most serious defoliator of broadleaved stands (mainly oak stands) in Slovakia. The outbreak range covers the lowlands in the south of Slovakia (Fig. 1). Outbreaks of this pest are repeated in cycles of 6 to 12 years. During the last outbreak of 1992 - 1994, gypsy moth damaged more than 18,000 ha of forest stands. The majority of these stands are characterized by bad health as a result of long-term oak decline. Defoliation can cause increased tree mortality in subsequent years. Therefore, attacked stands are treated by a biopesticide (B.t. FORAY 48 SC).

There are two reasons to find a new method for monitoring population density:

1) Gypsy moth population densities are measured using the Turcek method in Slovakia. Using this method, it is possible to get accurate data on pest abundance if the population density is higher than 1.0-1.5 egg masses per tree. However, at such population densities, the pest defoliates stands to such an extent before aerial application of biopesticides (B.t. mainly) that the biopesticide might not be captured by the canopy and falls to the forest floor.

2) Applications named "advance control" or "control in advance" are made when pest population densities have not reached an outbreak level yet, but the trend of increasing abundance has begun.

Pages 70-82 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

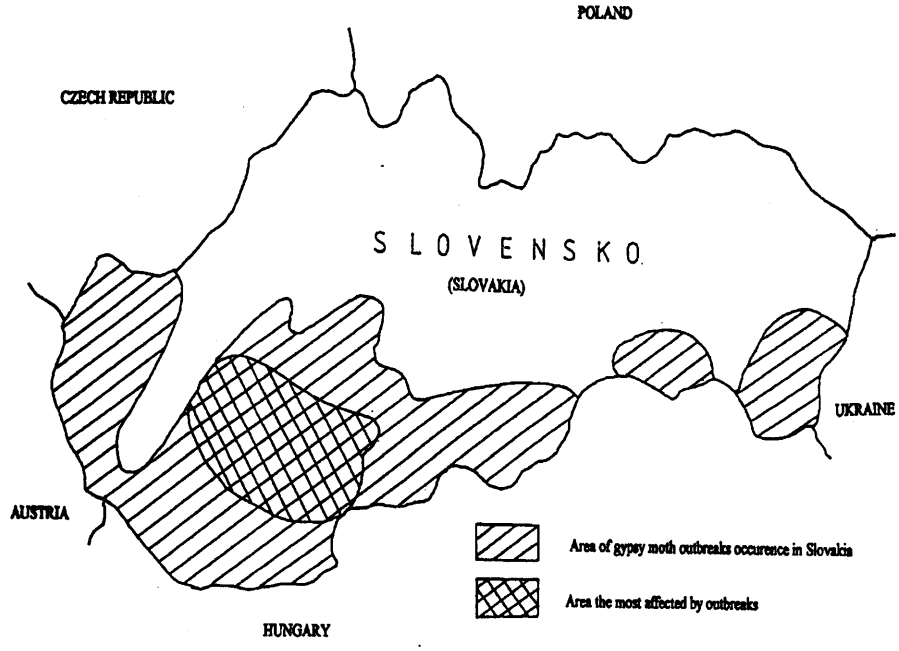


Figure 1. Outbreak area of gypsy moth in Slovakia.

Research on the use of pheromones to study low population densities can be divided into the following steps:

1. Optimization of pheromone (attractant, trap and dispenser);
2. Determination of the minimum number of sample trees and pheromone trap sets required for statistical evaluation;
3. Long-term assessment of population densities and gypsy moth males captured by pheromone traps; and
4. Specification of relationships between population density and numbers of gypsy moth males captured by pheromone traps by means of correlation analysis.

Material and Methods

Pheromone optimization started in 1985. Basic information about field experiments is provided in Tables 1 and 2 and Figure 2. Disparlure in different concentrations was used as an attractant. The types of traps used in the experiments are illustrated in Figure 3. The numbers of gypsy moth males captured at different doses of attractant using different types of traps and dispensers were compared and evaluated statistically.

Criteria for the optimal trapping set (attractant, trap and dispenser) include:

- low variability in numbers of captured males among traps, and
- time efficiency

Table 1. Basic information on the experiments during optimization

Date of experiments	Localities of experiments	Arrangement of testing points	Point spacing	Distance of testing group	Frequency of checking
7/17-9/14	Cifare Tesárske Mlynany	8 components 2 strips	50 m	100 m	14 days
7/15-7/23 7/15-9/3	Èifáre	latin square 9 components, 3 squares	100 m	200 m	every day 14 days
7/27-9/28	Cifare Dolné Semerovce Duzavska lúka	latin square 9 components, 3 squares	50 m		
7/19-9/20	Cifare Bušince Rátka	8 components 2 strips	50 m	100 m	
7/20-9/21	Cifare	latin square 9 components, 2 squares	100 m	200 m	
7/15-8/31	Cifare Rátka Kurinec Nitra Vojnice Levice	5 triangular points in every locality	100 m	minimally 200 m	without checking

In 1990, we tried to estimate the variability of gypsy moth egg masses in a stand. Egg masses were counted on sample trees at different population density levels. We have used the following formula for calculating the minimum sample size of trees and traps.

$$N = \frac{z^2 \cdot s_x^2}{Sypr^2}$$

Where: N = minimum number of samples needed with x% reliability, y% reliability and y% accuracy

z = coefficient of reliability level with P = x%

s_x = coefficient of variation

Sypr = accuracy of assessment

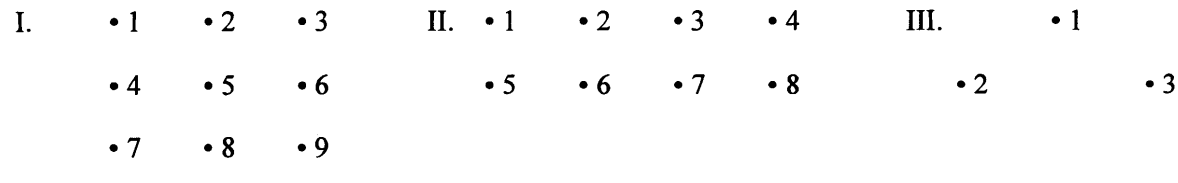


Figure 2. Array of testing components in the experiments: I - Latin square, II - Array in strips, III - Triangular array.

Table 2. Data on pheromones, dispensers and traps used in the optimization process

Pheromone trade name	Dose in µg	Dispenser	Attractant	Producer of pheromone and dispenser	Type of trap	Trap producer
NŠ 0,05	50	PO	cis-7,8-epo- 2 Me-18 Hy disparlure (D)	VNIIBMZR Kišinev	DK+1	VNIIBMZR Kišinev
LMS	100	PZ		AK Slušovice		
LM86	100	PZ		CSAV UOCHB	PPT	VÚLHM Jíl.
LM61	100	KK	D	Praha	ÈBL	Strn.
LM62	10	KK				VNIIBMZR
LM63	1	KK			DK+1	Kišinev
					DK-1	
Lymodor	300	PZ		PAN Warszawa	DKO,	
					PL	PAN Warzsawa
					WT	Albany,USA
LMD			D	AK Slušovice	DK+1	VNIIBMZR
Etokap	100	KK				Kišinev
NŠ Kišinev	10	GH		VNIIBMZR Kišinev		
Lymodor	300	PZ		PAN Warzsawa		
LMD			D		DI	SAV ÚEFE
Etokap	100	KK		AK Slušovice		
					HI	LVÚ VS B. Štiavnica
					DK+1	VNIIBMZR Kišinev
LMD					DK+1	VNIIBMZR
Etokap	100	KK	D	AK Slušovice		Kišinev
					PK	AK Slušovice
LMD					DK+1	VNIIBMZR
Etokap	100	KK	D	AK Slušovice		Kišinev

[1]Dispensers: GH - Rubber hose, KK - Rubber conical cup, PO - Plastic rectangular dispenser, PZ - Penicillin plug

Traps: CBL = Czech barrier lantern (dry), DI = Disc (dry, insecticidal), DK + I = Delta Kishinyev with window (dry, insecticidal), DK - I = Delta Kishinyev with window (without insecticide, dry), DKO = Delta Kishinyev open (sticky), HI = Mushroom (dry + insecticide), PK = Plastic container (dry), PL = Polish lantern (dry), PPT = Zinc - coated sheet (sticky), WT = Wing Trap (sticky)

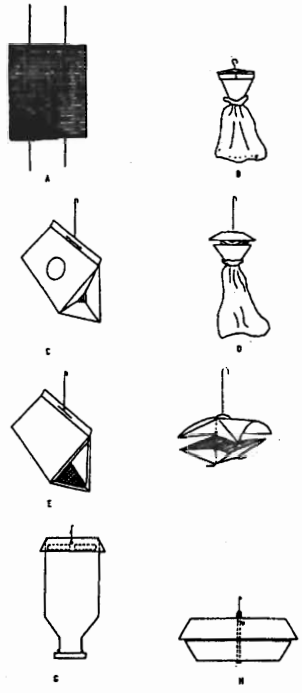


Figure 3. Types of traps used in testing experiments.

A - Zinc coated sheet (sticky)
B - Polish lantern (dry)
C - Delta Kishinyev + insecticide (dry)
D - Czech barrier lantern (dry)
E - Delta Kishinyev open (sticky)
F - Wing trap (sticky)
G - Mushroom + insecticide (dry)
H - Disk + insecticide (dry)

Since 1991, the population density has been measured on fixed plots. Pheromone traps have been installed in the same plots since 1991 (Fig. 5).

From 1991 - 1995, we have graphically compared the mean egg mass number per tree and mean number of males captured per trap.

We conducted a correlation analysis to determine relationships (coefficient of determination) between mean population densities obtained by means of the traditional method and mean number of gypsy moth males captured. We conducted a correlation analysis for every year and all localities as well as for each locality across all years.

Two methods were applied. In the first method "a" data on catches were correlated with the arrangement of traps in the experimental plot. In the second method "b" the data from four traps placed in the internal space of the experimental plot were used (Fig. 4).

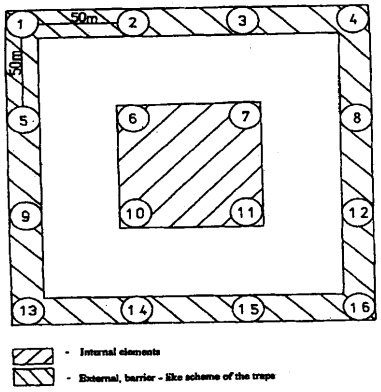


Figure 4. Scheme of pheromone traps on monitoring point.

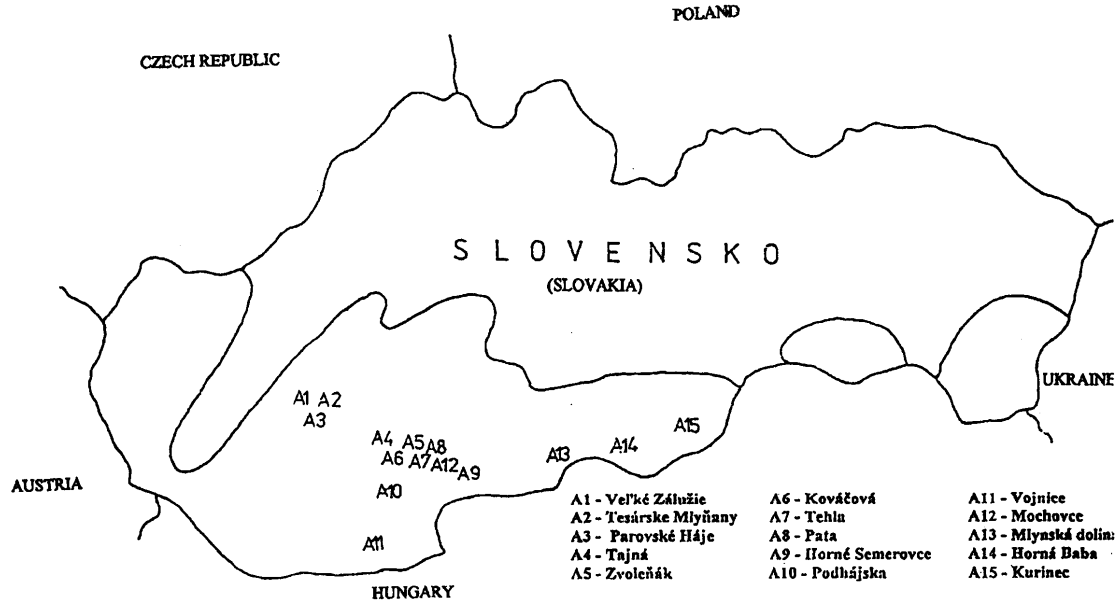


Figure 5. Scheme of experimental plots for monitoring gypsy moth population density.

Results

Pheromone, Dispenser and Trap Optimization. The optimal trapping set that has been used for the last 6 years is the: Pheromone LMD ETOKAP with 1OO g disparlure. The pheromone is formulated in a rubber conical dispenser. The trap is a Delta Kishinyev trap with window + insecticide.

Determination of the Minimum Number of Sample Trees and Pheromone Traps Required. As indicated in Table 3, when population densities are low (below 0.2) a large sample of trees is necessary (more than 300). We obtained a large minimum number of pheromone traps as well (Table 4).

Based on data collected, we determined that the minimum number of sample trees needed is 480 (30 trees in 16 points). For pheromone monitoring, a Latin square (16 pheromone traps with 50 m spacing) was established. The experimental design is presented in Figure 4.

Table 3. Minimum number of trees needed for detection of population density with different measurement accuracies

Population density (Egg masses/ tree)	Selected accuracy 60%	70%	80%	90%
1.00	52	92	207	830
0.40	100	178	400	1,599
0.30	125	222	439	1,997
0.20	171	304	658	2,739
0.10	306	344	1,224	4,896
0.05	560	996	2,241	8,962
0.01	2,454	4,363	9,816	39,266

Table 4. Minimum number of pheromone traps needed for statistical data processing.

Population density (Egg masses/ tree)	Selected accuracy 60%	70%	80%
0.00	5	9	20
0.01	12	21	46
0.05	12	21	46
0.10	6	11	24
0.20	2	3	5
0.40	8	15	33

Long-term Assessment of Population Densities and Gypsy Moth Males Captured by Pheromone Traps. Changes in population density and number of males captured by traps are presented in Figures 6, 7, 8, 9 and 10.

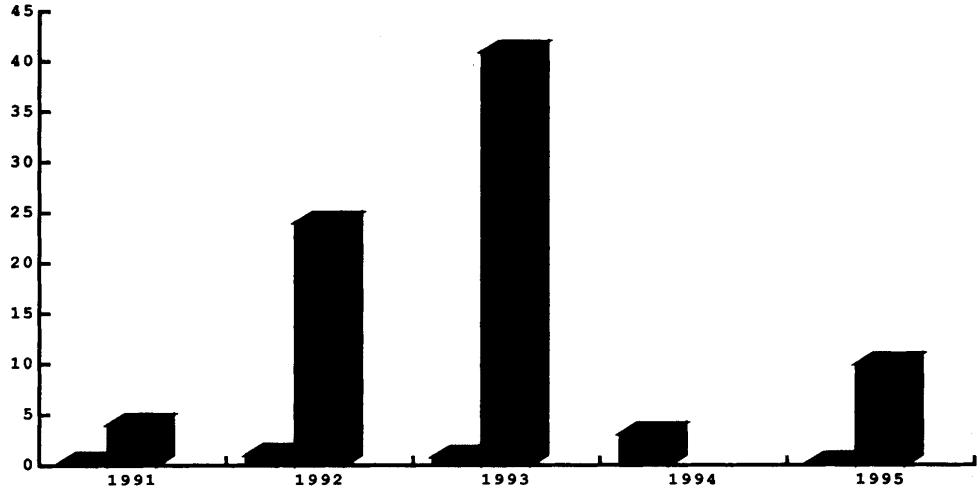


Figure 6. Comparison of mean population density (darker columns) and mean catch of gypsy moth males (lighter columns) in pheromone traps (locality Bušince I). X - axis = years; Y - axis = egg masses / 10 trees and mean number of gypsy moth males captured by 1 pheromone trap.

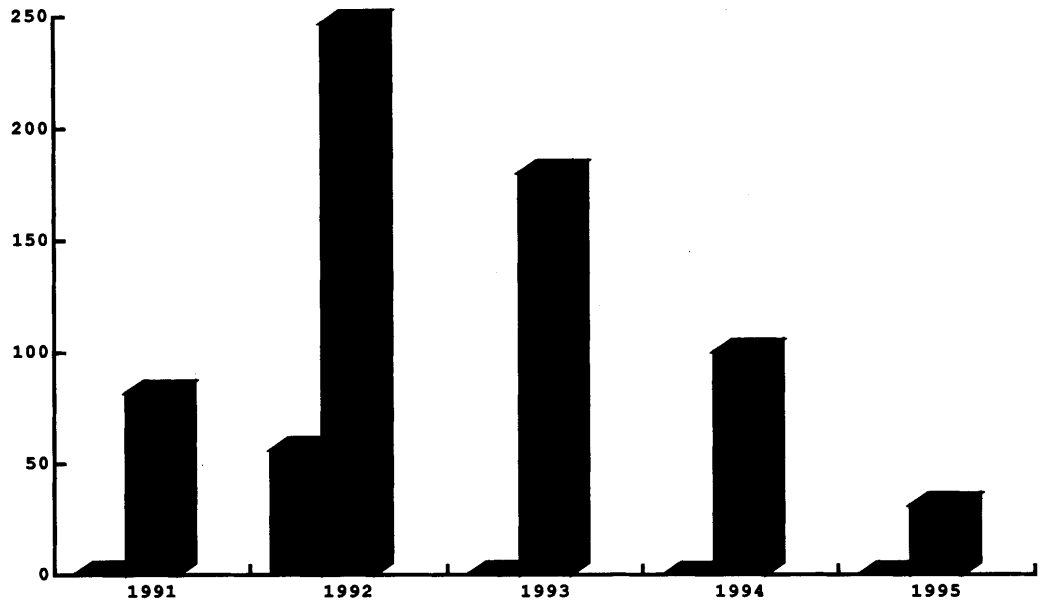


Figure 7. Comparison of mean population density (darker columns) and mean catch of gypsy moth males (lighter columns) in pheromone traps (locality Pata). X - axis = years; Y - axis = egg masses/10 trees and mean number of gypsy moth males captured by 1 pheromone trap.

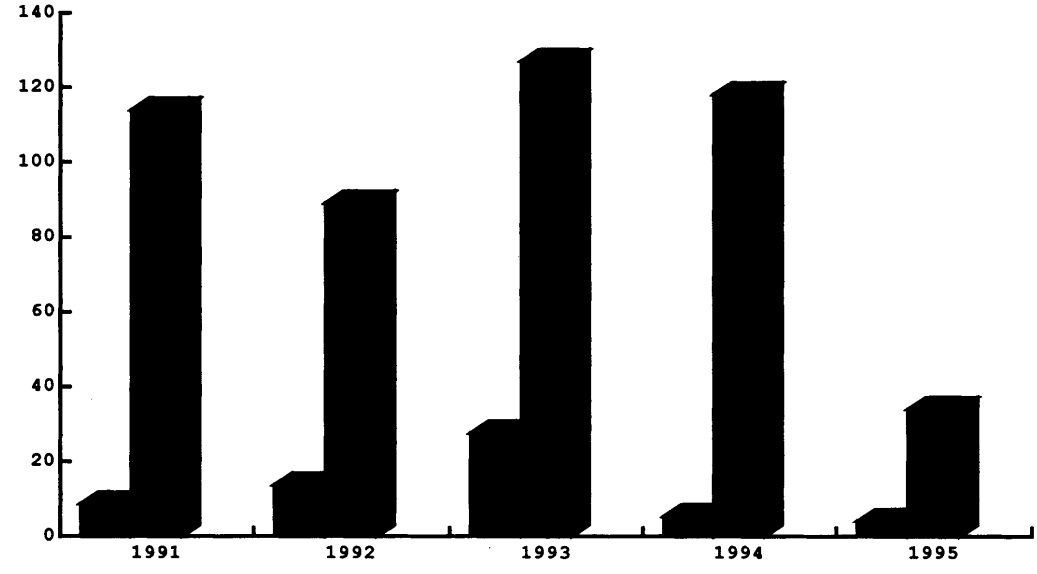


Figure 8. Comparison of mean population density (darker columns) and mean catch of gypsy moth males (lighter columns) in pheromone traps (locality Kovacova). X - axis = years; Y - axis = egg masses/100 trees and mean number of gypsy moth males captured by 1 pheromone trap.

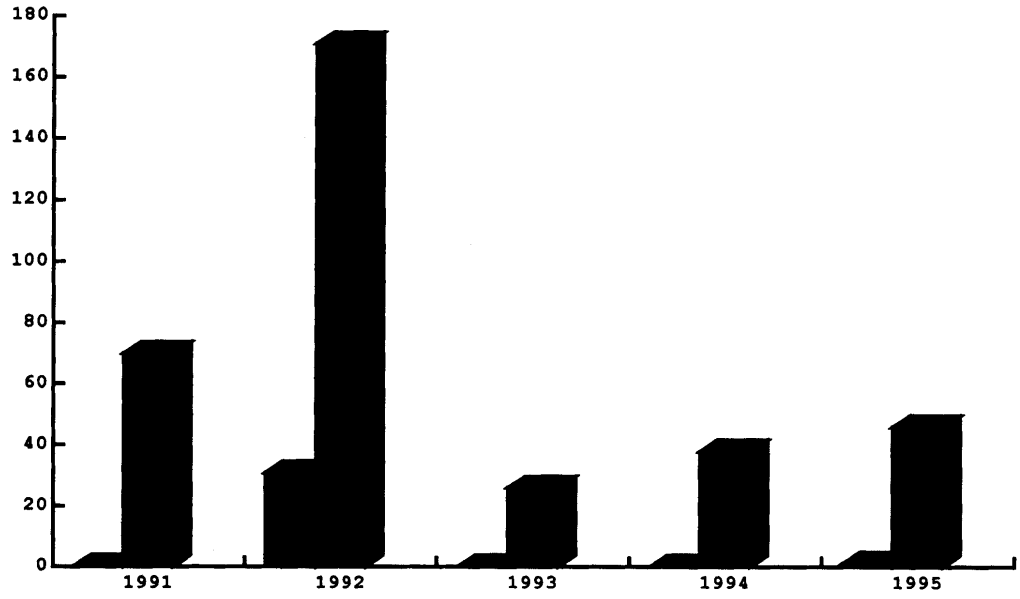


Figure 9. Comparison of mean population density (darker columns) and mean catch of gypsy moth males (lighter columns) in pheromone traps (locality Mlynany). X - axis = years; Y - axis = egg masses/1 tree and mean number of gypsy moth males captured by 1 pheromone trap.

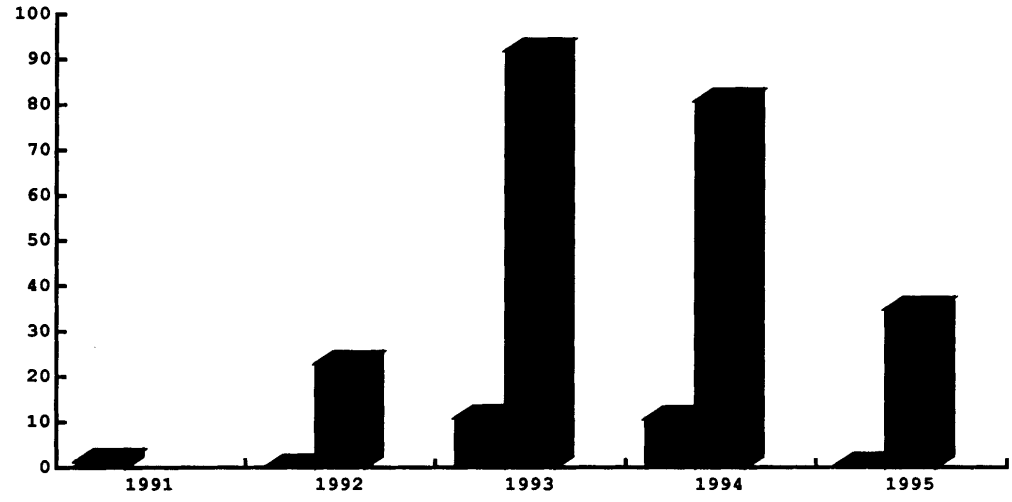


Figure 10. Comparison of mean population density (darker columns) and mean catch of gypsy moth males (lighter columns) in pheromone traps (locality Kurinec). X - axis = years; Y - axis = egg masses/100 trees and mean number of gypsy moth males captured by 1 pheromone trap.

It is possible to conclude that population density trends measured by traditional methods correspond to some extent with the catches of gypsy moth males in pheromone traps, mainly in the latency phase period and in the beginning of an outbreak.

Specification of Relationships Between Population Density and Catch of Gypsy Moth Males Captured by Pheromone Traps - Correlation Analysis. In 1991, we used this technique to calculate a coefficient of determination (R^2) of 0.24 for the "a" variant and 0.79 for the "b" variant (Fig. 11). The first value indicates a poor correlation, while the second one indicates a high correlation. In 1992, the coefficient of determination was 0.26 for "a" variant and 0.42 for "b" variant. Hence, the correlation in 1991 was not very high (Fig. 11).

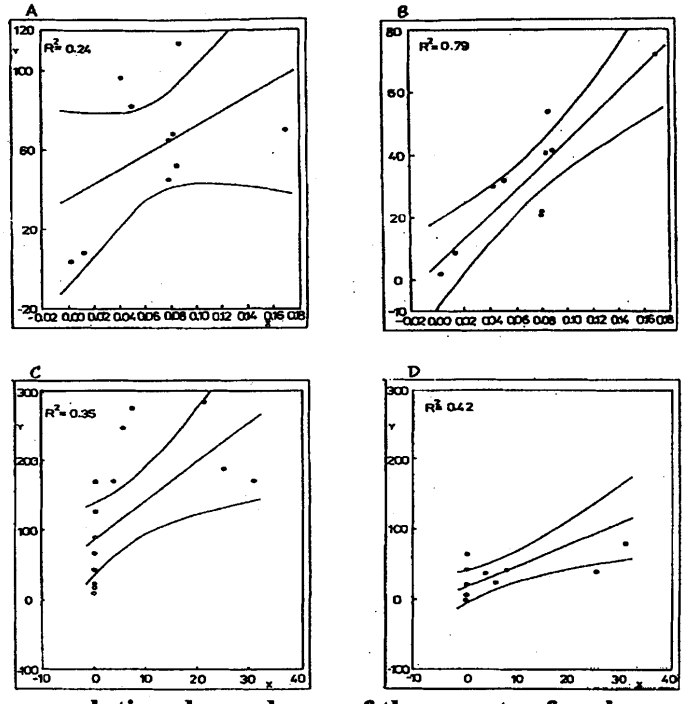


Figure 11. Linear correlation dependence of the counts of males captured in pheromone traps and population density.

A-year 1991 all traps B-year 1991 internal traps
C-year 1992 all traps D-year 1992 internal traps
(x-axis = mean number of egg masses per tree)
(y-axis = mean number of gypys moth males per trap)

The situation in 1993 was entirely different. It can be documented by the results for both variants (a: CD = 0.03, b: CD = 0.002), which indicated an absence of any correlation (Fig. 12). In 1994, the CD reached a value of 0.26 for the "a" variant which is judged as a poor correlation (Fig. 12). In 1995, we recorded 0.47 for the "a" variant and 0.38 for the "b" variant; the correlation was judged as not very high (Fig 13). For individual localities across all years, the R^2 was generally higher than corresponding values for all localities together in the same year. (Tesárske Mlynany = 0.93 from 1991 - 1995, Pata = 0.61 from 1991 -1995, Zvolenak = 0.90 from 1991-1994, and Kurinec = 0.98 from 1992-1994). These data are illustrated by Figure 14.

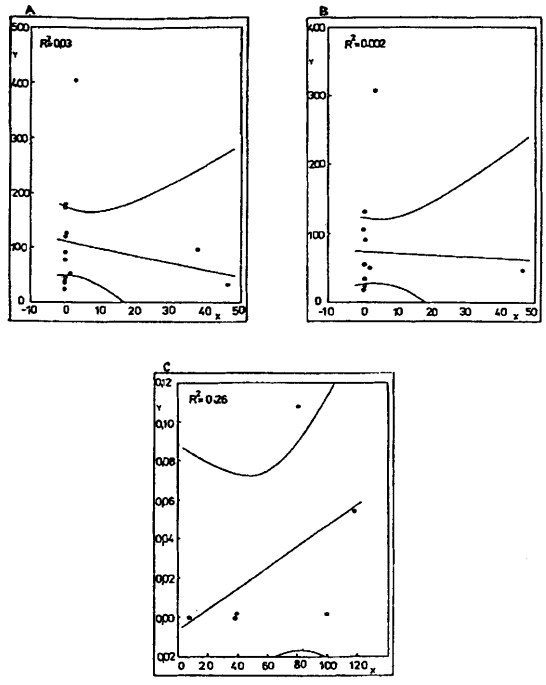


Figure 12. Linear correlation dependence of the counts of males captured in pheromone traps and population density.

A-year 1993 all traps B-year 1993 internal traps
(x-axis = mean number of egg masses per tree)
(y-axis = mean number of gypsy moth males per tree)
C-year 1994 all traps
(x-axis = mean number of gypsy moth males per trap)
(y-axis = mean number of egg masses per trap)

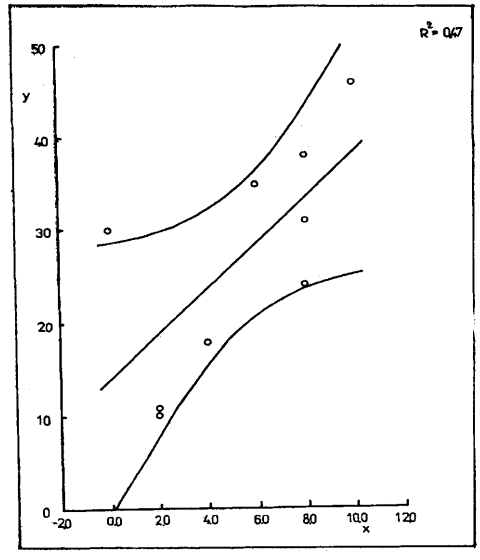


Figure13. Linear correlation dependence of the counts of males captured in pheromone traps and population density (year 1995).

(x-axis = mean number of egg masses per tree)
(y-axis = mean number of gypsy moth males per trap)

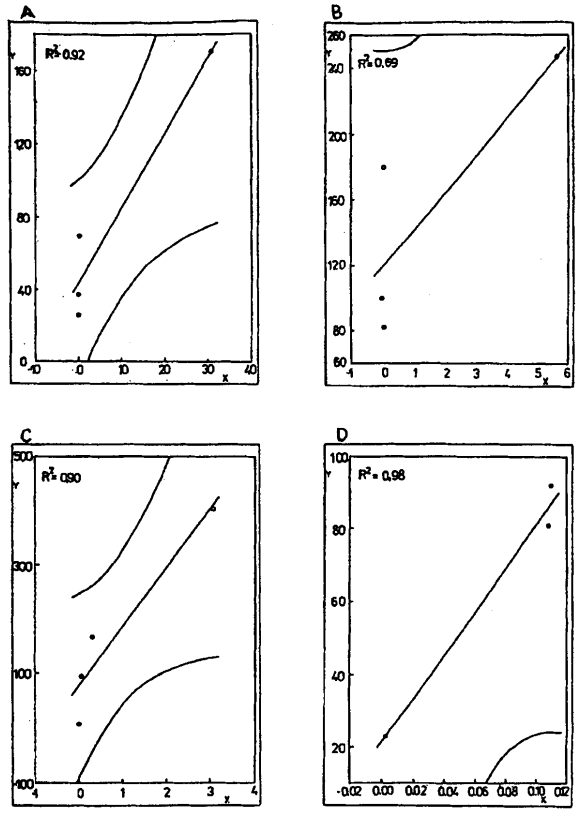


Figure 14. Linear correlation dependence of the counts of males captured in pheromone traps and population density (Period 1991 - 1994.)
A-study plot Tesarske Mlynany B-study plot Pata
C-study plot Zvolenak D-study plot Kurinec
(x-axis = mean number of egg masses per tree)
(y-axis = mean number of gypsy moth males per trap)

Conclusion

Based on the results obtained, the applicability of pheromones depends on the outbreak phases. In Slovakia, which represents the margin of a outbreak area, it is possible to use pheromone monitoring during the latency and ascendency phases. In some cases, results suggest a close correlation between population density and gypsy moth catches in traps. But these results are not universal. A considerable part of the results may be influenced by inaccuracies, e.g., relatively low sample sizes due to physical feasibility limitations of the study and immigration of males.

In Slovakia, the outbreak area of gypsy moth is divided by non-forest areas into many isolated forest areas and thus results should not be substantially affected by male moth migration. Pheromone monitoring can be used as a suitable, complementary method for investigating and predicting population density. Whole design of the application of particular methods during the gradation cycle is illustrated by Figure 15. In the future, the following measures should be implemented to improve pheromone-based monitoring:

- include other methods of data collection for low population densities to compare them with catches in pheromone traps (jute sacks, frass sheets...);
- complete the study of the variability of egg mass occurrence, determining the final set of sample trees needed;
- test new types of attractants, traps and dispensers which would reduce variability of catches;
- field test the proposed monitoring system during an outbreak cycle under field conditions in Slovakia;
- elaborate the standard design of pheromone monitoring for main gradation areas;
- verify correlations between trap catches and population densities in large and closed forest complexes;
- test the barrier effects of pheromone traps; and
- verify time limited monitoring (installing traps for 1 day - 1 month during the flight period) to eliminate the effect of male moth migration from surrounding stands.

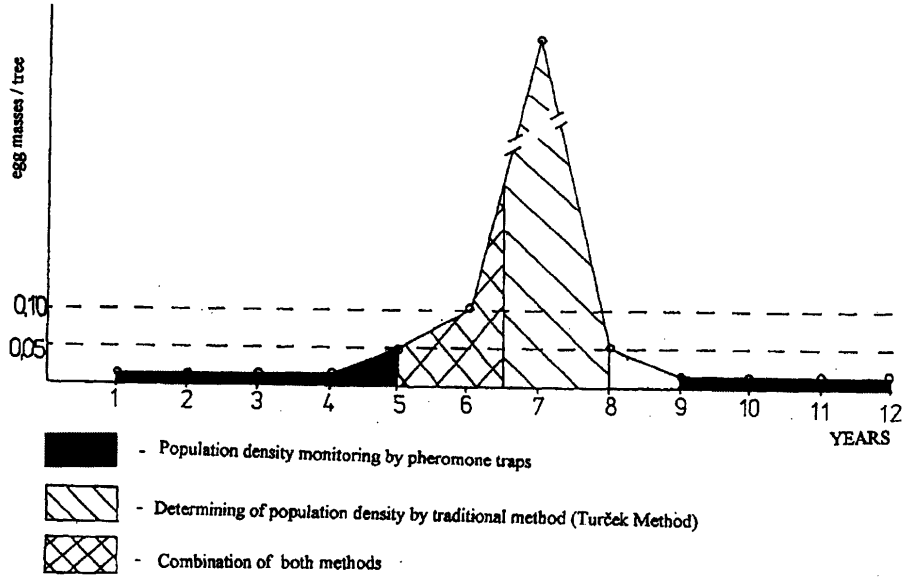


Figure 15. The scheme of the possibilities of methods use for detecting gypsy moth population density during gradation cycle in Slovakia.

In the following gradation cycle of the gypsy moth, the proposed system will be completed and, including recently gained knowledge, it will be used as a component of integrated pest management of gypsy moth in Slovakia.

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Cytological Investigations with Regard to Population Dynamics of the Pine Sawfly, *Diprion pini* L. (Hym.: Diprionidae)

J. ROUSSELET[1,2], C. GERI[1], F. GOUSSARD[1], S. MOUSSET[1], S. MARETHEU[1] AND F. LEMEUNIER[2]

[1]Station de Zoologie Forestière, Institut National de la Recherche Agronomique, Centre de recherches forestières d'Orléans, Ardon 45160 Olivet, France
[2]Laboratoire Populations, Génétique et Evolution, Centre National de la Recherche Scientifique, avenue de la terrasse, 91198 Gif-sur-Yvette, France

ABSTRACT The occurrence of diploid males is demonstrated in the pine sawfly, *Diprion pini*. Inbreeding experiments and cytological investigations were designed to investigate this phenomenon. The cytological study shows an unexpected chromosome complement (n=14, 2n=28) in this diprionid species and suggests a karyotype evolution by centric fission. The expected significance of diploid males to *D. pini* population dynamics is discussed.

DIPRION PINI IS an arrhenotokous sawfly whose gregarious larvae defoliate Scots pine, *Pinus silvestris*. In France, long periods of low population level are punctuated by short and spectacular outbreaks. These outbreaks cause considerable damage, reducing the growth of the trees and sometimes leading to tree mortality. *Diprion pini* is consequently responsible for occasional extensive economic loss.

Geographic variation in environmental conditions often results in variation in life cycles and in diapause intensity (Géri and Goussard 1988, 1991). Furthermore, diapause, parasitism and foliage availability (in quantity and quality) are significant regulative factors of population level during outbreaks and their collapses (Géri 1988). However, we cannot explain what triggers outbreaks.

Never the less, several experimental observations suggest an effect of inbreeding on sex-ratio and on diapause rates (Beaudoin et al. 1994, Géri et al. 1995). They suggest the influence of genetic factors. A male-biased sex ratio was notably observed in the rearing strain and following sibmatings while a female-biased sex ratio was generally observed in the field (Beaudoin et al. 1994, Géri et al. 1995). In natural populations, the variations in consanguinity and maybe consequently in sex ratio can affect the population dynamics because the females constitute the demographic potential.

Several mechanisms of sex determination may affect the sex ratio. It is well accepted that hymenoptera reproduction is mostly based on arrhenotokous parthenogenesis: females develop from fertilized eggs and are diploid, whereas males develop from unfertilized eggs and are haploid. In fact, sex determination is not merely a haplo-diploid determination at the cytogenetical level. Whiting (1943) proposed that sex is determined by a series of multiple complementary alleles of one locus (Fig. 1a). Diploid individuals possessing two different sex alleles are females, whereas hemizygous as well as homozygous individuals are males.

Pages 83-90 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Crozier (1971) extended this scheme to several loci (Fig. 1b). Complementary Sex Determination (CSD) yields several testable predictions. A simple qualitative prediction is that inbreeding should increase diploid male production because it increases homozygosity. Furthermore, the use of controlled matings between relatives permits quantitative predictions. Using mainly inbred crosses, diploid males have been detected to date in about 35 species (Cook 1993b). In some other cases, the sex ratio due to the primary sex determination can be modified by parasitic factors, microorganisms or behavioural control of fertilization. In the parasitic wasp *Nasiona vitripennis,* a supernumerary chromosome causes the condensation of the paternal genome in fertilized eggs. Consequently, the offspring are only haploid males (Beukeboom and Werren 1993).

It's now well known that diploid males have important consequences for population biology in Hymenoptera. In the fire ant *Solenopsis invicta,* diploid males significantly contribute to mortality because they reduce the rate of growth of new colonies and lead consequently to single-queen colony mortality (Ross and Fletcher 1986, 1993). In the parasitic wasp *Diadromus pulchellus*, diploid males modulate the variations in sex ratio due to larval competition in the host (El Agoze et al. 1986). Furthermore, diploid males are increasingly considered as a factor of failure in biological controls using parasitoids (Cook 1993a, Stouthamer et al. 1992).

Several facts assume the occurrence of diploid males in *Diprion pini* and call for cytological investigations to reveal them:

- The single locus CSD is considered ancestral and CSD is clearly widespread in Hymenoptera (Cook 1993b).
- A cytological study (Smith and Wallace 1971) revealed the occurrence of diploid males in another species of Diprioninae, *Neodiprion nigroscutum.*
- In *Diprion pini*, diploid males could account for the sex ratio inversion following inbreeding.
- Heterozygous males have been detected by enzymatic electrophoresis (Beaudoin et al. 1994).

This paper includes the preliminary description of *D. pini* chromosome complement and the results of research on diploid males in this species.

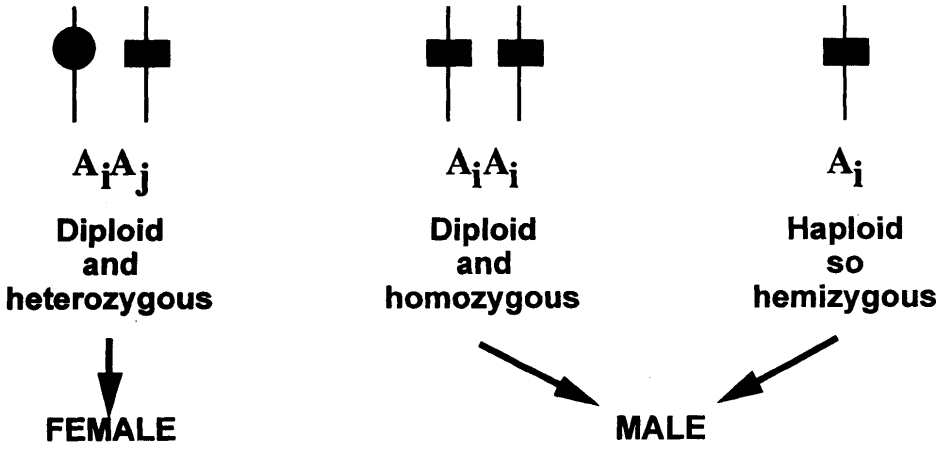


Figure 1a. Single locus CSD; 1 locus, n alleles.

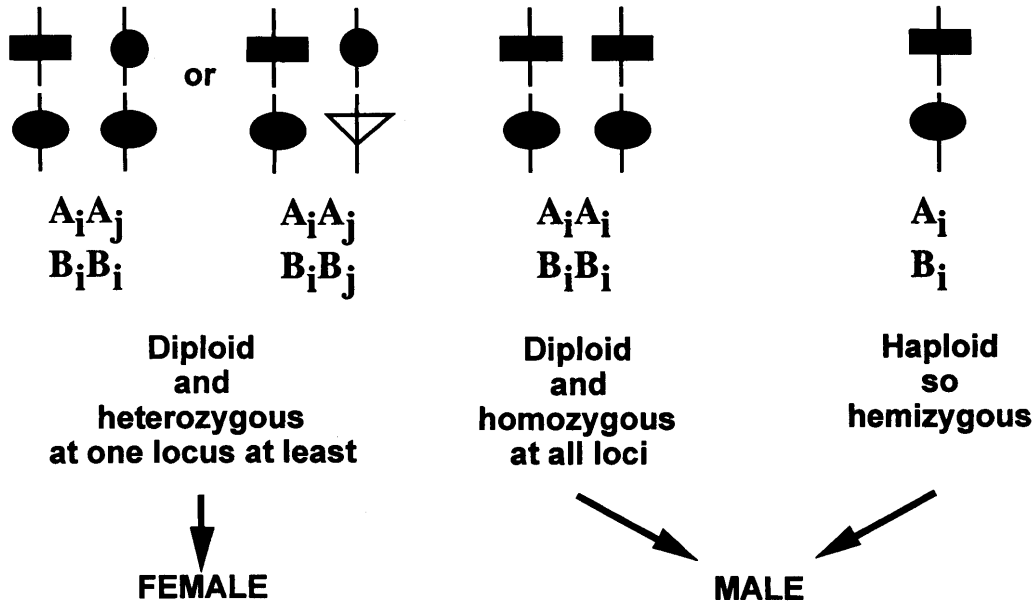


Figure 1b. Multilocus CSD (example of two loci).

Materials and Methods

Under CSD models, well-defined proportions of diploid males are expected following crosses between relatives. Our objective was to produce diploid males by inbreeding and to reveal them cytologically. The main part of the cytological study consisted of finding a tissue at the right time in order to observe as much mitosis as possible. It was necessary to observe many metaphase spreads, because several artifacts are possible, such as a juxtaposition of two chromosome complements that can look like a diploid set.

A. Cytology

Materials. Individuals used in this study were from a rearing strain (native to Sologne, France) or came from France (Fontainebleau Forest and Alps), Finland and England.

Chromosome Preparations. The chromosome number counts were made from the gonads of young prepupae. The gonial mitosis at the beginning of gametogenesis enables the observation of many metaphase spreads without polyploidy problems. We have parallel gametogenesis with eye development, which is a good external marker for dissecting at the right time. Testicles or ovaries were treated in colchicine-PBS solution, then in hypotonic solution for 15 minutes before fixing in an ethanol-acetic acid mixture for 30 minutes. The fixed tissue was then transferred to a drop of 60% acetic acid on a clean slide. Finally, the slide was placed on a warm hotplate and the drop was allowed to evaporate. The preparation was finally stained in a 3% Giemsa solution. Karyotyping followed the standard procedure and centromere position was described according to the nomenclature of Levan et al. (1964).

***In Situ* Hybridization (ISH).** The ribosomal probe used was Py12 cloned in pBr 322. It contains the 18S, 5S, and 28S genes plus intergenic spacers of *Drosophila melanogaster*. Methods for pretreatment, ISH and probe detection followed the procedure described in Engels et al. (1986) with minor modifications.

B. Sibmatings

We performed single-pair matings. Under single-locus CSD, a sister has one chance out of two to mate with one of its brothers possessing one of its alleles, so two kinds of brother-sister crosses occur (Fig. 2). If the female and the male share the same sex allele, their progeny contains diploid males. Consequently, we expected 50% of the colonies to have diploid males. Furthermore, 50% of fertilized eggs in these colonies are expected to be diploid males. Under the two-locus model, we expected 25% of the broods to contain 25% diploid males.

In these experiments, the colonies used for sibmating were descended from mated females collected in the Fontainebleau Forest.

first crosses (in order to obtain brothers and sisters) :

P : **F1 :**

AiAj x Ak → AiAk + AjAk + Ai +Aj

brother-sister crosses (in order to obtain diploid males) :

F2 :

AiAk x Ai → AiAi + AkAi +Ai + Ak 50% of diploid males (within the diploid offspring)

AiAk x Aj → AiAj + AkAj +Ai + Ak no diploid males

AjAk x Aj → AjAj + AkAj +Aj + Ak 50% of diploid males (within the diploid offspring)

AjAk x Ai → AjAi + AkAi +Aj + Ak no diploid males

Figure 2. Expected proportions of diploid males under a single-locus model.

Results and Discussion

A. Cytology

Our results contradict the study by Maxwell (1958) who karyotyped several samples from an English population of *D. pini*. She described it with a chromosome set of 7. At the beginning of this work, only the males were karyotyped and all had 14 chromosomes. According to Maxwell's description, all the males would be diploid, but our study revealed that all the females have 28 chromosomes. Several populations (see Materials and Methods) were studied, including an English population. All the populations share the same karyotype. So, Maxwell's determinations were not correct concerning *Diprion pini.* In a parallel example, *Diprion similis* was described with a haploid complement of 7 chromosomes by Maxwell (1958) and of 14 chromosomes by Smith (1941, 1960). These discrepancies forced us to redescribe *D. pini* karyotype as a prerequisite.

The 14 chromosomes of the haploid complement are acrocentric. A small chromosome carries a dot-shaped segment which appears similar to a B-chromosome. It is not a supernumerary chromosome but a satellite that is always present once in haploid males and twice in diploid females.

The chromosome number in *D. pini* is twice the basic number in Diprionidae. Two simple hypotheses can be considered to explain this karyotype evolution: polyploidization or centric fission. *In Situ* Hybridization (ISH) was carried out in order to differentiate between haplo-diploidy and diplo-tetraploidy. The rDNA probe hybridizes once in males and twice in females. Haplo-diploidy and centric fission are consequently more likely than diplo-

tetraploidy and polyploidization. This result is interesting from the fundamental and applied points of view (repercussions on sex determination and diploid male production).

B. Sibmatings and Detection of Diploid Males by Means of Cytology

Two series of sibmatings were carried out. Each time, some diploid males were revealed by karyotyping.

Diploid Male Characteristics. In the first experiment, all the individuals were weighed, dissected and karyotyped. Only four colonies (F2) were obtained from fertilized females (F1) and these colonies were not descended from the same "grandmother" (P). Only one progeny contained diploid males. In this colony, 40% of diploid individuals were male. The diploid males were clearly heavier than haploid males (33% on average), but the weight distributions slightly overlap each other (Fig. 3). Diploid males were responsible for sex ratio inversion. Because of homozygosity at the sex locus (or loci), the proportion of males at the prepupae instar was 56% while it would have been 27% if all the fertilized eggs developed into females.

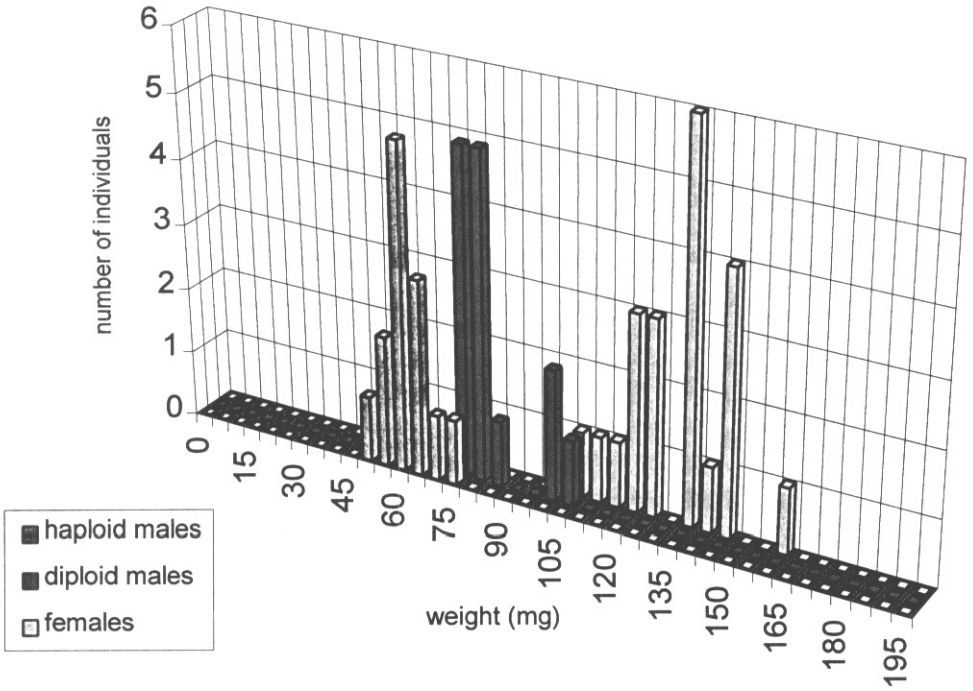


Figure 3. Weight distribution in a colony containing diploid males.

A second experiment was carried out in order to obtain diploid male adults. Because the weight of haploid male cocoons is rarely higher than 90 mg, individuals were graded by weight: < 90 mg and ≥ 90 mg. In this experiment, only a sample was dissected and karyotyped. All the dissected males among the heaviest males were diploid. Consequently, all the non-dissected males in this range were assumed to be diploid. So, it was confirmed that diploid male prepupae were heavier than haploid male prepupae (Fig. 4). The presumed diploid male imagos as a whole were clearly heavier and bigger with regard to many morphological features, but it was not possible to discriminate between a haploid male and a diploid male. Each time, the distributions overlapped and no typical marker was found until now.

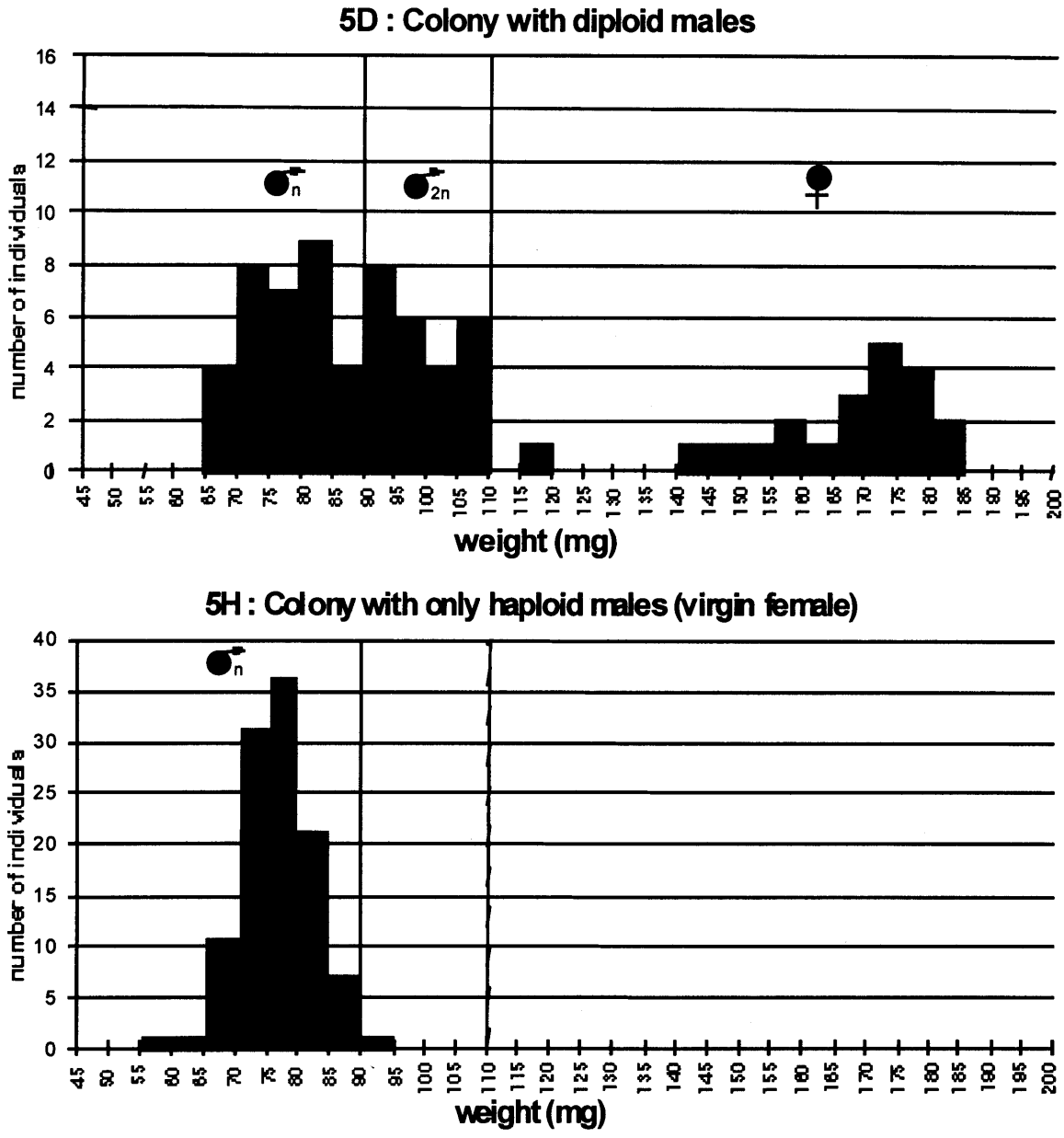


Figure 4. Distribution of prepupae belonging to colonies with or without diploid males as a function of cocoon weight.

Sex Determination. It is generally very difficult to succeed in mating and to obtain a sufficient number of colonies descended from the same grandmother (P) to test the expected proportions (50%-50% or 25%-75%). Many brother-sister crosses didn't succeed and produced progenies with only haploid males from unfertilized eggs. Furthermore, we were confronted with high diapause and mortality rates.

Our data does not permit us to arrive at a conclusion concerning sex determination models. The two experiments show that two-locus CSD is more likely with regard to the proportion of colonies containing diploid males, whereas the diploid male proportion is

consistent with the single-locus model. In the second experiment, for example, two colonies among eight progenies contained diploid males. It's completely consistent with the two-locus model (25%-75%). On the other hand, if diploid males are as viable as females, the expected proportions are 50%-50% under the single-locus model and 25%-75% under the two-locus model. In this experiment, there are approximately as many diploid males as females (53%-47%). Furthermore, diploid males are generally known to be less viable. So, single-locus CSD seems more likely from this point of view.

Possible Impact of Diploid Males on Population Dynamics. It is well known that diploid males affect the population biology of Hymenoptera (Cook and Crozier 1995). They are usually sterile or their sperm are mostly diploid and their progeny are triploid and not viable (except in the sawfly *Athalia rosae* - Naito and Suzuki 1991). Furthermore, they reduce population growth because they develop from eggs that are "normally" female.

With regard to *D. pini,* it is assumed that diploid males could interfere in diapause rates (Géri et al. 1995). On the other hand, it is possible that the very small size of *D. pini* populations between outbreaks entails a high level of consanguinity which could entail a considerable production of diploid males. Consequently, diploid males would reduce population growth and maintain a low population level. In this scheme, diploid male production would be stopped only when new alleles enter into the population (by migration or prolonged diapause emergences) thereby starting outbreaks.

Conclusion

It is concluded that diploid males occur in *D. pini* and we can suppose that these males play a prominent part in population dynamics. With the use of the sex pheromone recently synthesized (Bergström et al. 1995), it is now possible to sample males in the field by pheromone trapping in order to estimate their frequency in the natural population. However, testing our hypothesis requires more advances in the identification of diploid male adults and in the study of their biology (especially their mating ability, sterility, ploidy level of sperm, viability and larval development).

It is also necessary to settle the problem of sex determination, because single-locus CSD is more consistent with a high frequency of diploid males in the natural population. So, it is essential to confirm the karyotype evolution by centric fission because chromosome number doubling by polyploidization assumes the existence of (a minimum of) two sex loci.

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Noxious Effect of Scots Pine Foliage on *Diprion pini* L. (Hym. Diprionidae) and Other Defoliators: Specificity and Prospects for Use in Forest Management

MARIE-ANNE AUGER-ROZENBERG[1], CLAUDE GÉRI[1], CHRISTINE QUENCEZ[2] AND CATHERINE BASTIEN[2]

[1]INRA, Station de Zoologie Forestière, 45160 Ardon, France
[2]INRA, Station d'Amélioration des Arbres Forestiers, 45160 Ardon, France

ABSTRACT Feeding bioassays were conducted with the foliage of Scots pine clones, previously identified as favorable or unfavorable to the sawfly *Diprion pini*, in order to observe their effect on different populations of *D. pini* and on two lepidoptera defoliators, *Thaumetopoea pityocampa*, an important and dangerous pest, and *Graellsia isabellae*, a scarce and protected moth. All populations of *D. pini* consumed less foliage on the unfavorable clones; variation in consumption was related to the age of the larvae and to the season of the experiments. Similarly, *T. pityocampa* mortality increased and its larval development slowed down. Biological performances of *G. isabellae* were disturbed, too, and in this case, consumption of favorable clones allowed this species to obtain better survival and development rates than in nature. These results are discussed with regard to Scots pine breeding.

THE LARVAE OF the pine sawfly, *Diprion pini*, cause dramatic defoliation on Scots pine, its main host in Europe. In France, infestations occur especially in plains, where the insect is bivoltine (Géri 1988). The effect of the foliage on *D. pini* mortality, development rate, weight, fecundity and diapause has already been investigated using bioassays that involved starvation (Géri et al. 1988a), age (Géri et al. 1985, 1988a,b) and quality of the foliage (Géri et al. 1990). Auger et al. (1990, 1991, 1994) showed the existence of an interclonal intraspecific variability. Scots pine clones which are very unfavorable to the development of this insect were discovered in breeding populations of Polish origin. In order to determine the chemical compounds of the needles which could be associated with these noxious properties, analyses were conducted on polyphenols. The phenolic content of the foliage of Scots pine clones unfavorable to the larval development and survival of *D. pini* was characterized by the presence of two flavonoïds: taxifolin and one of its glucosides. These compounds were absent from the majority of the French clones and from some Polish clones favorable to the insect's performance (Auger et al. 1992, 1994). Furthermore, an induced reaction was shown when Scots pine trees were defoliated. Defoliation resulted in a decrease in the amount of needle taxifolin and an increase of its glucoside. However, this response is not limited to defoliation by *D. pini* larvae; Bastien et al. (1995) and Auger et al. (1994, and unpublished results) observed the same results after artificial defoliation with scissors. The reaction of the trees seemed to be localized near the wound. Nevertheless, it is currently difficult to evaluate the impact and mode of action of these phenolic compounds and the exact part they could play in Scots pine resistance mechanisms to insect pests. Because of the prospective use of

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resistant Scots pine in forest management, it was important to know the potential noxiousness of those clones for different populations and species of defoliators.

This article discusses experiments conducted to investigate clone foliage toxicity effects on different populations of *D. pini* and on two other Lepidopteran Scots pine defoliators: *Thaumetopoea pityocampa* Schiff. (Lep. Thaumetopoeidae) and *Graellsia isabellae* Graells (Lep. Attacidae). *Thaumetopoea pityocampa* is an economically important pest in Mediterranean forests and dermal irritations caused by larvae hair are harmful to humans. *Graellsia isabellae* is a scarce and protected beautiful moth located in the South Alps. Scots pine clones were used in feeding bioassays with *D. pini* larvae and associated with the phenolic content of the needles. In order to observe the specificity of foliage noxiousness, the effect of the foliage was comparatively observed on *D. pini* populations from different origins. Clones were then tested with caterpillars of *T. pityocampa* and *G. isabellae*.

Materials and Methods

Plant Material. Different clones of Scots pine of French (Alsace) and Polish (Mazurie) origin, used as breeding populations in an INRA breeding programme conducted at Orléans Station, were used in the following experiments. Each clone, identified by a code number, is represented by several grafted copies present at Orléans.

Feeding Bioassays With *D. pini*. Different bioassays, including several experiments and repetitions, were conducted from 1990 to 1993 with first instar larvae (which were more sensitive to feeding conditions) from a permanent laboratory strain reared from generation to generation (Goussard and Géri 1988) and from field populations near Orléans. Batches of 30 larvae were formed. The larvae were placed in transparent polystyrene boxes, which were closed with lids that allowed aeration, then placed in a growth chamber (15.30 / 8.30 h photoperiod, 16°C temperature). They were fed every 3 days with shoots taken from clones of the INRA nursery. The foliage was renewed by placing new shoots on the preceding ones, which were removed when the larvae had all moved to the fresh shoot. Larvae were fed for 12 days, and larval mortality rates were determined at the end of the test. Up until now, 37 clones were tested for their edibility for young *D. pini* larvae. For some clones, tests were completed by feeding bioassays using older larvae, in order to measure other biological characteristics, such as development rates, pupal weight, diapause rate and fecundity (Auger et al. 1990). We defined two groups of clones: one group of unfavorable clones and one group of favorable clones.

In 1994 and 1995, populations of *D. pini* larvae were collected in different forests and fed with different clones using the same method described above (two batches of 30 larvae per clone). They were collected at the first instar just after hatching or at the end of the first instar in the Fontainebleau forest (in the Parisian Basin), in the Alps and in a population of Finish origin, and immediately used in feeding tests. Feeding tests were conducted with the rearing strain at the same time for comparison.

Feeding Bioassays With *T. pityocampa*. *T. pityocampa* caterpillars live in colonies. They cause considerable damage, especially on black pine, but also attack Scots pine. From the 4th instar, they are highly irritating to humans and animals. This pest is present in southern France; the Orléans region represents the northern limit of its distribution. Two

experiments were conducted during the fall of 1992 and 1994. In 1992, colonies of first instar larvae (each of them corresponding to one egg laying) were collected in forests near Orléans after eggs were counted. Then, they were placed in the field on the branches of 10 clones: four clones (356, 632, 721 and 864) unfavorable to the survival and development of *D. pini* and six clones (129, 20, 16, 15, 14 and 13) that were favorable. Two colonies (one per tree) were placed on two trees per clone. In 1994, we used the same method with four clones: two favorable (16, 129) and two unfavorable (147, 136). Three colonies were placed on three trees per clone (one colony per tree) under natural conditions. In order to avoid climatic risks and itches, colonies were collected when larvae reached the fourth instar. Mortality and the development rate of the caterpillars were estimated by counting the survivors and observing the larval instars affected.

Feeding Bioassays With *G. isabellae.* This beautiful moth is known in Spain and in France where the subspecies *gallieglória* Oberthür, located in some valleys of the South Alps, is protected. Scots pine is its main host. Feeding bioassays were performed with a population reared at INRA since 1990, from eggs given by the OPIE (Office of Entomological Information) without catching insects in the wild. Caterpillars were fed cut shoots in transparent boxes as previously described from the time of hatch to cocoon spinning and kept in an outside shelter. Feeding bioassays were performed in the spring of 1992, 1993, 1994 and 1995. In 1992 and 1993, caterpillars were fed with five clones and for each clone, two batches of five caterpillars were formed: three unfavorable clones (356, 588 and 721) and two favorable (129 and 14) in 1992, and two unfavorable clones (627 and 721) and three favorable (129, 614 and 875) in 1993. In 1994, eight clones were used (721, 646, 588, 356 and 649 unfavorable and 129, 14 and 875 favorable). For each clone, four batches of five caterpillars were formed except for clones 875, 721 and 356 (two batches of five caterpillars). In 1995, three clones were used (147 unfavorable, and 129 and 20 favorable) with twelve batches of eight caterpillars for each clone. The biological characteristics of *G. isabellae* taken into account were: the percent larval survival, the sex ratio (% male cocoons), the length of larval development and the weight of the male and female chrysalis.

Biochemical Methods. In order to analyze the phenolic content, needle samples were collected at random in the trees before feeding bioassays, frozen immediately after collection in liquid nitrogen and then freeze-dried and ground to a powder before storage in dry conditions under a vacuum. The phenolic compounds were analyzed by HPLC and the presence or absence of the two compounds, identified as taxifolin and taxifolin glucoside, was observed for the whole clone employed in feeding bioassays. Extraction, elution programme and identification modalities are described by Auger et al. (1994).

Results

Experiments On *D. pini.* The percentages of young larvae surviving after 12 days of feeding on the different clones from 1988 to 1993 and the presence or the absence of taxifolin in the needles (when the phenol content of the foliage was analyzed) are shown on Figure 1. We can observe an important interclonal variability and higher mortality with clones containing taxifolin and its glucoside.

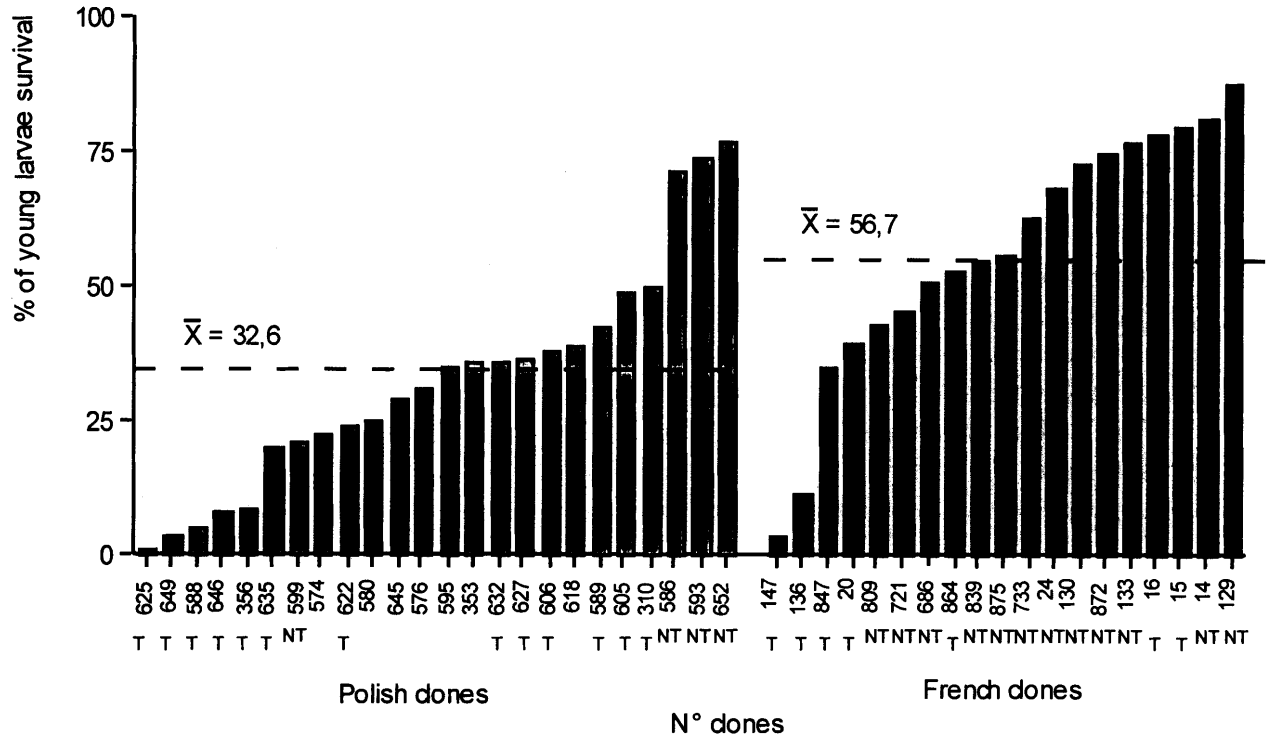


Figure 1. Mean survival (%) of *D. pini* larvae when young larvae fed in the laboratory on several Scots pine clones. Experiments were conducted from 1988 to 1993. For clones whose phenol content was analyzed: T = with taxifolin and taxifolin glucoside; NT = without the compounds.

Table 1 shows the results of feeding bioassays conducted with different populations of *D. pini* in 1994 and 1995. Mortality is always higher for larvae fed with unfavorable clones, whatever the origin of the population or the date of the test. When surviving larvae existed on unfavorable clones, we noted a decline in larval development and a decrease of both diapause rate and female fecundity. However, if the edibility of clones which were previously classified as very favorable (129) or very unfavorable (646, 588) is quite stable, differences existed for some clones with regard to the age of larvae, the season when tests were conducted, and the origins of *D. pini* populations. Thus, clone 20 caused high mortality of larvae from the rearing strain or Finland, but not of larvae from the Alps or the Fontainebleau Forest; clones 147 and 136 also showed variable mortality depending on populations. Whatever the population, foliage was unfavorable to larvae in November and mortality was important even with favorable clones (129). On the other hand, mortality was higher when the test was performed with L1 than with older larvae (L2). The effect of the intermediate clones on different populations needs to be confirmed.

Table 1. Feeding bioassays conducted in 1994 and 1995 with different populations of *D. pini*. Mean survival of larvae fed with different Scots pine clones. G: clones favorable to *D. pini* survival B: clones unfavorable to *D. pini* survival. T: clones with taxifolin and taxifolin glucoside. NT: clones without the compounds

Date of bioassays	Origin of *D. pini* population	Larval instar	N° clones							
			733 G NT	129 G NT	872 G NT	20 G NT	16 B T	147 B T	136 B T	646 B T
06/07/94	Rearing strain	L2	71,7							
13/09/94	Rearing strain	L1	50	66,3	53,3				0	
01/03/95	Rearing strain	L1		53,3		2,5		5		
15/11/94	Alps	L1		20	50		0	0		0
21/11/94	Alps	L2		76,7			6,7		0	0
21/04/95	Alps	L1		89,4		82,7		56,7		
03/03/95	Fontainebleau	L1		76,7				56,7		
10/03/95	Fontainebleau	L1		75		82,5		35		
18/10/94	Finland	L2		85	58,3				73,3	15
21/04/95	Finland	L1		71,7		30		26,7		

Experiments On Other Scots Pine Defoliators. The results of feeding bioassays on *T. pityocampa* (Pine processionary) are presented in Figure 2 for the experiments conducted in 1994. Important significant variations in caterpillar mortality and length of development were shown among the different clones. Foliage unfavorable to survival and development of *D. pini* larvae caused high mortality and slower larval development. The same results were observed in 1992; however, clone 864 (unfavorable to *D. pini*) caused only a drastic decrease of the larval development rate, and clone 14 (favorable to *D. pini*) caused high mortality. Therefore, we observed variability between different clones, but mortality was always higher with unfavorable clones than with favorable clones and linked with the presence of taxifolin.

The results of feeding bioassays on *G. isabellae* caterpillars were very consistent from year to year. They are presented in Figure 3 for the year 1994. During the four years, the effect of the consumption of clones was highly significant for all biological characteristics studied. The clones that were unfavorable to *D. pini* were unfavorable to *G. isabellae* caterpillars. They caused higher mortality (but not as high as that for *D. pini*), slower larval development and smaller pupal weight, whatever the year of the experiments. The worst performances (survival and development) were always observed with very unfavorable clones and, conversely, clones favorable to *D. pini* produced lower mortality, faster development and heavier *G. isabellae*. Very heavy female chrysalises, superior in weight to those observed in natural populations, were obtained when insects were fed clone 129, which was also very favorable for *D. pini*. As in the case of the previous species, performances of clones with *G. isabellae* were linked with the presence of taxifolin in the needles.

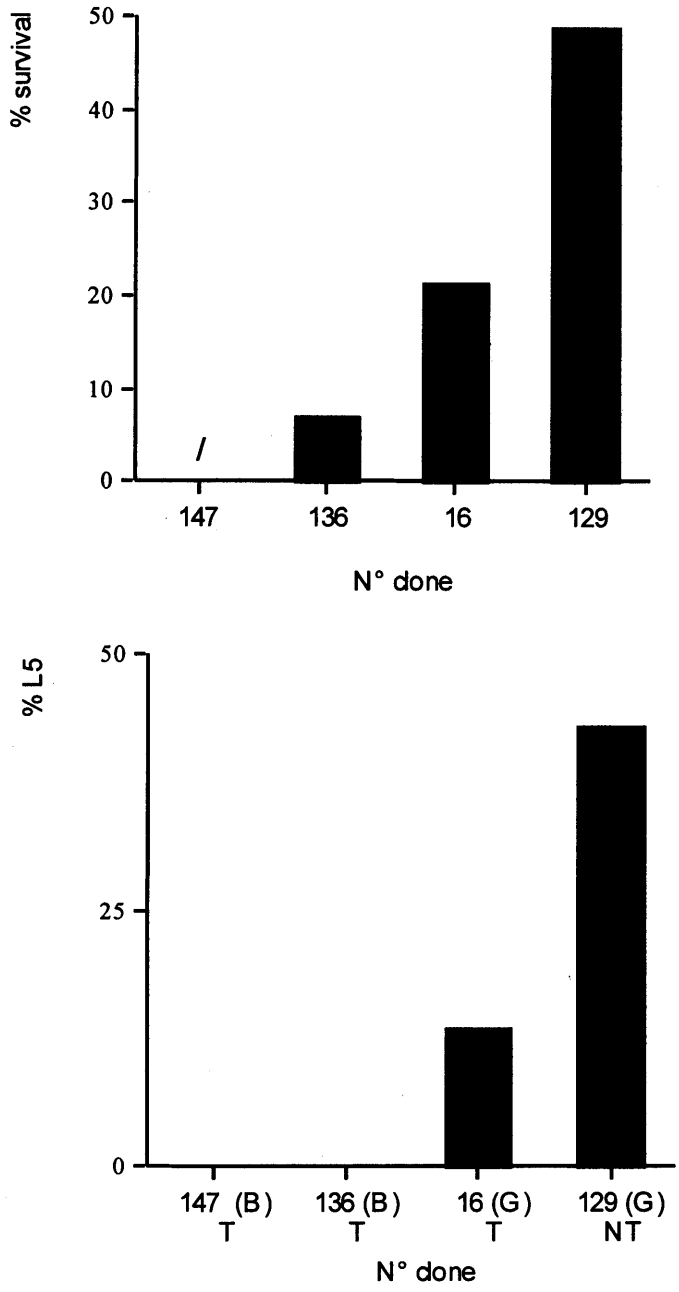


Figure 2. Mean larval survival and mean duration of development for caterpillars of *T. pityocampa* reared on different Scots pine clones in natural conditions. Experiments were conducted in 1994. B: clones unfavorable to *D. pini* survival. G: clones favorable to *D. pini* survival. T: clones with taxifolin and taxifolin glucoside. NT: clones without the components.

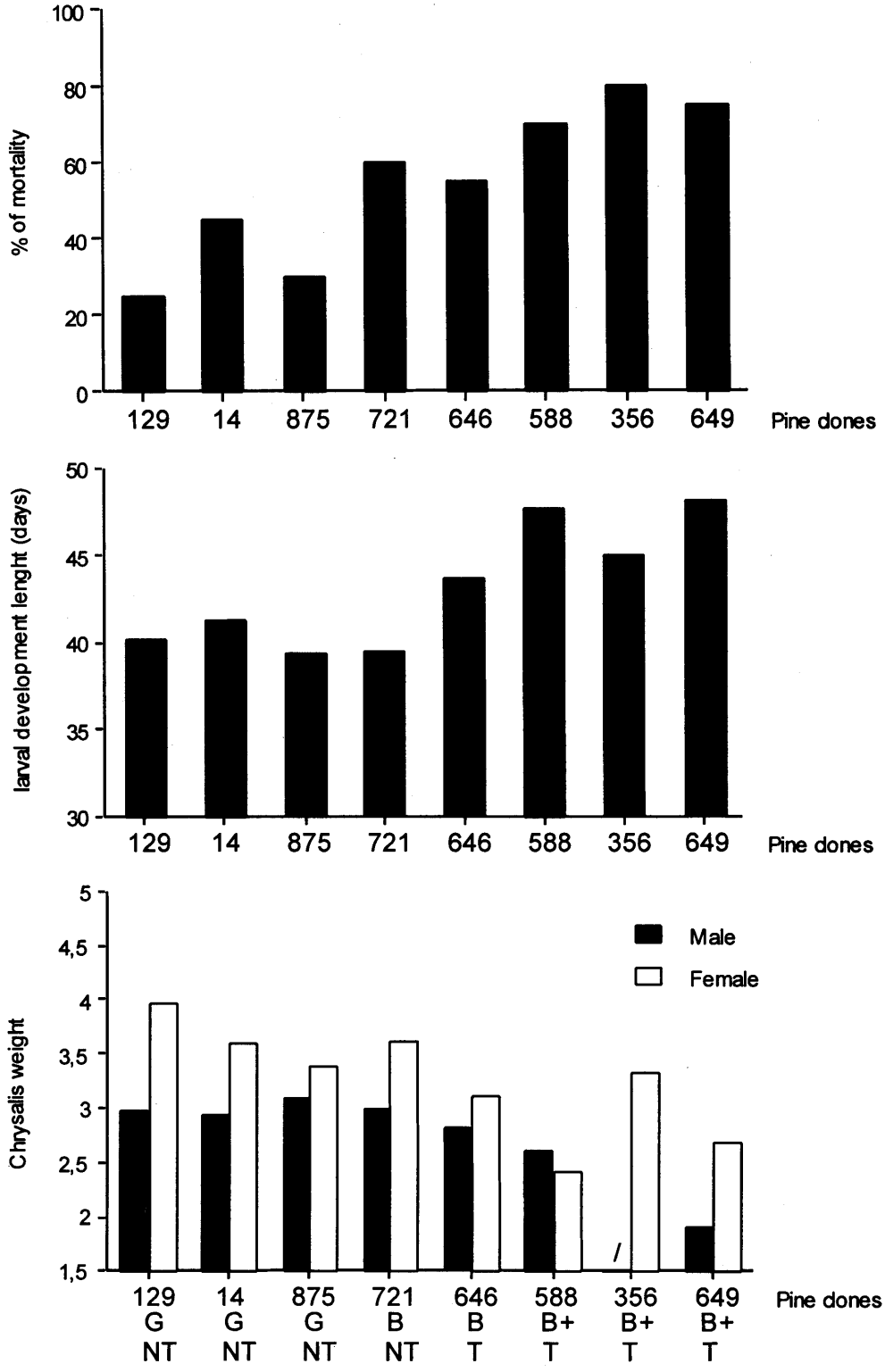


Figure 3. Performances of *Graellsia isabellae* fed with different Scots pine clones (experiments conducted in 1994). G: clones favorable to *D. pini* suvival. B: clones unvaforable to *D. pini* survival. B+: clones very unfavorable to *D. pini* survival. T: clones with taxifolin and taxifolin glucoside. NT: clones without the compounds.

Discussion and Conclusion

The results of these experiments on feeding show that the noxiousness of Scots pine clones is rather non specific and stable, not only for various populations of *D. pini*, but also for distant species of Scots pine defoliators. However, this needs to be confirmed with other pests.

The interclonal variability is notable for four different populations of *D. pini*, but needs to be verified by feeding tests with other populations. Some differences exist between populations, allowing one to assume that individual variations in the aptitude of insects to eat different foliage and perhaps genetic possibilities to overcome needle noxiousness exist. However, those differences need more precise investigations that consider others factors, such as insect age and seasonal variations in foliage quality. Nevertheless, clones previously noted for very favorable or very unfavorable characteristics presented homogenous results. We have to note that larvae of the rearing strain, usually fed with favorable foliage, showed higher mortality rates than larvae of field populations.

The results of feeding tests with *T. pityocampa* must be treated with caution because of the small number of experiments. Only first larval instars were observed and the tests were conducted under natural conditions, which confound the foliage effect. However, even if tests conducted at the end of insect development have to be made to prove the effect of clones on biological characteristics, such as pupal weight or fecundity, our results are in accordance with clone aptitudes observed with *D. pini*. Big differences between clones were shown for caterpillar mortality and development length. For *G. isabellae*, the results were repeated each year, and, as with *T. pityocampa*, the results clearly indicate the effects of Scots pine clone consumption on survival and development: their biological performances can be disturbed by consumption of clones which are known to be unfavorable to *D. pini*. The feeding effects of unfavorable clones were less important for *G. isabellae* than for the two insect pests used in the tests, but we have to be careful with the use of clone progeny obtained in a breeding program. They have a general effect on total fauna and they don't have to be introduced in the living area of this protected species. Moreover, some clones lead to really good insect survival and development, especially for chrysalis weight directly linked with fecundity, that were better than we can observe in nature. Those favorable clones can be used to rear scarce and protected species. However, we must ask ourselves if those clones wouldn't also be very favorable to the development of different insect pests. If breeding programs don't take this into account, trees selected for good growth criteria could also be very favorable for the breeding of efficient pests.

The species studied belong to very different families and these results are really interesting with regard to prospective use in forest management. In fact, if breeders want to obtain resistant trees, it is important to appreciate their effect on different species of defoliators. But environmental consequences on non-pest species and risks to select resistant insects need to be considered. It's comforting to note that the least affected species is the protected one.

Nevertheless, breeding strategy for Scots pine resistance is still to be achieved, and there is a need to experiment with others pests and to consider the long-term adaptations of insects to unfavorable trees.

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Sensitivity of the More Important Forest Defoliating Insects in Poland to Insecticides

HENRYK MALINOWSKI

Forest Research Institute, Department of Forest Protection, Bitwy Warszawskiej 1920r. nr 3, 00-973 Warsaw, Poland

ABSTRACT The susceptibility of the most important forest defoliating insects, such as nun moth, *Lymantria monacha* L., pine moth, *Dendrolimus pini* L., pine beauty moth, *Panolis flammea* Schiff. and conifer sawflies, Diprionidae, to approved and experimental insecticides (pyrethroids, arylpropylether, acylureas, diacylhydrazine) and biopreparations (based on a bacterium, *Bacillus thuringiensis* Berliner) was evaluated under laboratory conditions. Two methods were used: topical application and exposure of insects to treated pine needles.

Results indicated that although there is some evidence of resistance to frequently used insecticides (mainly to pyrethroids) in some insect populations, the above species can be controlled effectively with pyrethroid insecticides. The studies also showed that the insect populations we studied are fully sensitive to acylurea and diacylhydrazine insecticides and biological preparations based on *B. thuringiensis*. However, the sensitivity of target pest species to chemical and biological insecticides should be evaluated regularly.

THE MOST SERIOUS forest pests in some European countries, especially in Poland, include the nun moth, *Lymantria monacha* L., pine moth, *Dendrolimus pini* L., pine beauty moth, *Panolis flammea* Schiff., and conifer sawflies, family Diprionidae. Their periodic outbreaks often affect vast areas of Scots pine, *Pinus sylvestris* L., and Norway spruce, *Picea abies* Link., and can cause severe damage. To protect forests effectively against the above mentioned pests, chemical and biological insecticides are frequently used. For background information, a short history of the use of insecticides in Poland for control of forest defoliation is provided. Between 1950 and 1980, chlorinated hydrocarbons (DDT, lindane, methoxychlor) were most frequently used to control forest defoliators; in addition, organophosphates and carbamates were also used between 1974 and 1980. However, since 1980, pyrethroids such as deltamethrin and alphamethrin have been used most frequently against defoliating insects.

Although biopreparations of *Bacillus thuringiensis* (Foray, Dipel, Ecotech Pro) and acylureas (diflubenzuron, teflubenzuron, triflumuron) have been available since 1990, these products were rarely applied or used on smaller areas. Therefore, it can be assumed that among the insecticides used since 1980, the selection pressure of the pyrethroids to forest pest defoliators has been greater. The purpose of these studies was to evaluate the sensitivity of our most important forest defoliating insects to a variety of operational and experimental insecticides under laboratory conditions.

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Materials and Methods

The following species of insects were used in laboratory bioassays:

- nun moth (*Lymantria monacha* L.) - second and third instars
- pine moth (*Dendrolimus pini* L.) - first through fourth instars
- conifer sawflies (Diprionidae) (mixed population of different species of Diprionidae, mainly *Diprion pini* L. and *Gilpinia frutetorum* F.) - second instars
- pine beauty moth (*Panolis flammea* Schiff.) - second and third instars and their parasites: *Rictichneumon pachymerus* Katz. and *Barichneumon bilunulatus* Grav.

Larvae of the above mentioned insect species were collected in Scots pine stands from different forest districts in Poland between 1990 and 1995.

The insecticides used were:

Pyrethroids

- alphamethrin as 100 g/l EC (Fastac 100 EC, Shell)
- bifenthrin as 100 g/l EC (Talstar 100 EC, FMC)
- betacyfluthrin as 25 g/l EC (Bulldock 025 EC, Bayer)
- deltamethrin as 25 g/l EC (Decis 2,5 EC, Roussel - Uclaf)
- esfenvalerate as 50 g/l EC (Sumi - Alpha 050 EC, Sumitomo)
- lambdacyhalothrin as 25 g/l EC (Karate 025 EC, Zeneca)
- zetacypermethrin as 100 g/l EC (Fury 100 EC, FMC)

Arylpropylether

- etofenprox as 100 g/l SC (Trebon 10 SC, Mitsui Toatsu)

Acylureas

- diflubenzuron as 480 g/l SC (Dimilin 480 SC, Solvay Duphar)
- flufenoxuron as 50 g/l EC (Cascade 5 EC, Shell)
- novaluron as 100 g/l EC (GR 572 EC, Agrimont)
- teflubenzuron as 150 g/l SC (Nomolt 15 SC, Shell)
- triflumuron as 480 g/l SC (Alsystin 480 SC, Bayer)

Diacylhydrazine

- tebufenozide as 240 g/l EC (Mimic 24 EC, Rohm and Haas)

Biopreparations of *Bacillus thuringiensis*

- Foray 48B (B.t. kurstaki, potency min. 11.000 i.u./mg, Novo Nordisk)
- Ecotech Pro 07.5 OF (strain EG 2348, transconjugant *Bt* kurstaki x *Bt* aizawai, potency 24,000 i.u./mg, Ecogen)

Two methods were used to test the sensitivity of insects to contact insecticides: direct topical application to larvae, and exposure of insects to treated pine needles. For stomach poisons such as *Bt* and acylureas, insects were exposed to treated pine needles.

Topical Method. Insecticides were dissolved in acetone to produce six to eight different concentrations (doses). Larvae were individually treated using the Arnold microapplicator. A 1-µl drop of insecticide solution was applied to the dorsal surface of larvae. Percent mortalities were calculated 48 or 76 hrs after application of insecticides. Controls were treated with acetone. Mortality data were corrected for mortalities in the control insects according to Abbott's formula and subjected to probit analysis (Finney 1952).

Exposure of Insects to Treated Pine Needles. Aqueous suspensions of each insecticide were prepared at seven different concentrations. Bouquets of Scots pine needles, about 15 cm long, were dipped for five seconds in each concentration and allowed to dry. The test larvae were placed on the treated foliage, whereupon the bouquets were placed in water under glass tubes covered with cloth. Two replications of 15 larvae each were used for each concentration. The same procedure was used for controls that were treated with water only. In the case of the pine beauty moth, the caterpillars were exposed to treated filter paper with deltamethrin only. Percent mortalities were calculated after 48 hours (pyrethroids and etofenprox), 4 to 6 days (*B. thuringiensis* biopreparations) or 10 to 12 days after treatments (acylureas and tebufenozide).

Calculations of percent mortality included both dead and severely affected individuals. Tests were conducted at a temperature of 20-25°C for all treatments.

Results and Discussion

Susceptibility of Insects to Pyrethroids and Arylpropylether (Etofenprox). Topical Application Method. The topical application method allowed us to produce regression lines that demonstrated the relationship between doses and mortalities. Data on the susceptibility of second to third instar nun moth larvae to pyrethroids and etofenprox were presented earlier (Malinowski 1996). Those data showed that nun moth caterpillars exhibited similar response to most pyrethroids, resulting in regression lines that were close together. Nun moth larvae responded similarly to etofenprox; however, higher doses were required to cause comparable levels of mortality (Malinowski 1996).

The sensitivity of third to fourth instar pine moth larvae to pyrethroids and etofenprox is illustrated in Figure 1. The shape of the regression lines with small slopes for pyrethroids is similar to that observed in nun moth larvae. LD_{50} values ranged from 0.0017 μg/individual (deltamethrin) to 0.004 μg/individual (bifenthrin), resulting in two-fold differences. The regression line for etofenprox is also placed in the scale of higher doses and its slope is similar to that of pyrethroids.

A similar situation was observed in the case of conifer sawflies, Diprionidae, treated with pyrethroids and etofenprox (Fig. 2). The slope of the regression lines for pyrethroids and etofenprox is similar to other forest defoliating insect species discussed previously. However, LD_{50} values between 0.00014 μg/individual (deltamethrin) and 0.00031 μg/individual (bifenthrin) were lower than those obtained from studies on pine moth larvae (Fig. 1). Diprionid larvae were less sensitive to etofenprox than to pyrethroids, which is similar to the results with other species.

These studies showed that in all cases, the slope of the regression lines for pyrethroids is similar. Some differences in LD_{50} values were observed among species; however, for a given species, the LD_{50} values between pyrethroids differed only about two-fold. These studies also showed that in all cases, the slope of the regression lines for etofenprox is similar to those for pyrethroids; however, higher doses were required to produce a level of mortality similar to the pyrethroids. The shape of the regression lines with small slopes for both pyrethroids and etofenprox indicates that a degree of heterogeneity exists among individuals of all species studied. These populations of insects are composed of a mixture of resistant,

sensitive and hybrid individuals, and the quantitative relationships between them determine the shape of the regression lines. This is caused by selection pressure of insecticides currently being applied, such as pyrethroids, and probably by other products that were used previously, for example DDT. It has been suggested that cross resistance between DDT and pyrethroids exists (Malinowski, 1988).

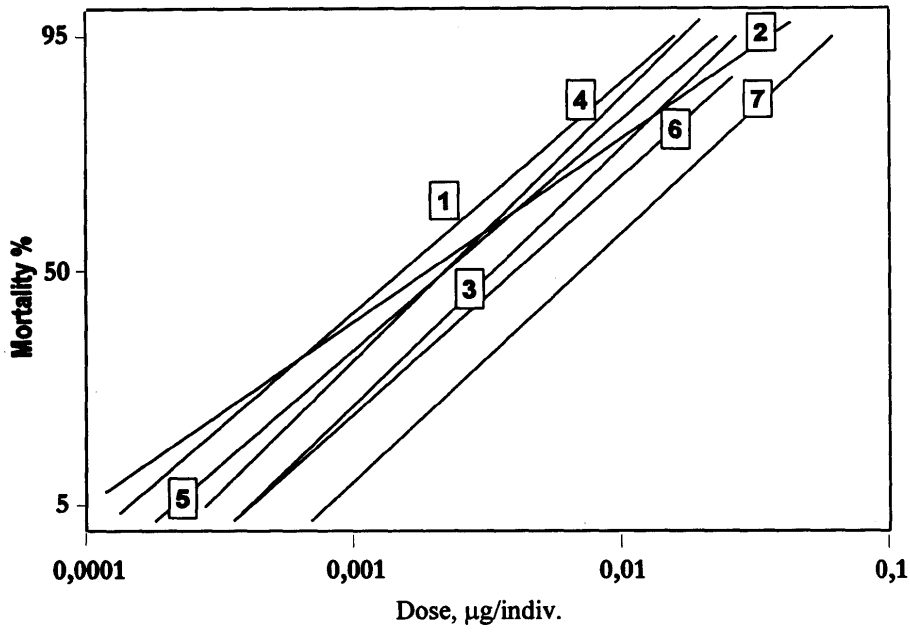


Figure 1. Regression lines obtained from studies on pine moth caterpillars L3/L4 instars treated topically with insecticides: 1-deltamethrin, 2-esfenvalerate, 3-zetacypermethrin, 4-lambdacyhalothrin, 5-alphamethrin, 6-bifenthrin, 7-etofenprox. Topical application method, assessment after 48 hrs. 1,2,5-studies on populations from Bialkow Forest District (1991, 1992), 3,4-studies on populations from Krosno Forest District (1993) and 6,7-studies on population from Ostrow Mazowiecka Forest District (1993).

Exposure of Insects to Treated Pine Needles. Although the insect populations tested are characterized by their heterogeneity in response to pyrethroids and etofenprox, they can be controlled effectively with these insecticides. Our studies conducted with the dipping technique showed that nun moth larvae that were exposed to a range of concentrations of pyrethroids and etofenprox suffered 100% mortality at three (0.01, 0.001, 0.0001 g/l) and two (0.01, 0.001 g/l) of the highest concentrations, respectively (Malinowski 1996). Similar results were obtained from studies on larvae of the pine moth and conifer sawflies. These results confirmed the data obtained by the topical application method which showed that pyrethroids were more effective than etofenprox against the larvae tested.

The comparative evaluation of the sensitivity of pine beauty moth larvae and their parasites *Rictichneumon pachymerus* Katz. and *Barichneumon bilunulatus* Grav. to deltamethrin, by exposing them to treated filter paper, showed differences between parasites and their host (Glowacka and Malinowski 1991). Parasites were less sensitive to deltamethrin

than as their host. Both parasites suffered 100% mortality only at the highest concentration (1 g/l) of deltamethrin. In the case of pine beauty moth larvae, 100% mortality was obtained at a 1000-fold lower concentration of deltamethrin. Results of this study also indicated that pine beauty moth caterpillars originating from different localities differed in their response to deltamethrin. It may be assumed that the lower sensitivity of some pine beauty moth caterpillars to deltamethrin can be attributed to the intensive use of pyrethroids in the past.

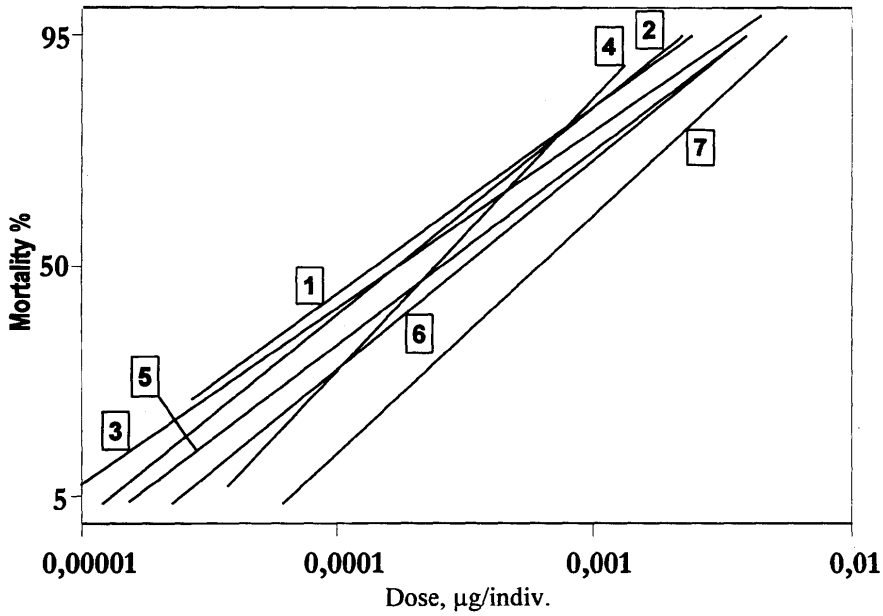


Figure 2. Regression lines obtained from studies on *Diprionidae* L2 instar larvae treated with insecticides: 1-deltamethrin, 2-zetacypermethrin, 3-alphamethrin, 4-lambdacyhalothrin, 5-esfenvalerate, 6-bifenthrin, 7-etofenprox. Topical application method, assessment after 48 hrs. 1,3,5-studies on populations from Bialkow Forest District (1991), 2,4,6,7-studies on populations from Podrodzie Forest District (1992, 1993).

Susceptibility of Insects to Acylureas. All larvae of species tested were susceptible to acylurea compounds such as diflubenzuron, flufenoxuron, novaluron, teflubenzuron and triflumuron (Malinowski 1995a). Nun moth larvae were equally susceptible to flufenoxuron, novaluron, teflubenzuron and diflubenzuron (Malinowski 1996). These compounds gave 90% larval mortality at a concentration of 0.0001 g/l, while 90% mortality with triflumuron occurred at a higher concentration (0.001 g/l). The response of pine moth and sawfly larvae (*Diprionidae*) (Table 1) was similar to that of nun moth larvae with one exception: diflubenzuron was effective at a higher concentration of 0.001 g/l. This group of insecticides was introduced more recently for control of forest insects and has been used on a small scale. Therefore, their selection pressure was too weak to produce resistant individuals in our test populations of insects.

Table 1. Toxicity of acylurea insecticides for L_2 instars of conifer sawfly (Diprionidae) larvae exposed to treated pine needles

Insecticide	LC_{90}*
flufenoxuron	0.0001
novaluron	0.0001
teflubenzuron	0.0001
diflubenzuron	0.001
triflumuron	0.001

*Concentration (g/l) giving minimum 90% population mortality after 10-12 days

Susceptibility of Insects to Tebufenozide. Tebufenozide (RH-5992) is a novel synthetic nonsteroidal ecdysteroid agonist, which represents a new class of insect growth regulators. It induces a premature and lethal larval molt by direct stimulation of the ecdysteroid receptors, especially in *Lepidoptera*. In this respect, it mimics the activity of the natural ecdysteroids (Heller et al. 1992, Smagghe and Degheele 1994, Slama 1995).

The sensitivity of *D. pini*, *B. piniarius* and *L. monacha* larvae to tebufenozide was tested in Poland under laboratory and field conditions (Malinowski and Glowacka 1996). Results of laboratory experiments using both methods--topical application to larvae and exposure of insects to treated pine needles--are given in Table 2. The data showed significant activity of tebufenozide against larvae of the above mentioned species of forest *Lepidoptera* at low concentrations.

Table 2. Toxicity of tebufenozide to larvae of some forest pest Lepidoptera

Pest	Method	Dose causing minimum 90% mortality
Dendrolimus pini		
larvae of second instar	exposure of insects to treated pine needles	0.001-0.0001%
larvae of first instar	topical application	LD_{50} < 1μg/larva
Bupalus piniarius		
larvae of second instar	exposure of insects to treated pine needles,	0.0001%
	topical application	LD_{50} < 1μg/larva
Lymantria monacha		
larvae of second instar	exposure of insects to treated pine needles	0.0001%

More detailed studies conducted in our laboratory (Pszczólkowski, personal communication) on the efficacy of tebufenozide against different larval stages of the pine

moth, using the same methods, gave the following results: the LD_{50} for L_5-L_6 instars was approximately 0.001 g/L (dipping technique, 10 days after treatment) and the LD_{50} for L_7 instars was between 0.004 - 0.04 µg/larva (topical method, 10 days after treatment).

Susceptibility of Insects to Biopreparations of *Bacillus thuringiensis*. Biopreparations of *B. thuringiensis*, which are typical stomach poisons that must be ingested by larvae, have been evaluated by Malinowski (1995b). Results of tests conducted on Foray 48 B against both nun moth and pine moth larvae (Fig. 3) suggest that both species are susceptible to this product.

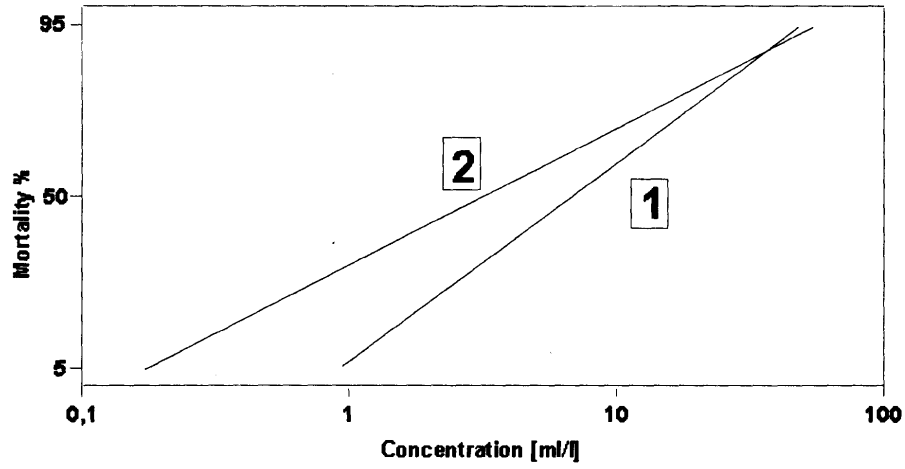


Figure 3. Regression lines obtained from studies on Lepidoptera caterpillars exposed to pine needles treated with Foray 48 B. (1) L2/L3 instars of nun moth caterpillars (assessment after 6 days), (2) L1/L2 instars of pine moth caterpillars (assessment after 4 days).

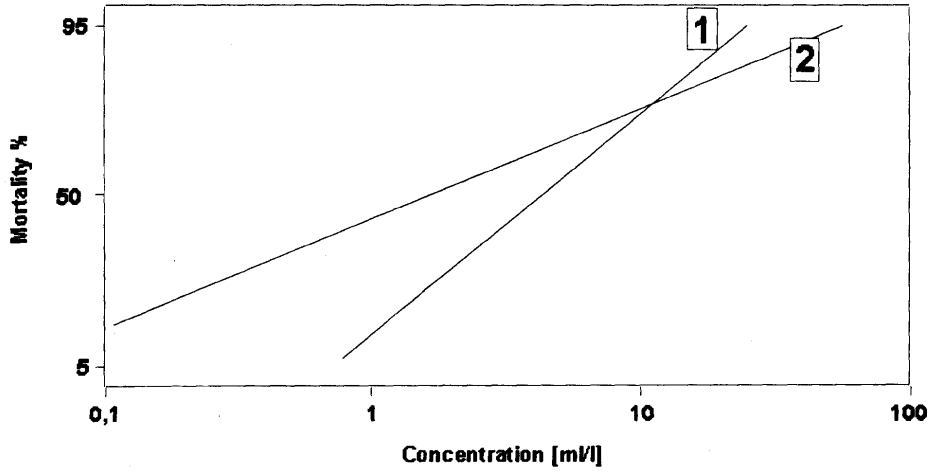


Figure 4. Regression lines obtained from studies on Lepidoptera caterpillars exposed to pine needles treated with Ecotech Pro 07.5 OF. (1) L2/L3 instars of nun moth caterpillars (assessment after 4 days), (2) L1/L2 instars of pine moth caterpillars (assessment after 4 days).

Results on the susceptibility of nun moth and pine moth larvae to Ecotech Pro 07.5 OF (Fig. 4) lead to the same conclusion. It may be concluded that larvae of nun moth and pine moth are equally susceptible to both Foray 48 B and Ecotech Pro. This is due to the strain specificity and low frequency of the use of other *B. thuringiensis* biopreparations against forest Lepidoptera in the past.

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The Control of the Nun Moth (*Lymantria monacha* L.) in Poland: A Comparison of Two Strategies

BARBARA GLOWACKA

Forest Research Institute, Bitwy Warszawskiej 3, 00-973 Warsaw, Poland

ABSTRACT The nun moth *Lymantria monacha* is a defoliator of coniferous trees in many European countries. In Poland, its cyclical outbreaks occur in Scots pine and spruce stands. In the last half of the century, insecticides were used to control the nun moth on a total area of 7.3 million ha.

During the course of an outbreak in 1993 and 1994, two different control strategies were utilized and the efficacy of treatments and side effects of the insecticides were estimated.

In 1993, pyrethroids were used against II-IV instar of nun moth larvae in stands where >90% defoliation was expected. The efficacy of treatments, calculated as larval mortality, was estimated to be ca. 87 %. The infested area increased by 7 times in the following year.

In 1994, stomach insecticides Dimilin 480 SC and Foray 48 B were used against I-II instars in stands where the expected level of defoliation ranged from 30% to 90%. Spraying was carried out in the stands in which a complete defoliation was predicted as well as in those stands where the outbreak just began. The treatment efficacy, based on larval mortality, was 100% and the nun moth outbreak collapsed.

The numbers of beneficial and other non-target arthropods killed and collected on 1 m^2 drop cloths in the stands treated with pyrethroids, were approximately 10 times higher than in the stands treated with stomach insecticides.

FORESTS IN POLAND cover 8.7 million ha, which accounts for about 28% of the country's total area. The composition of the forests includes: Scots pine (*Pinus sylvestris*; 70.0%), Norway spruce (*Picea abies*; 6.0%), Silver fir (*Abies alba*; 2.5%), Others (1.0%), Oak, beech, birch and others (20.5%).

Scots pine defoliating insects are major economic pests of Poland's forest stands. The main defoliators are the pine beauty moth (*Panolis flammea*), pine lappet (*Dendrolimus pini*), pine looper (*Bupalus piniarius*), nun moth (*Lymantria monacha*), and Diprionid sawflies.

The nun moth occurs in Scots pine, spruce and larch stands. At very high population densities larvae attack both conifer and deciduous species.

In the second half of the century, six nun moth outbreaks were recorded in Poland, and aerial treatments with insecticides were applied over a total area of 7.3 million ha. The largest outbreak occurred in 1978-1984 (Fig. 1), and covered 3.7 million ha of pine and spruce stands. The outbreak peaked in 1982, when over 2.3 million ha were sprayed with contact pyrethroids (95% of the treated area) and the stomach insecticides diflubenzuron and *Bacillus thuringiensis* (5%).

Pages 108-115 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

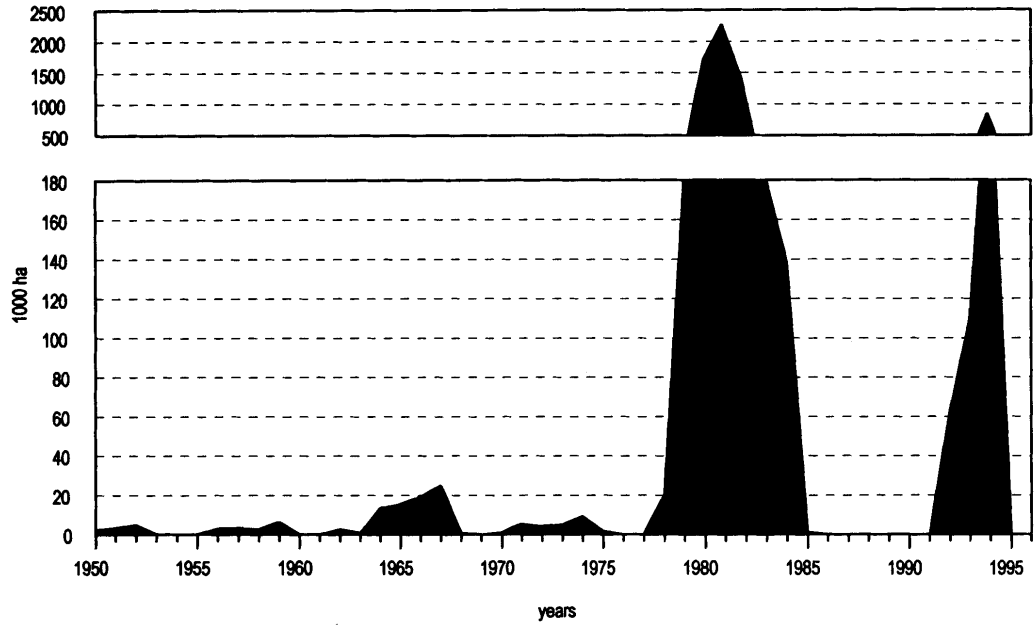


Figure 1. Aerial control treatments against the nun moth in Poland.

Table 1. Level of infestation with *Lymantria monacha* (females per tree)

Stand age (in years)	Warning numbers[1]	Numbers necessary to cause weak and/or moderate infestation (+ or ++)[2]	Critical numbers necessary to cause severe infestation (+++)[3]	
			Full foliage II and III class of quality site	Damaged foliage IV and V class of quality site
to 20	1	2 - 4	5	3
21-40	3	4 -19	20	10
41-60	6	7 - 39	40	20
61-80	10	11 - 59	60	35
81-100	15	16 - 79	80	50

[1]Warning numbers indicate a high probability of outbreak development.

[2]Numbers necessary to cause a weak or moderate infestation (+ or ++) with an estimated 30-90% stand defoliation.

[3]Critical numbers necessary to cause severe infestation (+++) with an estimated 90-100% stand defoliation.

The number of female moths observed on check trees during a swarm flight in July and August was used to forecast the infestation in the next year. Control treatments were recommended if the number of females observed on check trees indicated a possibility of complete (>90%) stand defoliation (Table 1).

The Nun Moth Control Treatments in 1993 and 1994

Since 1991, an increase in the density of nun moth populations was observed and in 1992, the infested area covered 160,000 ha of Scots pine stands. Control treatments were

carried out on an area of 62,600 ha using pyrethroids. In spite of the satisfactory efficacy of the spraying, the forested area infested with the nun moth increased in the following year.

In 1993, control treatments were carried out using the contact pyrethroids Sumi-Alpha 005 UL, Decis 2,5 EC, Fastac 10 EC and stomach insecticides Dimilin 480 SC and *B. thuringiensis* (Fig. 2). The treatments were performed against II-IV instar nun moth larvae. An aircraft equipped with Micronair AU 3000 nozzles sprayed 110,000 ha of Scots pine stands in which heavy (>90%) defoliation was expected.

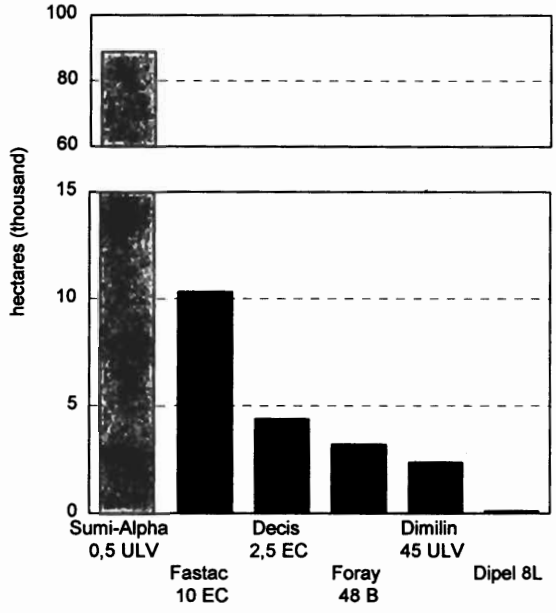


Figure 2. Insecticides used in nun moth control treatments in 1993.

In 1994, a new control strategy was developed to suppress pest outbreak. A project "The integrated control of nun moth in Polish forests," financed by Polish and foreign funds, was implemented. The new approach was aimed at reducing nun moth larval populations through the use of stomach insecticides. The use of pyrethroids was reduced to 10% (Fig. 3). The 757,000 ha of infested Scots pine stands were sprayed with an aircraft equipped with Micronair AU 5000 nozzles. The level of infestation based on predicted defoliation ranged from 30% to 90% and included stands where the nun moth outbreak was just beginning. The treatments were applied at the beginning of May, as soon as the nun moth larvae began hatching.

The Efficacy of Control Treatments in 1993 and 1994

Nun moth mortality following treatments was estimated in 1993 and 1994 using linen 1 m^2 cloths that were placed beneath check trees (420 cloths in 1993, and 450 in 1994). The number of dead nun moth larvae dropping from the crowns was counted over a period of 7 days in the stands treated with pyrethroids, and for a few weeks in those stands treated with stomach insecticides. Trees were then cut and placed on large linen sheets. The remaining larvae that were stuck to needles were collected and percent mortality was calculated by

multiplying the number of the larvae dropped/m^2 by the area of crown projection, and including the number of both living and dead larvae found in the crown.

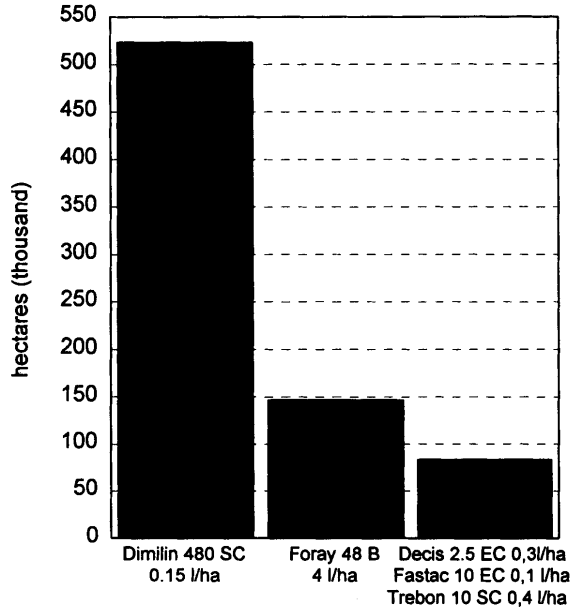


Figure 3. Insecticides used in nun moth control treatments in 1994.

In 1993, the mortality of the nun moth was calculated 1-2 weeks following treatment. The average number of dead larvae dropped per m^2 linen cloth was determined after each treatment (Fig. 4). In the stands treated with Dimilin 480 SC. an average of 18 larvae were found per m^2 cloth, and in the stands treated with Fastac 10 EC, the average number of dead larvae was more than 80. Nun moth larval mortality ranged from 17% to 100% (Fig. 5) with an average mortality nearing 87%. However, the infested area increased 7 fold in the following year.

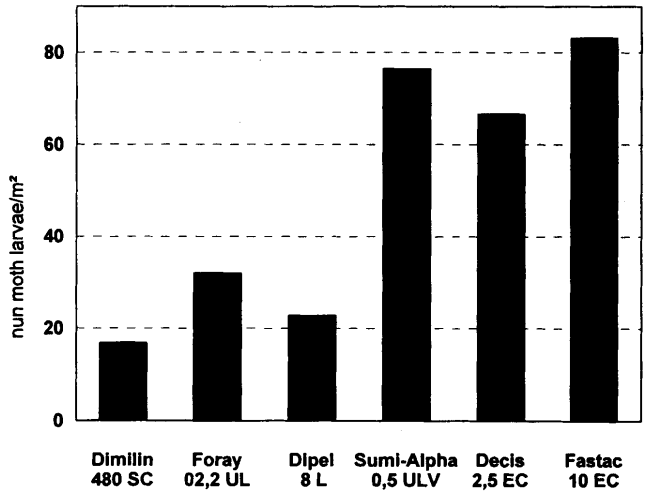


Figure 4. The mean number of nun moth larvae/m² in 1993.

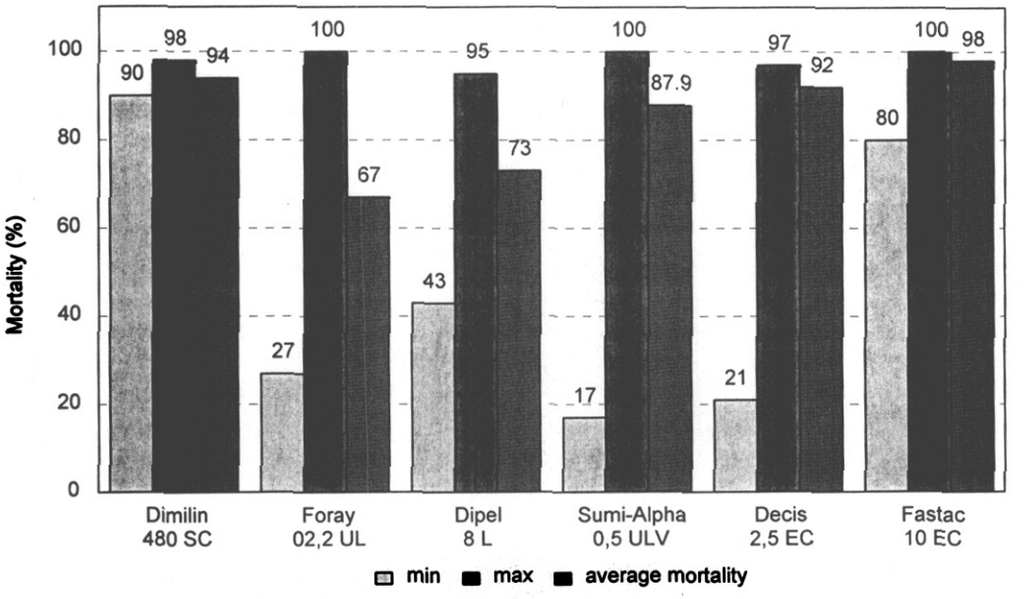


Figure 5. Mortality of nun moth larvae in 1993.

In 1994, the mortality of the nun moth on check trees was calculated 2 and 4 weeks following the treatment. The average number of dead larvae collected per m^2 ranged from 37 in the stands treated with Foray 48 B to 250 in the stands treated with Decis 2,5 EC (Fig. 6). Ultimately, the mortality approximated 100% (Fig. 7) and resulted in the cessation of the outbreak.

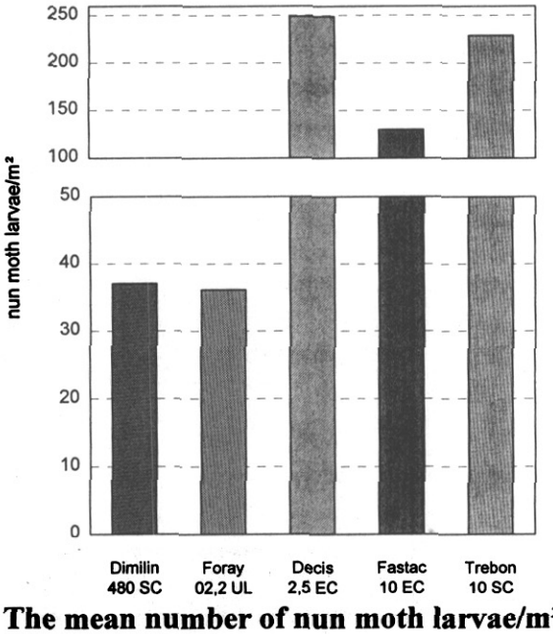


Figure 6. The mean number of nun moth larvae/m^2 in 1994.

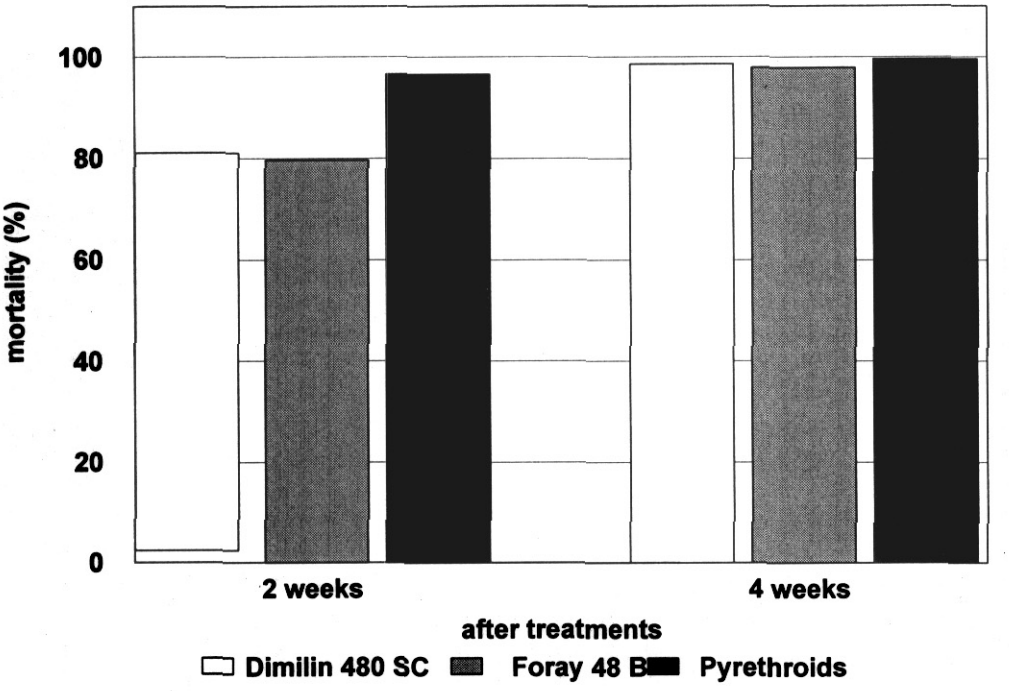


Figure 7. Mortality of nun moth larvae in 1994.

The additional factor that favored high nun moth mortality in 1994 was the poor synchrony between the development of pine and nun moth larvae caused by above normal temperatures in April and below normal temperatures in May and June (Table 2).

The early hatching of larvae and delayed development of young pine shoots and male inflourescences resulted in a continued deficit of suitable food for young larvae; this may have caused the reduced viability observed in the nun moth populations.

Mortality of Non Target Arthropods

An estimation of the environmental impact of the control treatments was carried out in 1993 and 1994. The impact of both stomach and contact insecticides on parasitoids, predators, and other non-target insects and spiders was assessed as the number of dead arthropods found after the treatment on 1 m^2 linen cloth placed beneath the crowns of 420 (1993) and 450 (1994) check trees.

The average numbers of dead beneficial and other non-target arthropods collected per m^2 in the stands treated with pyrethroids were approximately 10 times higher (Figs. 8-9) than in the stands treated with *B. thuringiensis*, diflubenzuron, and in the control plots.

Table 2. Thermal characteristics of successive decades of April (Ap), May and June in 1993 and 1994 (acc. IMiGW)

Meteorological station	1993							1994						
	Month													
	Ap	May			June			Ap	May			June		
	Decade													
	3	1	2	3	1	2	3	3	1	2	3	1	2	3
Bialystok	A	A	A	a	N	B	B	A	b	A	B	b	B	N
Chojnice	A	A	A	A	a	b	B	A	N	a	B	b	B	a
Gdansk	A	A	A	A	a	b	B	A	b	a	b	b	B	N
Katowice	A	A	A	A	A	b	B	A	b	A	b	b	B	A
Kielce	A	A	A	a	a	b	B	A	b	A	b	b	b	a
Koszalin	A	A	A	A	N	N	B	A	a	a	b	b	B	a
Kraków	A	A	A	a	A	b	B	A	b	A	b	b	B	A
Lublin	A	A	A	a	a	b	B	A	B	A	B	B	B	a
Lodz	A	A	A	a	A	b	B	A	N	A	B	b	B	A
Olsztyn	A	A	A	A	N	b	B	A	b	A	B	b	B	N
Opole	A	A	A	a	A	b	B	A	b	A	b	N	B	A
Poznan	A	A	A	a	a	B	B	A	N	A	B	b	B	a
Rzeszów	A	A	A	a	a	b	B	A	b	A	b	b	b	A
Szczecin	A	A	A	a	a	b	B	A	a	A	b	b	B	a
Warszawa	A	A	A	a	a	b	B	A	b	A	B	b	B	a
Wroclaw	A	A	A	a	A	b	B	A	N	A	b	b	B	A
Zielona Góra	A	A	A	a	A	B	B	A	N	A	b	b	B	A

A	much above normal
a	above normal
N	normal

B	much below normal
b	below normal

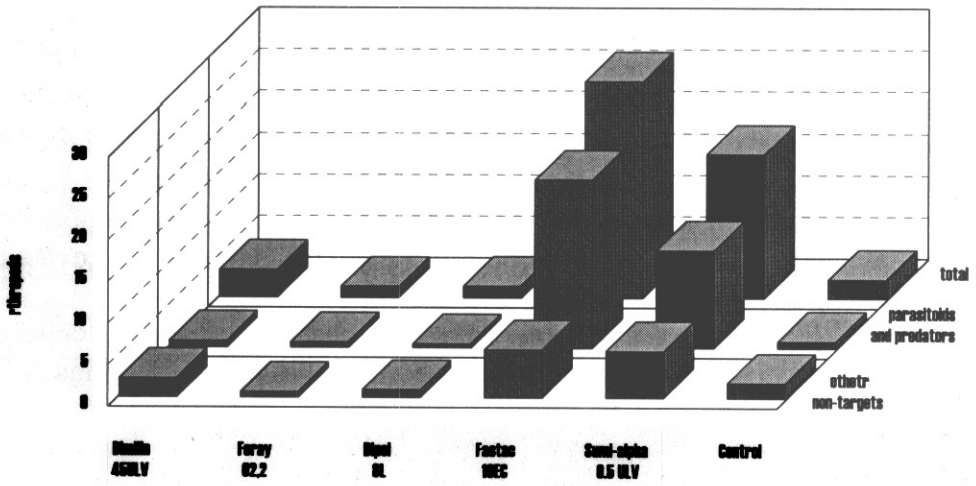


Figure 8. Average number of beneficial and indifferent arthropods dropped per m^2 in treated stands in 1993.

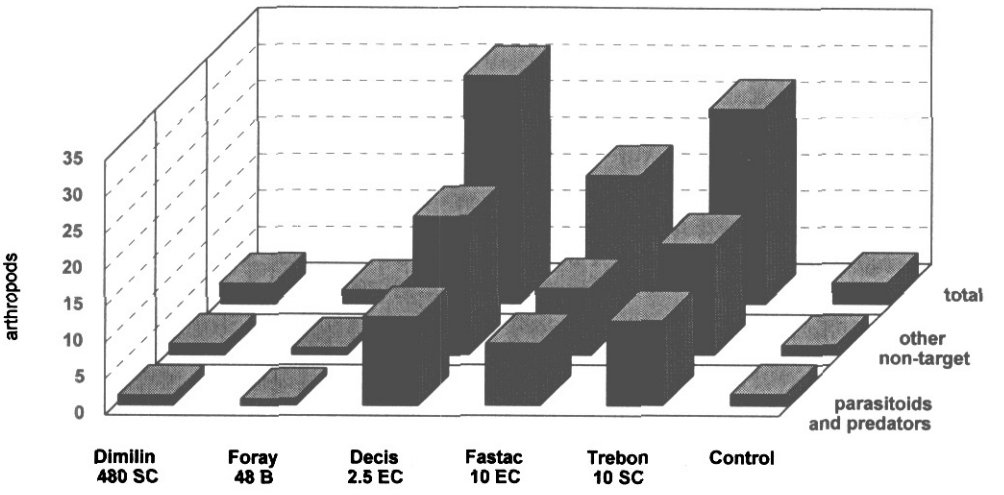


Figure 9. Average number of dead beneficial and other non-target arthropods collected per m^2 in treated stands in 1993.

Conclusions

In 1993, the II-IV instar nun moth larvae were controlled with pyrethroids in stands in which the population density of the pest was expected to cause >90% defoliation. However, the area of infested stands increased in the following year by 7 times.

The use of stomach insecticides Dimilin 480 SC and Foray 48 B against newly hatched larvae in 1994, not only in the stands in which complete defoliation was expected, but also in those stands with lower density nun moth populations, caused high mortality of the larvae and resulted in the cessation of the outbreak.

The comparison of the side effect of the insecticides used here showed that the mortality of parasitoids, predators and economically indifferent arthropods in the stands treated with pyrethroids was 10 times higher than in the stands treated with stomach insecticides and in untreated stands.

The Effect of Pesticides Applied Aerially to Forest Stands on Four Species of Native Hymenopterous Parasitoids

JACEK HILSZCZAŃSKI

Forest Research Institute, Department of Forest Protection, ul. Bitwy Warszawskiej 1920r. nr 3, 00-973 Warsaw, Poland

ABSTRACT Studies were conducted on the Ostrow Mazowiecka Forest District in central Poland to assess the impact of aerially spraying four pesticides (Decis 2.5 EC, Trebon 10 EC, Foray 48B, and Dimilin 480 SC) against the nun moth (*Lymantria monacha* L.) on the dynamics of four species of hymenopterous parasitoids that are common inhabitants in Scots pine forests. Results are discussed in relationship to the behavior and bionomics of the individual parasitoid species and to their hosts.

THE SUPERFAMILY *ICHNEUMONOIDEA* is one of the largest groups of insect parasitoids, and contains many species that attack a wide variety of insect hosts and that possess many behavioral adaptations. These attributes contribute to their importance in the biological control of many forest insect pest species. Outbreaks of many forest defoliators occur in Poland, requiring at times the application of pesticides to thousands of hectares in order to prevent defoliation and tree mortality. There is concern about the effect of aerially-applied pesticides on forest ecosystems, and specifically on non-target species such as native parasitoids. Consequently, the Department of Forest Protection, Forest Research Institute, initiated studies to determine the impact of pesticide treatments used against the nun moth, *Lymantria monacha* in Scots pine (*Pinus sylvestris*) stands on select species of parasitoids.

Methods

Studies were conducted in 1994 and 1995 in the Ostrow Mazowiecka forest district in central Poland. Four treatment plots and a control plot were established in a 40 year old even-aged stand of Scots pine. Four pesticides were applied aerially on May 22, 1994, using ULV equipment (Micronair AU 5000): Trebon 10 EC, Decis 2.5 EC, Foray 48B, and Dimilin 480 SC.

In order to estimate the mortality after treatments five, 1 m^2 linen drop cloths were placed in each plot under the average trees. The cloths were checked on six successive days post-treatment in the plots sprayed with contact pesticides Trebon 10 EC and Decis 2.5 EC. In the plots sprayed with Foray 48B and Dimilin 480 SC, the cloths were checked every third day post-treatment over a period of 2 weeks.

Changes in the abundance of native parasitoids were estimated by deploying Moericke's yellow pan traps (6/plot) in the middle of tree crowns at 5 to 8 m above ground depending on tree height. The traps were checked every 2 weeks during the period of May 5 to October 20 in both 1994 and 1995.

Pages 116-121 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Four species of parasitoids were chosen for analysis based on their differing behavior, biology, and effect on their hosts. *Agrypon flaveolatum* (Grav.), *Idiogramma euryops* (Foerst.), and *Lestricus secalis* (L.) are koinobionts, which are proovigenic and have a relatively short Spring flight period (Askew and Shaw 1988). Two species of ichneumonids that are closely related biologically, *Pimpla turionellae* (L.) and *P. contemplator* (Mueller) were combined because of questions about their taxonomy. These species are characteristic of idiobionts, which are synovigenic and have a prolonged flight period.

Results and Discussion

The analysis of collections from the linen drop cloths indicate that none of the pesticide treatments had an effect on any of the chosen species of parasitoids. Because the treatments were applied early in the morning prior to the period of activity of adult parasitoids, there was very low mortality caused even by the contact pesticides Trebon 10 EC and Decis 2.5 EC. This was further confirmed by the large number of ichneumonids that were recovered in the plots (Fig. 1).

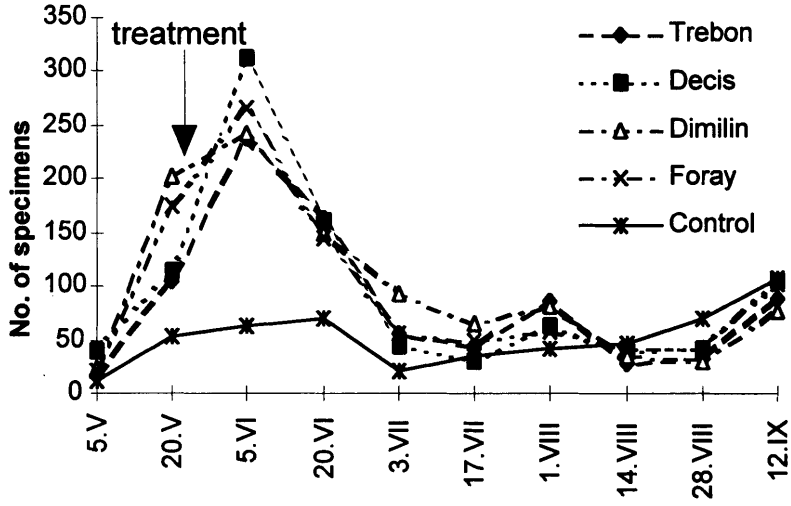


Figure 1. Abundance of *Ichneumonidae* collected in Moericke traps, Ostrów Mazowiecka forest district, 1994.

Based on collections from the pan traps, the pesticide treatments had either no effect or a positive effect on populations of the koinobiont species *A. flaveolatum, I. euryops,* and *L. secalis*; the idiobiont species (*Pimpla*) declined in 1995, the year after the plots were treated. The results are discussed in relationship to the behaviors of these species and the dynamics of their host populations.

Females of the koinobiont species are proovigenic, that is, they contain completely developed eggs at the time they emerge, and therefore do not require supplementary feeding prior to parasitizing their host larvae. Therefore, they spend most of their adult life searching for suitable hosts in which to oviposit. This contributes in part to their relatively short flight period (Figs. 2, 3, 4). In addition, they are univoltine and, thus, well adapted to their individual host species. *A. flaveolatum* is a Palearctic species in the subfamily anomaloninae

and is known to parasitize larvae of many lepidopteran species, especially within the families Tortricidae, Noctuidae and Geometridae. This species is an important natural enemy of the winter moth, *Operophtera brumata* L., and was introduced successfully into North America to control this forest pest (Barrons 1989). Females of *A. flaveolatum* deposit their eggs into early instar larvae of their hosts whereupon the parasitoid larva hatches, completes its development within the host, and then emerges from the host pupa. Although populations of free living host larvae might be reduced by the pesticide treatments, thus having a negative effect on the parasitoid, this was not observed since numbers of *A. flaveolatum* recorded from traps were similar in both years on all plots except the plot treated with Dimilin, where a significant increase occurred in 1995 (Fig. 2). Since many of the geometrid larvae were in the late instars at the time of spraying, it is possible that *A. flaveolatum* larvae were able to complete their development successfully prior to the death of their hosts. It has been reported that diflubenzuron, the active ingredient in Dimilin, can cause an increase in progeny of some parasitoids (Khoo et al. 1985). This could possibly account in part for the high abundance of *A. flaveolatum* in the Dimilin plot in 1995. However, additional research studies are needed to confirm that this phenomenon occurs in this species.

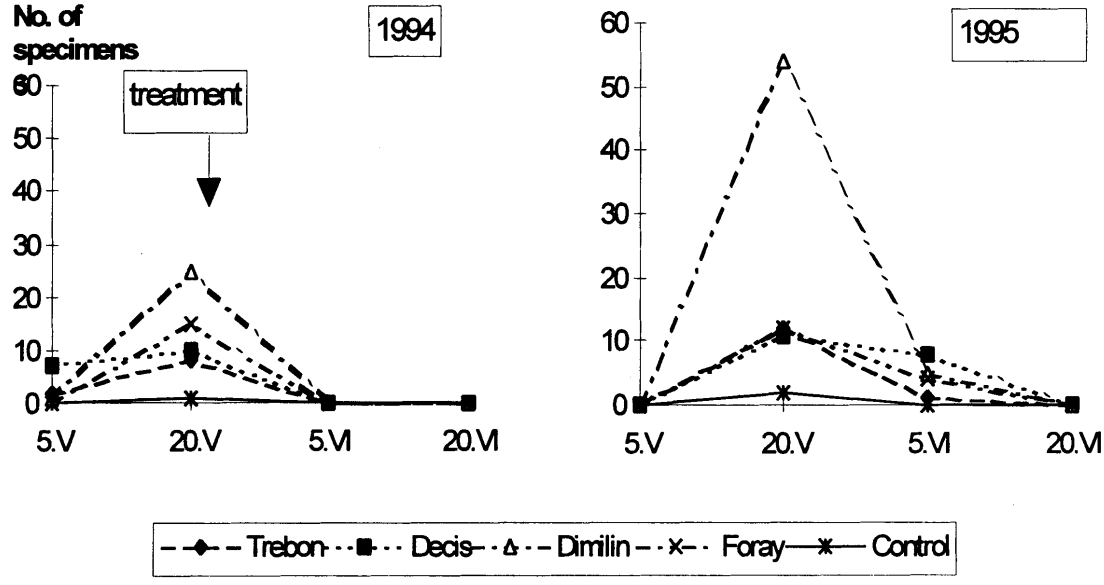


Figure 2. Abundance of Agrypon flaveolatum (Grav.) collected in Moericke traps, Ostrów Mazowiecka forest district, 1994-95.

Idiogramma euryops is a small tryphonine that is known to parasitize xyelid (Hymenoptera: Xyelidae) larvae that live concealed in male inflorescens of *Pinus* sp. Although the pesticide treatments should not have directly affected the xyelid hosts of this parasitoid, the treatments may have effectively eliminated the nun moth first instars that also feed upon and destroy pine inflorescens, and thus compete with the xyelid larvae for suitable habitats. Reduction in nun moth populations may have benefited both from the xyelid population and *I. euryops* and, thus, account for the increased abundance of *I. euryops* that was recorded in 1995 (Fig. 3).

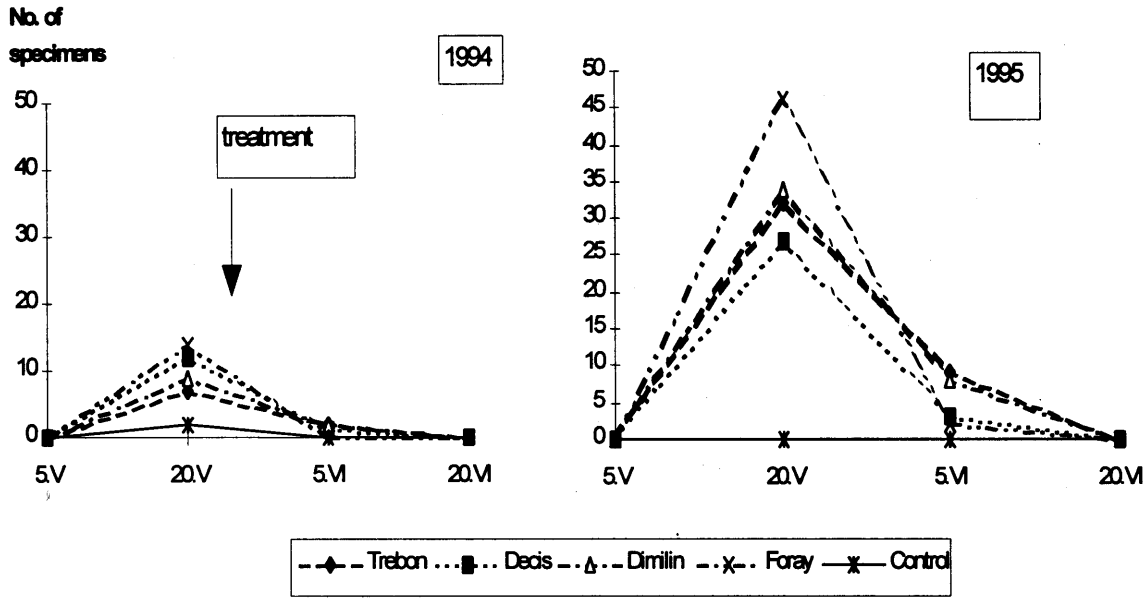


Figure 3. Abundance of *Idiogramma euryops* (Foerst.) collected in Moericke traps, Ostrów Mazowiecka forest district, 1994-95.

The other koinobiont, *L. secalis*, is a small braconid wasp in the small world-wide subfamily Cenocoeliinae, that parasitizes small wood-boring beetle larvae (Shaw and Huddleston 1991). In our plots, we recovered this species from *Pogonocherus decoratus* Fairm. and *P. fasciculatus* (DeGeer) (Coleoptera: Cerambycidae), whose larvae live in dead and dying twigs of conifers. Therefore, these hosts should not be affected by treatments of aerially applied pesticides. However, the abundance of populations of *P. decoratus* and *P. fasciculatus* might be affected more strongly by outbreak nun moth populations that cause death and weakening of *P. sylvestris* and thus provide more host material for the cerambycids. In fact, the abundance of *L. secalis* was lower in the control plot (Fig. 4) where nun moth populations also were low (Glowacka 1994).

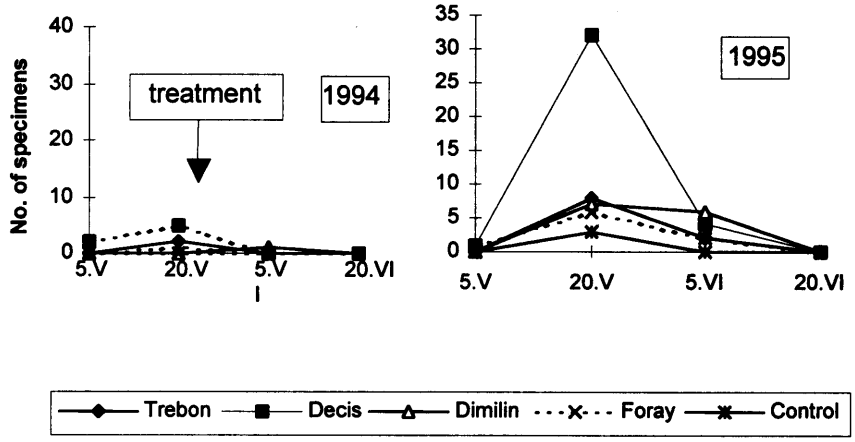


Figure 4. Abundance of *Lestricus secalis* (L.) collected in Moericke traps, Ostrów Mazowiecka forest district, 1994-95.

Pimpla turionellae and *P. contemplator* are idiobionts, which are synovigenic. The adult females are obligated to take supplementary food, and therefore, the time required for completion of egg development is prolonged. In addition, both species are bivoltine with peaks of abundance occurring at the beginning of June and toward the end of July (Fig. 5). Both species are polyphagous and parasitize small- and medium-sized pupae of many species of Lepidoptera in the families Geometridae, Tortricidae, Noctuidae, and Lymantriidae (Fitton et al. 1988). The abundance of *Pimpla* sp. was not affected by the treatments in 1994, however significant reductions were observed in 1995. These reductions apparently were caused by significant decreases in the host populations caused by the pesticide treatments.

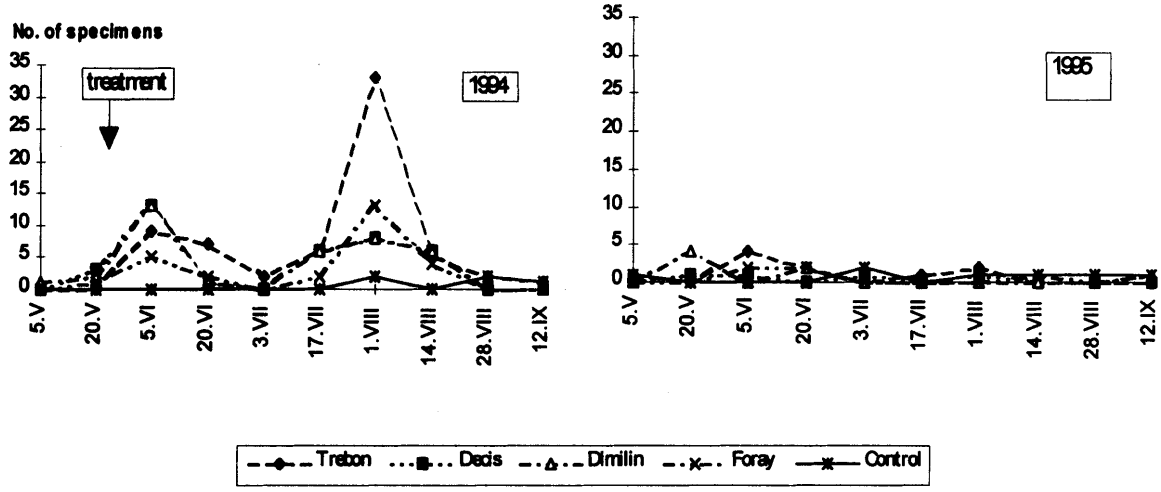


Figure 5. Abundance of Pimpla sp. collected in Moericke traps, Ostrów Mazowiecka forest district, 1994-95.

Although aerial application of pesticides to control forest defoliators may have many direct and indirect effects on populations of natural enemies, these effects will vary depending on the behavior and dynamics of both hosts and parasitoids. Adult hymenopteran parasitoid species that are active in tree crowns may be particularly susceptible to contact pesticides such as Trebon 10 EC and Decis 2.5 EC. However, their susceptibility to these products varies depending on their period of flight activity and the timing of the pesticide application. The abundance of the four parasitoid species in this study probably was affected more by the abundance of their host populations, which in turn varied according to their distribution in the forest and their susceptibility to the pesticide treatments.

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Evaluating the Impact of Insect Communities on Pine Caterpillar Density under Different Stand Conditions

TIANSHENG LI[1] AND GUOFA ZHOU[2]

[1]Research Institute of Forest Protection, Chinese Academy of Forestry, Beijing 100091, P.R.China
[2]Department of Applied Mathematics, Branch Campus of Peking University, Beijing 100083, P.R.China

ABSTRACT Natural enemies play an important role in inhibiting the population dynamics of the pine caterpillar, but their roles are difficult to incorporate into systematic management models. This paper attempts to use selected forest stand factors to substitute for the effects of natural enemies, for use in management models. From studies that include more than 200 plots under different stand conditions in Qu County, Changshan County and Longyou County of Zhejiang Province, 16 predominant species groups from the insect community were selected, and the canonical correlation coefficient between the insect diversity index, number of insect species, number of predominant insect species and stand factors was determined. The results indicated that both canopy density and vegetation condition are the key stand factors that characterize the dynamics of the insect community. The forest area was classified into four types according to variation in canopy and vegetation conditions using systematic cluster analysis. There were significant differences in the insect diversity index, number of insect species, number of predominant insect species and population density of the pine caterpillar among the four types. Regression models between pine caterpillar density and forest factors, including canopy density and vegetation cover were developed for each type of forest. The correlation coefficients of the four regression models were rather high (r=0.924-0.964). This indicates that the classification of forest stands is reasonable and stand factors may be used to simulate the effect of natural enemies in the field.

THE PINE CATERPILLAR, *Dendrolimus punctatus* (W.), is a serious defoliating pest of masson pine forests in the southern part of China and occurs in 15 provinces and regions. The population dynamics of the pine caterpillar are a major component of the integrated management system of this insect. Natural enemies play an important role in inhibiting the population density of the pine caterpillar, but past research work has centered on natural enemy classification, individual biology and evaluating their effect by constructing life tables. (Wu 1979, Cheng 1984, Wang1984, Chai and Li 1985, Zha 1988, Chen and others 1990). The results were difficult to use in systematic management models. Past research work has shown that in the field, forest plant and insect communities interact with each other (Bach 1980, Frances 1982, Lawton 1978, MacArthur 1964, Southwood and others 1979). Stand factors affect insect communities, which further affect pine caterpillar population dynamics. In this paper, we focus on the impact of the insect community on pine caterpillar density with the goal of identifying forest stand factors that simulate the effect of insect communities on this pest and are easy to use in management models.

Pages 122-128 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Materials and Methods

Field work was conducted between 1992 to 1994 in masson pine forests located in Longyou County, Qu County and Changshan County of Zhejiang Province. Most of the pine forests are pure pine and distributed on hillsides. Stand ages ranged from 5 to 20 years, tree heights ranged from 2 to 6 meters, and diameter at breast height ranged from 5-12 centimeters. Canopy densities varied from 0.3 to 0.8, and vegetative cover varied greatly, with herbs or shrubs being predominant. From 1992 to 1994, ground surveys were conducted on 222 experimental plots six times per year.

Survey Period. The survey time frame encompassed the late larval and pupal stages following overwintering, the early larval, late larval, and pupal stages of the first generation, and larval stages of the second generation before overwintering.

Sampling Methods. Two sampling methods were used. The first involved covering a pine branch sample with a net, cutting the branch with long-stem scissors, then counting the number and species of insects. Two branches were cut on each of 50 trees for a total of 100 samples per plot. A total of 70 groups of insects was found using this method. Another method involved sweeping insects on the ground vegetation with a sweepnet.

Factors of Investigation. Factors of investigation included pine caterpillar density; tree age and canopy density; elevation, slope and aspect; and vegetative conditions, including the height of shrubs and herbs, percent herb and shrub cover, total percent cover and average percent cover.

Data Analysis. Predominant Species or Species Group Determination: The selection criteria for the predominant species or species groups included: the individual number of insects per sampling unit more than 5 and the value of the correlation coefficient between the density of predominant species groups and density of the pine caterpillar. Most predominant species or species groups are natural enemies of the pine caterpillar. According to the above selection criteria, 16 species or species groups were selected as predominant species. These include: Pantatomidae, Reduviidae, Coreidae, Carabidae, Meloidae, Aphididae, Formicidae, Chalcididae, Ichneumomidae, Braconidae, Coccinellidae, spider, Lymantriidae, Chrysopidae, Syrphidae and Alydidae.

Expression of the Function of Predominant Species Groups. The individual number of insects is denoted by N, the number of species or species groups is denoted by S and the diversity index is denoted by H. These variables were chosen to represent the dynamics of the predominant species or species groups. H was calculated using the Gini-Simpson method. The correlation coefficients between N, S, H and the density of the pine caterpillar, D, were calculated.

Table 1. Correlation coefficients between N, S, H and D

R	Min	Max	Average
N-D	0.32	0.83	0.51
S-D	0.23	0.63	0.43
H-D	0.28	0.69	0.45

The results showed that all of the coefficients are higher than the critical point at the 5% (0.25) significance level (Table 1). Therefore, using N, S and H to describe the impact of the insect community on pine caterpillar populations was suitable.

The Selection of Key Stand Factors. The canonical correlation analysis method was adopted to evaluate the effect of stand factors on the insect community. This method can delete relative effects among the factors and analyze the relative of each factor against N, S and H. The canonical correlation coefficient between N, S and H of the 16 predominant species groups and each stand factor was analyzed. The results showed that canopy density and vegetation condition were the principal stand factors for characterizing the dynamics of the insect community. The results are shown in Table 2.

Table 2. Key stand factors

County	Number of Factors	Key Stand Factors
Qu	4	canopy density, shrub coverage, herb height, total coverage
Longyou	3	canopy density, herb height, total coverage
Changshan	3	canopy density, shrub coverage, shrub height

Classification of Forest Stands. The forest area was classified into four types, denoted as type I, II, III, and IV, by using systematic cluster analysis according to the above conditions. The two-dimensional presentation of the classification is shown in Figures 1 and 2.

The results of the classification for the three counties were consistent. In order to see if the classification was reasonable, we first compared the values of N, S, H and D of forest type (I, II) (i.e., forest type I and type II together) and forest type (III, IV). The calculation results indicated that there were significant differences between type (I, II) and (III, IV) forests (Table 3). Then, on the basis of the first step, we compared the difference between type I and II and between type III and IV. The results indicated that there were also significant differences between type I and II as well as between type III and IV (Table 4). These results demonstrated that the classification of forest stands was reasonable, because there was a different inhibition effect on the pine caterpillar among the four types of forest. Furthermore, this effect among the four types of forest could be expressed as function of Nt, St, Ht and D(t).

Modelling Community Indices and Stand Factors. By denoting $Y_t = D(t+1)/D(t)$, that is, the ratio of the population density of the pine caterpillar at time t+1 and time t, then the linear regression models of Y_t on N_t, S_t, H_t and D(t) are:

Forest Type I: $Y_t=5.356-1.589N_t+2.280S_t-5.457H_t$ R=0.701

Forest Type II: $Y_t=-3.968+1.407N_t-4.446S_t-22.225H_t$ R=0.981

Forest Type III: $Y_t=2.992-0.155N_t-0.385S_t+1.375H_t$ R=0.771

Forest Type IV: $Y_t=4.092+0.021N_t-0.493S_t+2.261H_t$ R=0.962 .

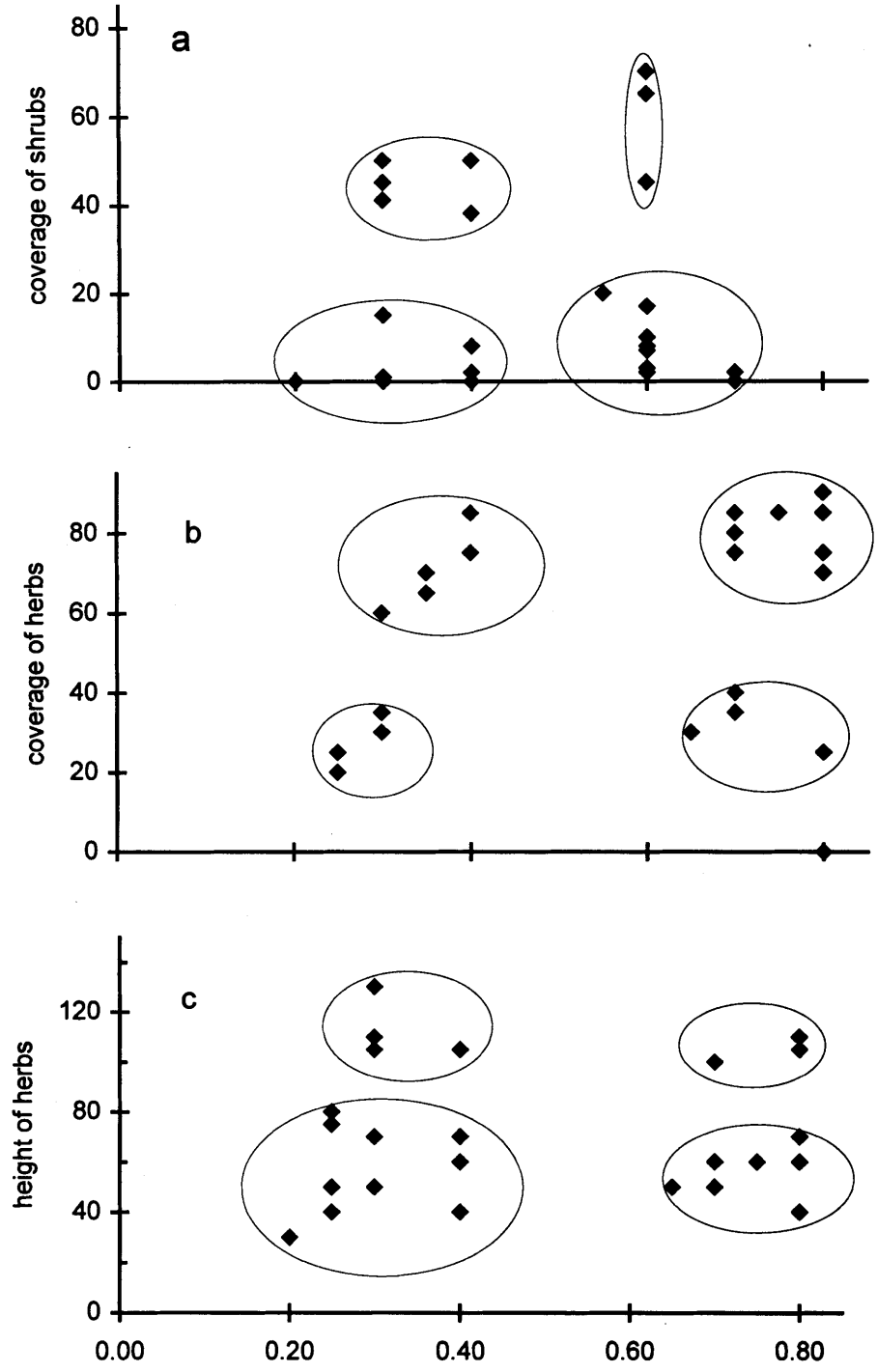


Figure 1. Classification for forest stand conditions. a: Changshan County, b: Longyou County, c: Qu County. Horizontal axis for all: canopy density.

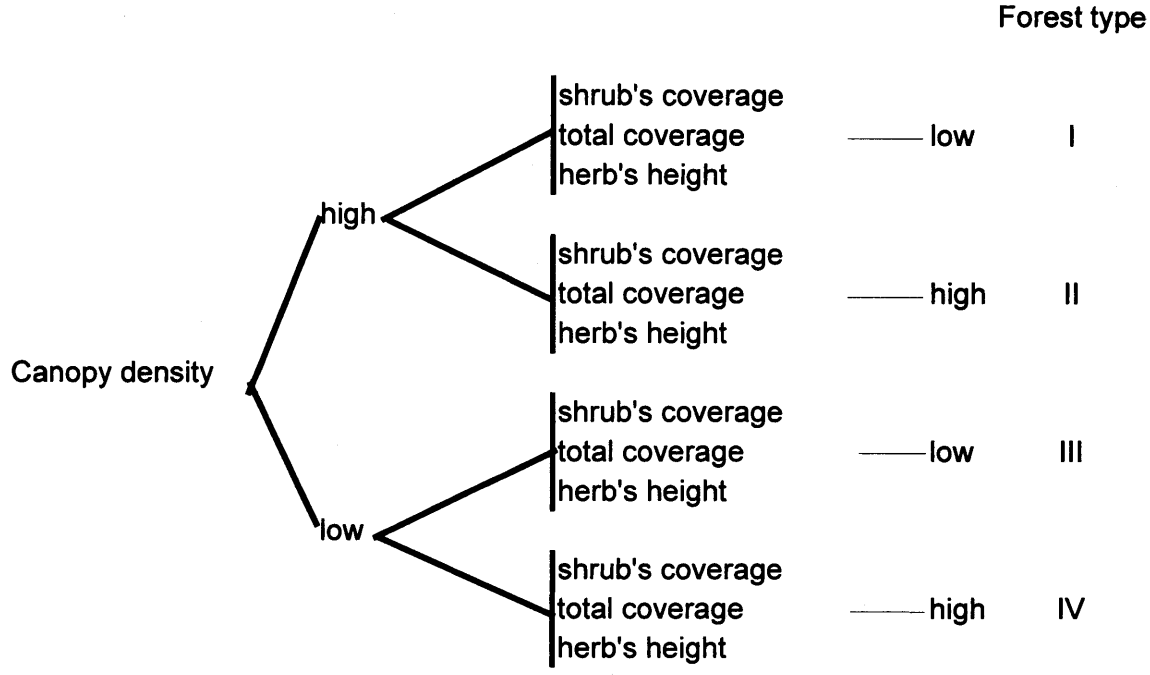


Figure 2. Result of classification for forest stand conditions.

Table 3. Comparison between type (I, II) and type (III, IV)

Statistics	N		S		H		D	
	(I, II)	(III, IV)	(I, II)	(III, IV)	(I, II)	(III, IV)	(I, II)	(III, IV)
mean	9.22	6.90	2.50	2.00	1.52	0.74	13.97	10.60
sample number	78	78	78	78	79	79	66	71
student t	14.49		3.12		4.91		19.76	
prob<0.01	yes		yes		yes		yes	

Table 4a. Comparison between forest type I and forest type II

Statistics	N		S		H		D	
	I	II	I	II	I	II	I	II
mean	9.92	8.59	2.33	2.61	1.83	1.46	15.93	12.20
sample number	37	41	36	41	37	41	31	35
student t	5.88***		-1.66**		1.25*		14.96***	

*** p<0.01, ** p<0.05, * p<0.10

Table 4b. Comparison between forest type III and forest type IV

Statistics	N		S		H		D	
	III	IV	III	IV	III	IV	III	IV
mean	6.33	7.38	1.81	2.17	0.61	0.87	12.14	9.25
sample number	36	42	36	42	36	42	33	38
student t	-4.61***		-1.59**		-1.25*		12.14***	

*** p<0.01, ** p<0.05, * p<0.10

The correlation coefficients between N, S, H and the population density of the pine caterpillar are large for all four formulas. The formulas above showed that the effects of N, S and H on population densities were different in different forest types; the negative and positive regression coefficients indicated that in an ecosystem, diversity may or may not be positively related to the stability of that ecosystem.

The relationship between the diversity and stability of an ecosystem is complex. It can be explained by structure analysis. There are serial connection and parallel connection structures. There also may be positive relations in parallel connection structures due to the increase of redundancy, and this may increase system stability. On the other hand, in series connection structures, diversity cannot increase the stability of the system (Liu 1991). Unfortunately, under natural conditions, N, S and H are not easy to survey; however, forest stand factors can be relatively easy to investigate., Actually, Y_t can be expressed as Y(t)=f (forest stand factors) =f (ybd, gh, gc, ch, zc) in which ybd is canopy density, gh is shrub layer height, gc is shrub coverage, ch is herb layer height and zh is total coverage. The stepwise regression results are listed below:

Forest Type I:

Y_t=3.620+7.933ybd-0.091gh-0.021gc+0.020ch-0.159zc-0.134D(t) R=0.961

Forest Type II:

Y_t=-29.148+0.346gh+63.011ybd-0.677ch+0.567zc R=0.924

Forest Type III:

Y_t=2.318+2.171ybd+0.006ch-0.089D(t) R=0.964

Forest Type IV:

Y_t=4.199-0.128ybd-0.097D(t) R=0.957

Obviously, the correlation coefficient between Y_t and the stand factors is higher than the correlation coefficient between Y_t and N, S and H of the insect community. The variable D(t) was left in the regression models, because the variation of insect density is related to former insect density.

Conclusion

The effect of the insect community on the pine caterpillar plays an important role in pine caterpillar population dynamics. Usually, the dynamics of an insect community can be described by insect diversity, the number of individuals, the number of species and other indices. Unfortunately, it is difficult to quantify these community indices. On the other hand, forest stand factors, such as canopy, vegetation coverage, etc., can be easily surveyed. Thus,

we tried to find a way to use forest stand factors instead of insect community indices to express the impact of the insect community on the pine caterpillar. We first used the 16 predominant species or species groups from previous studies to identify key forest stand factors, then used these key stand factors to classify forest stand, and finally, established relationships between the variation in pine caterpillar density and stand factors. The results showed that canopy density and vegetation condition were the key stand factors for characterizing the dynamics of the insect community.

Forest stands can be classified into four types according to variations in canopy density and vegetation. This classification of forest stands was reasonable according to statistical analysis. The correlation coefficient between the variation rate of population density, Y_t, and major stand factors was larger than that of Y_t and the insect community indices. The results indicated that stand factors can be substituted for the effect of natural insect enemies of the pine caterpillar. Stand factors are easy to collect in the field and can be easily used in management models.

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Towards an Integrated Management of *Dendrolimus pini* L.

ALICJA SIERPIŃSKA

Forest Research Institute, ul. Bitwy Warszawskiej 1920 r. No. 3, 00-973 Warszawa, Poland

ABSTRACT The pine moth *Dendrolimus pini* L. (*Lepidoptera: Lasiocampidae*) is one of the most serious forest insect defoliators in Poland. During the period 1946-95, more than 200,000 hectares of forests were treated in order to control this pest. In this paper, we present a historical background of pine moth outbreaks in Poland and review what is known about the biology of the insect and attempts to manage it. Important natural enemies and pathogens also are discussed. The idea of "the focus-complex method" and approaches to incorporate silvicultural methods into forest protection also are described.

OUTBREAKS OF THE pine moth *Dendrolimus pini* L. (*Lepidoptera: Lasiocampidae*) were first recognized in Poland at the beginning of the 17th century. The frequency of outbreaks appears to have increased over time (Szujecki 1993) (Table 1). During the period 1946-95, the pine moth was controlled in Poland on a total area of 233,000 hectares (Fig. 1), although there were 20 years during that period when no treatments were required.

Table 1. Pine moth outbreaks in Poland, 1791-1996

Years	Region of occurrence
1791 - 1792	West Pomerania
1863 - 1872	from Saxony to Masuria
1905 - 1909	Zagan Forest
1925 - 1927	Pomerania and Mazovia
1936 - 1937	Kurp Forest, Tuchola Coniferous Forest and Poznan province
1946 - 1952	West Pomerania, Zagan Forest, Kurp Forest and White Forest
1956 - 1957	Poznan and Tarnow provinces
1964 - 1975	from Notec Forest on the west to Augustow Forest on the north-east and Solska Forest
1982 - 1985	Pomerania and Zielona Gora province
1992 - 1996	Zielona Gora province, Tuchola Coniferous Forest, White Forest and Green Forest

The pine moth is a monophagous insect that feeds on Scots pine, *Pinus sylvestris* L. According to a 1996 report, Scots pine stands occupy approximately 69.4% of the forested area in Poland (Raport 1996). In the past, pure Scots pine stands were planted on sites that were both suitable and unsuitable for this species (Zasady 1994). The pine moth does not occur in stands that were planted on unsuitable sites which, according to Szujecki (1992), comprises 2.5 million hectares, or about 30% of the forested area in Poland. Long-term

Pages 129-142 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

observations indicate that young coniferous forests are most often infested by mass outbreaks of the pine moth. However, the pattern of pine moth outbreaks differs between western and eastern Poland (Lesniak 1976b).

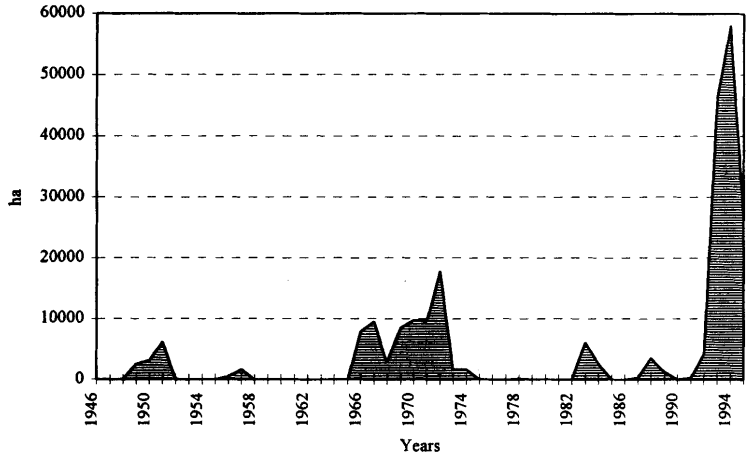


Figure 1. Control of pine moth in Poland, 1946-1996. Source of data: Department of Forest Protection, Forest Research Institute.

Lesniak (1976a) analyzed data from six meteorological stations between 1949 and 1970, and characterized abiotic conditions of the six identified centers of pine moth outbreaks. He suggested that climatic variation among different areas of Poland might significantly affect the course and intensity of outbreaks. He identified several climatic factors that were most important in population processes of the pine moth. These included: higher mean annual temperatures (particularly those during autumn and winter), lower wind velocities, less precipitation, fewer days with snow cover, the low mean long-term values for Seljaninov's coefficient[1], greater duration of summer and vegetation season, and higher frequency of dry months. Results of this research suggest that abiotic factors do not affect the pine moth directly, but rather the pine moth population dynamics indirectly, through the host plant.

Szujecki (1993) suggested that management systems in forestry (clear-cutting), positive thermal influences, and eutrophization of coniferous forest ecosystems, which deposit between 10 and 20 kg of nitrogen each year (Stachurski and Zimka 1984) may explain the increasing frequency of pine moth outbreaks. Contrary to studies by Luterek (1969) and Lesniak (1984), Szujecki (1993) showed that nitrogen fertilization positively influenced the development and fecundity of the pine moth.

[1] **Seljaninov's hydrothermal coefficient provides an example of a joint action of two fundamental abiotic factors. It is calculated according to the formula: (precipitation total x 10) divided by temperature (active) total. The coefficient values from 1.0 to 1.5 characterize an optimal humidity of a region, above 1.6 – its excess and below 1.0 – deficit. The most dangerous outbreaks of pine moth occur on areas in Poland with the lowest (1.2) value for Seljaninov's coefficient (Lesniak, 1976a).**

Biology of Pine Moth in Poland

D. pini moths emerge from pupae in midsummer. Flight is observed from the beginning of July until the middle of August. Females usually do not fly before they mate, and they rest on the lower parts of pine tree trunks. Mating begins at night and lasts a few hours. Females can fly after having deposited most of their eggs, an activity that takes place in the early evening and at night. The moths live for 9-10 days. The females oviposit 150-250 eggs in groups of 20-100 on twigs without needles, on needles, or on the bark of Scots pine. It is very rare that females will deposit eggs on trees other than Scots pine.

Egg embryonation lasts 16-25 days. Larvae usually begin hatching in early September and are about 5 mm in length. When larvae complete their development, they are about 70-80 mm long and have increased their weight by about 700x. During the first 10 days, hatching larvae begin feeding on pine needles; at first, they feed only on the margin of the needles, and later, they consume entire needles. Before winter, larvae usually molt 2-3 times. Autumn feeding lasts until the first frost occurs (November). Then larvae move down the tree trunks to overwintering sites that are between the mineral soil and litter layer. About 85% of all larvae can be found in the immediate vicinity of tree trunks.

Early in the spring, usually in March, when soil temperature reach about 3°C, larvae begin to move upwards into the crowns. Depending on the weather condition, this activity can occur until the middle of April. In spring, the larvae consume 3-5 times more pine needles than in the autumn and they also can feed on the bark of young shoots. The studies carried out by Lesniak (1976c) confirmed that the spring-feeding larvae develop better on Scots pine needles from the previous year, whereas the autumn-feeding larvae develop best on the current year's needles. Before pupation, pine moth larvae are more active and can crawl for distances of several hundred meters to neighboring stands.

Pupation begins in May-June and lasts 4-5 weeks. Pupae are formed inside loose, partially transparent cocoons, and can be found in tree crowns, on the bark of trunks and on understory vegetation (Koehler 1961, Sliwa 1992).

Natural Enemies

The stabilizing influence of natural enemies in ecosystems has been reviewed by numerous authors (Sitowski 1928, Szmidt 1951, Szmidt 1955, Glowacka-Pilot 1974, Sliwa 1992) although there is lack of agreement about the relative importance of parasites, predators, and microorganisms in the natural control of the pine moth. The theoretical basis for the use of biological methods in forest protection were summarized briefly by Koehler (1968a).

Bacteria. The role of entomogenous bacteria and fungi in the regulation of pine moth populations in Poland was studied extensively by Glowacka-Pilot (1974). During 4 years, she isolated 374 strains of bacteria from 343 larvae (Table 2). Non-spore-forming species of bacteria were most responsible for disease in larval populations, and the most frequently isolated species was *Aerobacter cloaceae*. Although 29 strains belonged to the genus *Bacillus,* none of the isolates produced both spores and crystals.

Table 2. Bacteria isolated from pine moth larvae, 1965-69 (Glowacka-Pilot 1974)

Species	No. of isolated strains
1. *Achromobacter* sp.	14
2. *Aerobacter aerogenes*	33
3. *Aerobacter cloaceae*	101
4. *Bacillus brevis*	13
5. *Bacillus cereus*	7
6. *B. cereus* var *mycoides*	1
7. *Bacillus megaterium*	8
8. *Klebsiella aerogenes*	12
9. *Proteus rettgeri*	37
10. *Pseudomonas aeruginosa*	32
11. *Pseudomonas chlororaphis*	18
12. *Sarcina flava*	5
13. *Serratia marcescens*	93

In an earlier study (Glowacka-Pilot and Swiezyñska 1967), the insecticidal activity of two bacterial preparations, Thuricide (*B. thuringiensis* subsp. *thuringiensis*) and Dendrobacillin (*B. thuringiensis* subsp. *sotto* biotype *dendrolimus*), was compared. Results suggested that the insecticide based on *B. thuringiensis* subsp. *sotto* biotype *dendrolimus* might be more promising for the control of pine moth. Our unpublished data on the estimation of insecticidal activity of *B. thuringiensis* strains against pine moth larvae suggest that *B. thuringiensis* subsp. *sotto* biotype *dendrolimus* is more effective than *B. thuringiensis* subsp. *kurstaki* HD-1, which is used in most commercial preparations for forest protection.

Fungi. The role of pathogenic fungi in reducing the population density of the pine moth increases during the course of an outbreak. During a 4-year study Glowacka-Pilot (1974) isolated 1826 fungi strains from 1794 larvae (Table 3). The most frequently isolated species were *Paecilomyces farinosus* and *Beauveria bassiana*. *Verticillium lecanii* also was commonly found. *Cordyceps militaris* is another entomogenous fungal species that can be important in limiting pine moth populations. During the period of observation, this species occurred naturally in the several dozens of hectares in half of the outbreak areas and, in some places, it caused 30% to 80% mortality of overwintering larvae. Infection of pine moth larvae with the isolated fungi in laboratory conditions showed that *P. farinosus* and *B. bassiana* had the strongest pathogenic properties.

It is generally known that successful infection by fungi is related to relative humidity. The results of field trials on the infection of overwintering pine moth larvae by *B. bassiana* suggest that *B. bassiana* could be used as a natural regulator of pine moth population in those outbreak areas that are localized on coniferous forest sites with higher values of Seljaninov's coefficient. In the first trial, located in the central part of Poland, the mortality of overwintering larvae treated with *B. bassiana* was about 80% (Cichoñska and Swiezyñska 1993). In the second trial, located in the western part of Poland on a dry coniferous forest site, the mortality of treated larvae was equal to the mortality of control larvae (unpublished data). This suggests that climatic conditions were responsible for the difference in the level of infection of *B. bassiana* against pine moth larvae.

Table 3. Fungi isolated from pine moth larvae, 1965-69 (Glowacka-Pilot 1974)

Species	No. of isolated strains
1. *Acremonium aranearum*	3
2. *Aspergillus parasiticus*	37
3. *Beauveria bassiana*	311
4. *Beauveria tenella*	7
5. *Verticillium falcatum*	10
6. *Verticillium lecanii*	179
7. *Verticillium* sp. I	1
8. *Verticillium* sp. II	1
9. *Cordyceps militaris*	542
10. *Fusarium* sp.	33
11. *Mucor* sp.	20
12. *Paecilomyces farinosus*	603
13. *Paecilomyces fumoso-roseus*	11
14. *Penicillium* sp.	30
15. *Scopulariopsis brevicaulis*	38

Parasites. The significance of insect species parasitizing the pine moth as natural regulators of pest population density differs depending on the stage of the outbreak and location. A listing of the more important pine moth parasites in Poland is provided in Table 4. For example, *Sarcophaga affinis* Fall. reduced pine moth larvae and pupae by 10% to 40%; similarly, *Exochilum giganteum* Grav. caused a reduction of 2% to 33% (Sitowski 1928). In 1947-48 and 1956-57, because of high parasitization of pine moth larvae by *Apanteles* sp. and *Meteorus* sp., the forest administration decided not to initiate control treatments (Sliwa 1992). In stands where sticky bands were used as a method of pine moth control, some activity by species of Muscidae was observed (Sitowski 1928). *Muscina pabulorum* Fall. parasitized 40-60% of pine moth larvae in the first year after applying sticky bands on tree trunks, and *Stomoxys calcitrans* L. parasitized up to 30% of the larvae.

Predators. The list of more important insect predators of pine moth is presented in Table 5. Birds also are important as pine moth predators, especially the cuckoo, golden oriole, starling, coal-tit, jay, thrush, rook, jackdaw, chaffinch and woodpecker. Among mammals, moles and bat are considered to be important (Koehler 1961).

Table 4. Parasites of nun moth (Sitowski 1928, Szmidt 1955, Koehler 1968a, Sliwa 1992)

Host stages	Order	Family	Parasite species
eggs	Hymenoptera	Proctotrupidae	*Teleas laeviusculus* Rtzb.
			Telenomus verticillatus Kiefer
			Trichogramma embryophagum Hart.
larvae	Diptera	Sarcophagidae	*Parasarcophaga harpax* Pand.
			Pseudosarcophaga monachae Kram.
			Sarcophaga affinis Fall.
			Sarcophaga tuberosa Pand.
		Tachinidae	*Tachina larvarum* L.
			Eriothrix rufomaculatus Deg.
			Sturmia scutellata R.D.
			Ernestia rudis Fall.
		Muscidae*	*Muscina pabulorum* Fall.
			Muscina stabulans Fall.
			Stomoxys calcitrans L.
			Amphiochaeta rufipes Meig.
	Hymenoptera	Ichneumonidae	*Exochilum giganteum* Grav.
			Pimpla inquisitor Scop.
			Pimpla instigator F.
			Pimpla holmgreni Schmiedekn.
			Theronia atalantae Poda.
			Pristomerus vulnerator Panz.
			Omorgus faunus Gr.
		Braconidae	*Apanteles ordinarius* Ratz.
			Meteorus versicolor Wesm.
		Chalcididae	*Tetrastichus xanthopus* Nees.
pupae	Hymenoptera	Chalcididae	*Tetrastichus xanthopus* Nees.

* Parasites found below sticky bands

Table 5. Predators of pine moth (Koehler 1961, 1968a, Sliwa 1992)

Host stages	Order	Family	Predator species
eggs	Raphidoptera	Raphididae	*Raphidia ophiopsis* L
larvae	Rhynchota	Pentatomidae	*Troilus luridus* L.
			Picromerus bidens L.
	Raphidoptera	Raphididae	*Raphidia ophiopsis* L
	Coleoptera	Carabidae	*Calasoma sycophanta* L.
			Carabus violaceus L.
			Carabus coriaceus L.
	Hymenoptera	Formicidae	*Formica polyctena* Forst.
			Formica rufa L.
pupae	Coleoptera	Carabidae	*Calasoma sycophanta* L.

Forecasting and Monitoring

Coniferous monocultures are especially susceptible to pest outbreaks and the application of sound forestry practices are required to assure their durability. According to Szujecki (1992), accurate forecasting of insect outbreaks and control of damaging insect populations are necessary to protect our forests against severe damage and economic losses.

Since 1946, yearly forecasts of the status of forest pest insect populations have been conducted in Poland. At present, it is based on the rules presented in "Forest Protection Guidelines" (1988). Data are collected on permanent plots in every State Forest District (SFD) (there are 443 SFD in Poland), and submitted, first to Regional State Forest Directorates (17), and then to the Forest Research Institute, Warsaw, where the actual forecast of the abundance of insect pests is developed.

Good knowledge of the biology of each pest allows us to formulate the most precise method for estimating the status of populations. If, for example, the number of larvae that collect below sticky bands that are placed on tree trunks of sampling trees exceeds the critical number for the stand (Table 6), aerial spraying is prescribed.

Table 6. Critical numbers of pine moth larvae (Burzynski 1988)

Stand age	No. of larvae per tree	Stand age	No. of larvae per tree	Stand age	No. of larvae per tree	Stand age
0 - 20	8 - 20	16 - 20	24 - 20	32 - 20	40 - 20	48 - 20
21 - 40	21 - 50	22 - 40	22 - 50	23 - 40	23 - 50	22 - 40
41 - 60	51 - 80	42 - 60	52 - 80	43 - 60	53 - 80	42 - 60
61 - 80	81 - 100	62 - 80	82 - 100	63 - 80	83 - 100	62 - 80
81 - 100	101 - 150	82 - 100	102 - 150	83 - 100	103 - 150	82 - 100

In the summer, observations of adult moth flight are performed at every SFD threatened with *D. pini*. The number of moths (females and males) that occupy trunks of control trees to a height of 4 m are counted. If mating is intensive, individual trees in the

threatened stands are cut after the larvae emerge and all larvae in the crowns are counted thoroughly. When the number of larvae found in crowns exceeds the critical number for the stand, aerial spraying can also be prescribed.

In order to optimize the forecasting of insect outbreaks, so-called "monitoring searching plots" were established in 1991. These plots were established to monitor populations in the stands where defoliation and discoloration of foliage has occurred. In 1991, there were 1,133 monitoring searching plots in pine stands in Poland (Ocena 1993). Methods of searching on monitoring plots have been developed so that the data obtained can be compared over time. At present, it is too early to reach conclusions about the effectiveness of these methods.

Past and Current Control of Pine Moth

Until the early 1960's, sticky bands were placed on tree-trunks in threatened stands as a means to control the pine moth. For example, in 1949 about 2,500 hectares of pine forest were protected against the pine moth using this method. Larvae that gathered below sticky bands attracted great numbers of parasites. Although the method was very effective, it also was very labor intensive. The first aerial spraying against the pine moth was conducted in 1951. Between 1951 and 1979, the insecticide DDT was used against the pine moth on a total area of 70,000 hectares (Sliwa 1992).

Table 7. Contact insecticides registered for ULV spraying in forestry in Poland (based on "Insecticides recommended for forest protection in 1996" ed. By Forest Research Institute, Warsaw)

			Recommended dose [l/ha]*	
Trade name	Common name	Active ingredient (%)	nun moth, *Acantholyda* sp., *Cephalcia* sp.	pine beauty moth, diprionids
Alfamor 05 SC	alphamethrin	5.0	0.15 - 0.20	0.12 - 0.15
Alfazot 05 EC	alphamethrin	5.0	0.15 - 0.20	0.12 - 0.15
Decis 2.5 EC	deltamethrin	2.5	0.25 - 0.32	0.15 - 0.25
Fastac 10 EC	alphamethrin	10.0	0.075 - 0.100	0.060 - 0.075
Karate 025 EC	lambda-cyhalothrin	2.5	0.25 - 0.32	0.15 - 0.25
Sumi-alpha 050 EC	esfenvalerate	5.0	0.20 - 0.25	0.15 - 0.20
Sumi-alpha 005 UL	esfenvalerate	0.5	2.00	2.00
Trebon 10 SC	etofenprox	10.0	0.40	0.30
Zorro 100 EC	zeta-cypermethrin	10.0	0.075 - 0.100	0.060 - 0.075

* Mixed with 0.70 l of mineral oil (IKAR 95 EC) and 1.50 - 3,00 l of water/hectare

In 1979, the use of DDT was prohibited in Poland in favor of synthetic pyrethroids. Pyrethroids are sill in use today (Table 7), together with insecticides that interfere with chitin deposition (Table 8), and commercial formulations of *Bacillus thuringiensis* (Table 9). Until the 1990's, diesel oil was often used as a carrier for chemical spraying; however, in 1994, we began to use an inflammable mineral oil as a carrier on large areas of sprayed forest (Biernacka et al. 1995). The two types of aircraft used most frequently for spraying the pine

moth are the PZL M-18 "Dromader," which has a maximum load of 2,500 kg and the Mi-2 helicopter, which has a maximum load of 400 kg. Since 1982, we have used ULV spraying to optimize control of pine moth populations.

Table 8. Chitin-inhibiting insecticides registered for forest managment in Poland (based on "Insecticides recommended for forest protection in 1996", ed. By Forest Research Institute, Warsaw)

Trade name	Common name	Active ingredient (%)	Recommended dose [kg or l/ha]	
			heavy infestation	normal infestation
Dimilin 480 SC	diflubenzuron	48	0.15	0.10
Dimilin 25 WP	diflubenzuron	25	0.30	0.25
Ekos 100 EC	heksaflumuron	10	0.50	0.40
Nomolt 150 SC	teflubenzuron	15	0.20	0.10

Table 9. *Bacillus thuringiensis* insecticides registered for forest management in Poland (based on "Insecticides recommended for forest protection in 1996", ed. By Forest Research Institute, Warsaw)

Trade name	B.t. strain	B.t. crystals (%)	Recommended dose [kg or l/ha]	
			heavy infestation	normal infestation
Bacilan(WP)	kurstaki HD-1	3.0	2.00	1.00
Bactospeine 16 000 WP	kurstaki HD-1	20.0	3.00	2.00
Dipel 8L	kurstaki HD-1	3.5	3.00	3.00
Dipel 3.2 WP	kurstaki HD-1	3.2	1.50	1.00
Ecotech Pro 07.5 OF	EG 2348	7.5	2.00	1.50
Ecotech Pro XL 015 OF	EG 2348	15.0	1.00	0.75
Foray 02.2 UL (48B)	kurstaki HD-1	2.2	4.00	2.50
Foray 03.3 UL (76B)	kurstaki HD-1	3.3	2.50	2.00
Thuridan-krem PA	kurstaki HD-1	3.0	2.00	1.50

There are two seasons during the year when pine moth can be treated effectively with insecticides: spring and autumn. There are advantages and disadvantages to spraying at these times. If the threatened area is well evaluated, spraying in autumn provides better foliage protection than spraying in the spring (Sliwa 1992). During the period 1946-1995, autumn spraying was conducted on about 10 occasions. Formulations of *B. thuringiensis,* toxicity of which is temperature-dependent, also can be applied in the autumn with satisfactory results (Fig. 2) (Sierpińska and Sierpiński 1994).

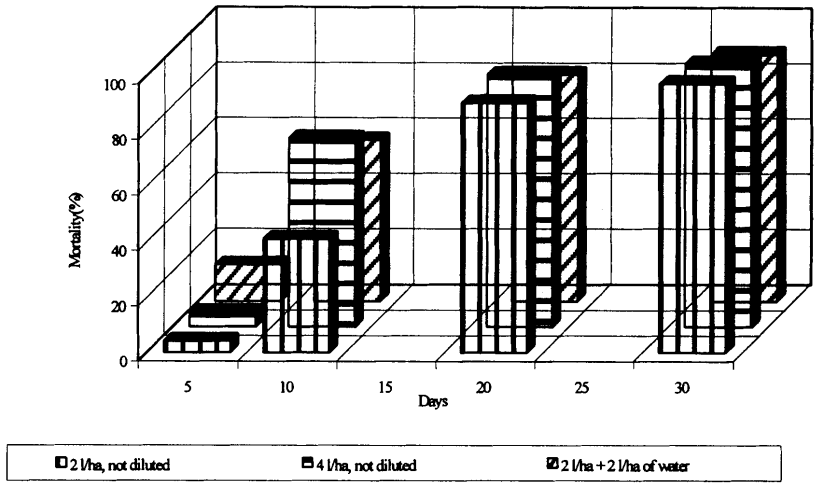


Figure 2. Mortality of pine moth larvae after treatment with Foray 48B, Autumn 1993 after Sierpinska and Sierpinski, 1994.

In August 1995, the efficacy of four ULV *B. thuringiensis* formulations and one pyrethroid was evaluated for the control of the pine moth. Aerial spraying was applied to 54 to 60 year old pine stands in which the mean number of larvae per tree was estimated to be 111 (21-161). An Mi-2 helicopter equipped with electric atomizers (AR 47.000) was used to apply the insecticide. Doses of insecticides and areas of sprayed plots are provided in Table 10. Before spraying, 1 m^2 linen cloths were placed under crowns of sample trees. The number of dead larvae on the linen cloths was checked on the 2^{nd}, 7^{th}, 10^{th}, 15^{th}, and 23^{rd} day after treatment and calculated for the whole crown. On the last day, the sample trees were cut down, all dead and live larvae in the crowns were counted, and the percent mortality was calculated. After 23 days, the mortality of larvae sprayed with *Bt* insecticides was 97% and it was comparable to the mortality measured after treatment with pyrethroids (99%). The only difference was the time when the mortality at this level was observed. The larval mortality of 84% for the least effective *B. thuringiensis* product was observed after 23 days. Of the *B. thuringiensis* insecticides tested, Ecotech Pro XL provided the highest efficacy at the lowest volume (Fig. 3).

Table 10. Doses of insecticides (L/ha) used in 1995 experiments, and area sprayed

Insecticide	Dose [l/ha]	Area of sprayed plots [ha]
Dipel ESNT	2.8 (undil.)	101
Ecotech Pro 07.5 OF	2.0 (water dil.: 2.0 l/ha)	52
Ecotech Pro XL 015 OF	1.0 (water dil.: 1.5 l/ha)	407
Foray 76B	2.0 (undil.)	241
Zorro 100 EC	0.1 (+ 0.61 l IKAR 95 EC + 1.2 l water/ha)	97

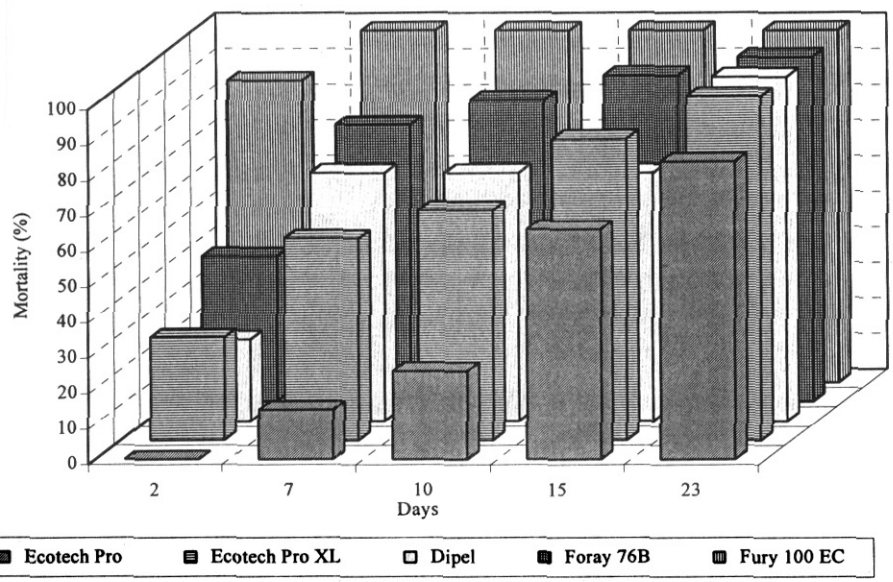


Figure 3. Mortality of pine moth larvae treated with four commercial formulations of *Bt* and a pyrethroid (Fury 100 EC).

Integration of Different Means and Methods

The first attempt at integrating different methods to protect forests and to apply prophylactic practices to improve the health of forests in Poland was referred to as the focal-complex (complex-center) method, which was formulated by Koehler (1968b).

The purpose of this approach was to initiate changes that develop gradually over time and lead to an equilibrium of less stable biocenoses in artificially regenerated stands. The "complex" depends on specific conditions of a definite forest area, e.g. diversity of the specific composition of the forest stand, protection of small mammals, increase in population density of bats and insectivorous birds, colonization of ants, concentration of parasitic insects, introduction of pathogens, etc. Intensive, integrated treatments were located in potential, primary centers of pest outbreaks.

The above described method applied not only to the pine moth situation, but resulted from an in-depth analysis of the causal sources of forest calamities and diseases in Poland.

One of the prescriptions of general importance in managed forest ecosystems to increase their resistance against insects attacks, is the utilization of silvicultural methods and the introduction of deciduous species to the understory of coniferous forests. Bernadzki et al. (1986) suggested that the introduction of lower forest layers favorably influenced the productivity of stands and the biocenotic potential of forest ecosystems, especially in more fertile habitats. They also suggest that this practice is justifiable in poor habitats because it reduces the economic risk, improves the quality of timber produced, influences the direction of succession processes, improves the state of the site, and also might create a microclimate that is unfavorable for insect pests and favorable for beneficial insects.

In 1994 the assumptions of the strategic government program designed to create a pro-ecological model of forestry were elaborated (Grzywacz 1994). The pro-ecological forest policy serves to integrate the protection of nature and forest management practices. The new, multi-functional model of forest management ensures the productivity, stability, and

usefulness of forest ecosystems for society (Rozwalka 1996). In agreement with the assumptions of the "Polish Policy of Integrated Protection of Forest Resources," Forest Promotion Complexes (FPC) have been established. At present, there are seven FPC in Poland which cover 300,000 hectares (5% of the forested area in Poland). The above mentioned assumptions of pro-ecological policy will become obligatory on state forest land in Poland; however, they will be introduced initially on the FPC areas (Szujecki 1996). The idea of establishing FPC seems to provide a good organizational framework for deploying Integrated pest management procedures and also for managing the pine moth.

Conclusions

Under existing conditions whereby Polish pine forest ecosystems are endangered by the repeated outbreaks of *D. pini*, the judicious use of insecticides is necessary in order to protect these forests from severe defoliation. During the past 50 years, a policy has existed whereby doses of chemicals used in forest protection should be the minimal dose required to provide effective control. During that period, insecticides like DDT, that were highly toxic to all elements of forest ecosystems, were withdrawn for control of pine moth and were replaced with more selective products such us *B. thuringiensis*-based preparations.

In Poland, *D. pini* has numerous natural enemies. Considering this, as well as the number and severity of forest protection problems in Poland, the creation of optimal conditions for naturally occurring pathogens, parasites and predators along with the use of silvicultural methods seems to be very important and can become an effective approach towards long-term sustainability.

Implementation of pro-ecological policy of "The Polish Policy for the Integrated Protection of Forest Resources" has created an organizational framework in which to implement integrated pest management.

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The Development and Operational Use of a Management System for Control of Douglas-Fir Tussock Moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), Populations at Pre-Outbreak Levels

IMRE S. OTVOS[1], JOHN C. CUNNINGHAM[2], LORRAINE MACLAUCHLAN[3], PETER HALL[4] AND NICHOLAS CONDER[1]

[1] Natural Resources Canada, Canadian Forest Service, Pacific, 506 W. Burnside Road, Victoria, B.C, Canada V8Z 1M5,
[2] Natural Resources Canada, Canadian Forest Service, 1219 Queen Street East, Sault Ste. Marie, Ontario, Canada P6A 5M7
[3] Kamloops Forest Region, B.C. Ministry of Forests, 515 Columbia Street, Kamloops, B.C, Canada V2C 2J7
[4] Forest Health Section, Silviculture Practices Branch, B.C. Ministry of Forests, 31 Bastion Square, Victoria, B.C., Canada V8W 3E7

ABSTRACT The Douglas-fir tussock moth is a native defoliator which periodically reaches outbreak proportions in western North America, causing economically important damage to its primary host, the interior Douglas-fir. The research and development of a management system for this defoliator over the past 15 years is reviewed in detail. The various data from field trials supporting this system are presented and components of this management system are briefly mentioned. The operational testing of this management system was successful, and supporting data are presented and discussed. It is recommended that this operationally proven management system be used as a template for the development of similar systems for other defoliators.

THE DEVELOPMENT OF a management system using a virus for the regulation of Douglas-fir tussock moth was the result of cooperative research efforts conducted over a number of years by the Canadian Forest Service (Pacific and Ontario Centres), the B.C. Ministry of Forests, and the USDA Forest Service (Stelzer et al. 1977; Shepherd et al. 1984a, 1984b; Otvos et al. 1987a, 1987b).

The Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* (McDunnough), belongs to the family Lymantriidae. It is an important indigenous defoliator in the interior dry-belt forests in British Columbia and the western United States. Although the larvae can feed on the foliage of several trees, the primary host in the interior of B.C. is Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco. The female moth is flightless, and after emerging from her cocoon and mating, lays all her eggs in a single mass on the cocoon from which she emerged. The eggs overwinter and the larvae hatch the following spring after the host trees flush (Wickman and Beckwith 1978, Shepherd et al. 1984). Dispersal of the tussock moth is limited. The small, hairy larvae spin silken threads and are blown to surrounding trees and adjacent stands; this is probably the reason for the patchy pattern of defoliation associated with this insect.

Pages 143-154 in M.L. McManus and A.M. Liebhold, editors. 199 Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

DFTM is a cyclic pest and outbreaks usually occur 7 to 11 years apart in western North America (Harris et al. 1985, Otvos and Shepherd 1991). DFTM populations increase rapidly, usually resulting in severe defoliation and tree mortality (Wickman 1963, 1978). Mature, severely defoliated trees are susceptible to attack by Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. Outbreaks in an area usually collapse after 2 to 4 years of defoliation (Mason and Luck 1978) due to a naturally occurring nuclear polyhedrosis virus (OpNPV), but by then tree damage is extensive (Dahlsten and Thomas 1969, Shepherd and Otvos 1986). NPVs are so named because they replicate within cell nuclei, and the virus produces an inclusion body which is many-sided, *i.e.* a polyhedral inclusion body.

Two morphotypes of OpNPV have been isolated from DFTM larvae and identified as the cause of epizootics (Hughes and Addison 1970). Unicapsid OpNPVs have rod-shaped virus particles embedded singly in the inclusion matrix. Multicapsid OpNPVs have bundles of five to 15 virus particles occluded in a protein envelope with several bundles per inclusion body. Both viruses belong to a group called Baculoviridae. These viruses are highly species-specific and most of them only infect the host target insect or closely related species of the same genus. Baculoviruses are generally slow acting, and some feeding damage can occur between ingestion of a lethal dose and death of the insect larva. Baculoviruses, like the bacterium, *Bacillus thuringiensis*, must be ingested to cause infection (Cunningham 1982). The inclusion body protein dissolves in the alkaline larval gut juices, releasing the viral particles. The viral particles penetrate the gut cells in susceptible species, after which they usually spread to other organs. In the final stages of infection, more inclusion bodies are produced in infected cells. Following the death of the larva, the cuticle ruptures and the polyhedral inclusion bodies (PIBs) are released into the environment. These may infect more larvae (horizontal transmission) or the next generation of larvae (vertical transmission). Some of these particles end up on other needles, which can then be ingested by additional larvae. Other inclusion bodies are washed off the foliage and end up in the soil. Inclusion bodies in the soil are basically lost from the infection cycle, but are a potential source of inoculum at the next outbreak. Although it is technically feasible to grow these viruses in cell culture, the medium is expensive and the yield is relatively low. It is more economical to produce the virus in host larvae.

The first aerial spray trial in British Columbia using OpNPV against DFTM was conducted jointly by personnel of the Canadian Forest Service, the USDA Forest Service, and the British Columbia Ministry of Forests in the mid-1970s (Stelzer et al. 1977, Shepherd et al. 1984, Cunningham and Shepherd 1984). High populations of DFTM larvae were treated aerially in the second year of the outbreak with laboratory-produced multicapsid OpNPV. The virus was applied as soon as all the larvae had hatched, dispersed, and were actively feeding. Such early application is essential for the second wave of virus infection, causing an epizootic and resulting in a high level of control. The treatments caused high larval mortality, but the treated stands still sustained considerable damage. After these trials, the multicapsid isolate of OpNPV, produced in the DFTM, was registered in the U.S. by the Environmental Protection Agency in 1976 under the name TM BioControl-1®. The same virus, produced in whitemarked tussock moth, *Orgyia leucostigma* (J.E. Smith), received registration in Canada in 1983 under the name Virtuss.® The recommended dosage in polyhedral inclusion bodies on both labels is 2.5×10^{11} PIB/ha (Otvos et al. 1995). Neither Virtuss® nor TM BioControl-1® products were used operationally (only experimentally) in

Canada until 1991, 1992 and 1993, when ca. 200 ha, 450 ha, and 610 ha, respectively, were treated with these products. From 1974 to 1982, the American product TM BioControl-1® was used on eight research plots, with a total area of 638 ha, in a joint project between the Canadian and USDA Forest Service. The Canadian product was used on 10 plots with an area of 150 ha in British Columbia, Canada.

The American product, TM BioControl-1®, was also registered in Canada in 1983 to facilitate its importation and use in British Columbia. The recommended dosage of Virtuss® of $2.5x10^{11}$ PIB/ha takes 200-300 whitemarked tussock moth, *Orgyia leucostigma*, larvae to produce. *O. leucostigma* is a closely related species that does not have an obligatory diapause, and is much easier to rear and handle than *O. pseudotsugata*. Therefore, in Canada, *O. leucostigma* is the preferred host for producing the virus. Virtuss® is also effective for control of whitemarked tussock moth. It was field tested in Newfoundland (West et al. 1987, 1989) and this species may be added to the label.

There are two main strategies for using viral insecticides. First, there can be a one-shot application, killing only larvae that ingest sufficient amounts of polyhedral inclusion bodies. Secondly, one can initiate an epizootic with horizontal and vertical transmission of the virus, as in the case of the DFTM. The strategy of combining pheromone detection and virus application led to the development of a system for integrated control of DFTM. It was considered desirable to introduce the virus at the beginning of the outbreak to initiate a viral epizootic before it would occur naturally, thus preventing the development of the outbreak and reducing tree damage. Another focus of the study was to determine whether or not it was necessary to spray the entire infested area, or if the virus would spread into untreated areas. In addition, experiments were conducted to determine if the recommended application rate could be reduced and still prevent damage. These points were investigated during the 1981-1984 and 1990-1993 outbreaks.

Materials and Methods

Early treatment of an infested stand is desirable, because the greatest tree mortality results from the first year's defoliation. Application on first and second instar larvae is essential to obtain secondary infection. Introduction of the virus at the beginning of an outbreak requires a reliable monitoring system. In a separate study, concurrent with the virus work, a dependable and sensitive pheromone monitoring system was developed for early warning of outbreaks (Shepherd et al. 1985). Pheromone-baited traps were placed in susceptible stands, which were defined by overlaying previous outbreak, forest type, and biogeoclimatic zone maps. The most susceptible stands tended to be located in the driest part of the range of Douglas-fir, where it mixes with ponderosa pine, *Pinus ponderosa* C. Laws. exo. Laws. Within this forest habitat, 18 permanent monitoring stations were selected and pheromone-baited traps monitored annually to measure male moth density (Shepherd and Otvos 1986). Population trends in pheromone-baited traps were followed from endemic to epidemic levels. The number of successive years of upward trends of male moths caught is used because it is a better indicator of impending outbreaks than the average number of male moths per trap in any one year. Three consecutive years in which the number of male moths caught in the pheromone-baited traps increases and exceeds 25 males/trap indicates that an outbreak is expected to occur within the next 1 or 2 years.

The pheromone-baited trapping program is followed by egg-mass surveys to monitor DFTM populations (Shepherd and Otvos 1986). The pheromone trap system only gives advance warning that an outbreak is imminent and signals that another, more precise, sampling system should be used in the area. Thus, after 2 years of upward trends, an extensive network of additional traps is deployed around the indicator stations to locate the foci of the developing outbreak. An egg-mass survey is then required during the fall or winter to determine the insect density at the centre of the developing infestation and to predict potential damage (Shepherd et al. 1984a).

1981-1984 Outbreak. A developing DFTM outbreak in south-central British Columbia was discovered in 1980 before any defoliation occurred. This led to the experiment conducted in 1981 (Shepherd et al. 1984b), when virus was applied both from the ground and air, at an early phase of the outbreak, to determine whether a viral epizootic can be initiated at low to moderate population levels before it would occur naturally, and to try to prevent or reduce defoliation.

During 1982, one water-based dosage and three dosages in an oil-based formulation containing OpNPV were compared. Four 10-ha plots were treated with the following viral dosages: one plot received the recommended dosage of $2.5x10^{11}$ PIB/ha in an aqueous formulation containing 25% molasses and 75% water, and a second plot received the same dosage in an emulsifiable oil formulation (25% Dipel 88 blank carrier and 75% water). The other two treatments involved reduced dosages of virus in oil, with Plot 3 receiving about 1/3 and Plot 4 about 1/15 of the recommended dosage (Otvos et al. 1987b). The virus was applied at 9.4L/ha to all four plots. An additional four plots were established as untreated checks. Tree mortality was monitored for 2 years after the treatments in 1982.

1990-1993 Outbreak. Pheromone trap catches followed by egg-mass surveys in 1990 indicated that nine Douglas-fir stands or areas in the Kamloops Forest Region would be defoliated in 1991. Results from the 1982 experiment indicated that a virus dosage of $8.3x10^{10}$ PIB/ha, which is one-third of the previously recommended dosage, would be adequate, and either tank mix was acceptable. In 1991, 12 infested stands were treated with the "blanket" type approach at the full dose ($2.5x10^{11}$ PIB/ha); four stands with a total area of about 100 ha were treated with ca. 10-year-old stored Virtuss®, four other stands with a total area of about 40 ha were treated with ca. 10-year-old stored TM BioControl-1®, and the remaining four stands with a total area of about 60 ha were treated with a batch of freshly produced Virtuss® to provide a basis for comparison.

In 1992, two new areas were treated with the "blanket" type application, one ca. 240 ha in area east of Kamloops, and one ca. 460 ha in area west of Kamloops. Both areas were treated with the stored Virtuss® at the recommended (full) dosage of $2.5x10^{11}$ PIB/ha in 9.4L/ha in 25% animal grade molasses, 75% tap water (aerated to get rid of the chlorine) and 6% Orzan LS (I.T.T. Rayonier, Inc., Seattle, WA) added as a sunlight/UV protectant.

The hypothesis that the widely spaced swath treatment approach would provide adequate population reduction and foliage protection was also tested in 1992. This experiment was conducted in the stand used as an untreated check in 1991 where the infestation increased both in size and intensity. The infestation expanded to about 260 ha and the average egg-mass density increased from an average of 2.5 egg masses per tree (based on three lower branches/tree) in the fall of 1990 to 21 per tree in the fall of 1991. Average egg-mass densities over 1.7 per tree (based on three lower branches/tree) indicated severe defoliation

was to be expected in 1992. To test the widely spaced swath treatment, flight lines were set 200 m apart.

Results

1981-1984 Outbreak. In 1981, virus was applied aerially to three DFTM population densities: high, moderate, and low, and an epizootic occurred at all three host densities. Although a natural epizootic also occurred in the check plots containing high and moderate DFTM populations, incidence of viral infection in the treated plots was considerably earlier and higher, indicating the beneficial effects of the virus spray. Treatment effects were excellent even at low population density, and a natural epizootic in the check plot occurred much later. The experiment showed that the virus can be introduced into DFTM populations at an early phase of the outbreak. A viral epizootic can be initiated both by aerial and ground treatment applied at a dosage of $2.5x10^{11}$ PIB/ha on first and second instar larvae.

Table 1. Population densities and larval reduction of DFTM in the experimental plots treated with Virtuss® at Veasy Lake, Kamloops Forest Region, B.C., 1982

Plot Number	Treatment (PIB/ha)[a]	Tank Mix	Larvae per m² foliage ($\bar{x}$ ± SE) Pre-spray	6 weeks post-spray	Population reduction due to treatment (%)[b]
T1	$1.6x10^{10}$	Emulsifiable Oil	182.8 ± 12.6	6.7 ± 1.8	64.7
C1	Check		197.5 ± 18.0	20.5 ± 2.9	-
T2	$8.3x10^{10}$	Emulsifiable Oil	145.8 ± 12.2	2.8 ± 0.7	90.8
C2	Check		136.9 ± 9.4	28.7 ± 2.8	-
T3	$2.5x10^{11}$	Emulsifiable Oil	302.0 ± 28.7	1.0 ± 0.4	95.0
C3	Check		360.6 ± 34.6	24.1 ± 4.6	-
T4	$2.5x10^{11}$	Aqueous	41.8 ± 5.3	2.0 ± 0.6	86.6
C4	Check		81.2 ± 16.5	28.9 ± 4.3	-

[a] PIB, polyhedral inclusion bodies

[b] Population reduction was calculated using a modified Abbott's formula (Abbott 1925).

The initial impact of the applications in 1982 was that 10-30% of larvae became infected 2 weeks after the spray. These infected larvae died, liberating polyhedra and increasing the amount of inoculum on the foliage. A secondary wave of virus infection then developed among the surviving larvae (DFTM larvae have a long feeding period) and within 6 to 7 weeks after spraying the population collapsed. Percent infection and the development of the virus epizootic among the larvae in the four treated plots were related to dosage. Population reduction was calculated using a modified Abbott's formula (Abbott 1925), which corrects for natural mortality. Population reduction was 64.7% in the plot receiving the lowest dosage ($1.6x10^{10}$ PIB/ha), 90.8% in the plot receiving the second lowest dose ($8.3x10^{10}$ PIB/ha), and 95.0% in the plot receiving the full dose ($2.5x10^{11}$ PIB/ha) formulated in emulsifiable oil; there was an 86.6% reduction in the plot treated with the water-based formulation at the full dose (Table 1). The lower population reduction in the plot treated with the water-based

formulation is believed to be due to the initial lower population density, about 42 larvae/m^2, compared to a range of 146-302 larvae/ m^2 in the other treated plots. Virus transmission was higher in plots with higher larval densities. In contrast, NPV infection was not detected in the four untreated check plots until 5 weeks after spraying and at a much lower level. Development of the viral disease is temperature dependent and the spread of the disease is influenced by host density.

Six weeks post-spray infection of larvae in the treated plots ranged from 88 to 100%. A high level of naturally occurring viral infection of larvae was found in only one untreated check plot, where it reached 43% at 7 weeks after the spray. Percent infection in the other three check plots was 1.4, 9.1 and 23.0% at this time. All the treatments were considered effective in reducing DFTM larval populations. The higher level of naturally occurring virus in two of the check plots (23% and 43%) was unexpected, because naturally occurring virus is usually not prevalent at the beginning of outbreaks. One additional benefit of the virus application was increased pupal mortality. An average of 11.6% of the pupae emerged as adults from the treated plots, compared to 35.4% emergence in the check plots. Adult emergence from the pupae collected from the four treated plots ranged between 4% and 20%, the latter being in the plot receiving OpNPV in an aqueous formulation (Table 2). The virus application effectively reduced emergence of adults from 45.2% to 86.9%.

Table 2. Reduction of adult emergence of DFTM in experimental plots treated with Virtuss® at Veasy Lake, Kamloops Forest Region, B.C., 1982

Plot Number	Treatment (PIB/ha)[a]	Number of pupae reared[b]	Number of adults emerged	Adult emergence (%)	Emergence Reduction (%)[c]
T1	$1.6x10^{10}$	107	19	17.8	58.6
C1	Check	219	94	42.9	-
T2	$8.3x10^{10}$	108	4	3.7	86.9
C2	Check	181	51	28.2	-
T3	$2.5x10^{11}$	105	10	9.5	71.4
C3	Check	117	39	33.3	-
T4	$2.5x10^{11}$	52	10	19.5	45.2
C4	Check	265	93	35.0	-
Average	Treatment	372	43	11.6	67.4
	Check	782	277	35.4	-

[a] PIB, polyhedra inclusion bodies.

[b] Collection included some larvae that pupated shortly after collection.

[c] Population reduction was calculated using a modified Abbott's formula (Abbott 1925).

Defoliation attributable to DFTM larvae was impossible to estimate in the test area because western spruce budworm, *Choristoneura occidentalis* Freeman, was also present in all the plots. The *C. occidentalis* population was not affected by the OpNPV application. A

comparison of results of egg-mass surveys conducted in the spring and the fall before and after the spray showed a drastic reduction of egg-mass numbers in all the treated plots. Egg-mass numbers remained the same in one of the check plots, and more than doubled in the other three check plots. The results from these experiments showed that virus can be introduced into a DFTM population at an early phase of the outbreak and a viral epizootic can be initiated by either aerial or ground application on early instar larvae. Levels of virus infection were monitored and all treatments were successful, even at a low population density.

Tree mortality was negligible in the four treated plots: it averaged 0.6% 1 year after treatment and 2.8% 2 years after treatment, compared with 37.8% and 40.7% in the check plots (Table 3) (Otvos et al. 1987a). These results indicate that it is feasible to control DFTM populations with OpNPV (at least at $8.3x10^{10}$ PIB/ha) at an early stage of an outbreak before significant damage occurs, and this can prevent, or at least minimize, tree mortality. It was concluded that virus treatments in 1982 were successful in preventing tree mortality. The data from ground treatments indicated that OpNPV spread from sprayed to unsprayed areas, and Virtuss® may be applied in widely spaced swaths. This would permit applying the virus aerially in swaths that are about 100 to 200 m apart (instead of the usual "blanket" type approach where the spray swaths are 30 to 40 m apart) and then allowing the spread of the virus into the unsprayed areas. This novel approach would result in considerable cost reduction of spray operations. The results of experiments conducted during the 1981-1984 outbreak provided data for the development of a pest management strategy which was tested operationally in the most recent (1990-1993) outbreak.

Table 3. Population densities and reduction of DFTM larvae in four Virtuss®-treated experimental plots in 1982, the year of application, and cumulative proportion of trees killed 1 and 2 years after treatment at Veasy Lake, Kamloops Forest Region, B.C

Plot		1982 pre-spray	% population	% sample trees killed by DFTM	
Number	Treatments	DFTM/m²	reduction 1982[a]	1983	1984
T1	$1.6x10^{10}$	182.8	64.7	0	0
T2	$8.3x10^{10}$	145.8	90.6	2	7
T3	$2.5x10^{11}$	302.0	95.1	0	4
T4	$2.5x10^{11}$	41.8	86.6	0	0
Average				0.6	2.8
C1	Control	197.5		53	60
C2	Control	136.9		logged	-
C3	Control	360.6		60	62
C4	Control	81.2		0	0
Average				37.8	40.7

[a] Population reduction was calculated using a modified Abbott's formula (Abbott 1925).

1990-1993 Outbreak. Two of the three treatments used in 1991 gave good population reduction (Table 4). Both the stored and newly produced Virtuss® gave good population reductions at 86% and 82%, respectively (corrected for natural mortality). However, population reduction in the stands treated with the old TM BioControl-1® was only about 8%.

This low and unacceptable population reduction was probably due to the low pre-spray larval population density. When the two untreated check plots with the lowest pre-spray population densities (2.1 and 8.9 larvae/m^2) are excluded from these calculations, the population reduction figures for the two remaining plots (with 27.4 and 23.4 larvae/m^2 in the pre-spray counts) increased to 27.7% (Table 4). The lower population reduction figure is believed to be the result of low population densities prior to the spray and suggests that it was not necessary to treat stands infested with such low densities of DFTM larvae. Egg-mass surveys in the treated stands taken in the fall revealed low counts, indicating a prediction of either no damage or only traces of defoliation in the year following treatment. This was confirmed by both aerial and ground defoliation surveys in 1992.

Table 4. Population reduction for operational application of OpNPV against Douglas-fir tussock moth in Kamloops Forest Region, B.C. 1991

		DFTM per m^2 at biweekly sampling times					Population reduction due to treatment (Abbott's formula) at biweekly sampling times[a]		
Treatment	Plot	0	1	2	3	4	2	3	4
Old Virtuss®	3	52.34	64.96	22.34	14.31	4.91	42.6	57.6	79.0
	7	163.13	164.88	40.77	3.10	2.57	58.7	96.4	95.7
	7b	39.07	96.70	37.56	30.11	19.12	35.2	40.0	45.0
	9	130.51	121.92	67.43	28.18	2.84	7.7	55.5	93.5
	Avg.	102.85	113.85	41.16	16.67	5.85	39.7	71.8	85.7
New Virtuss®	1	7.92	39.76	14.28	7.47	3.09	40.1	63.8	78.4
	4	51.33	52.32	57.04	11.11	4.50	0	59.1	76.1
	5	86.57	179.70	64.62	15.80	10.36	40.0	83.1	84.0
	6	60.35	102.05	96.31	17.59	6.22	0	66.8	83.1
	Avg.	53.07	90.13	64.69	13.58	5.89	0	71.0	81.8
TM BioControl-1®	8	20.15	27.44	24.71	7.23	4.35	0	49.3	55.9
	10	30.98	23.35	19.04	14.25	8.85	0	0	0
	11	0.64	2.10	2.11	2.11	0.82	0	0	0
	12	7.25	8.85	9.48	7.10	5.49	0	0	0
	Avg.	13.41	13.89	12.45	7.25	4.58	0	0	8.4
Average		61.75	75.16	36.93	12.83	5.44	18.0	67.1	79.9
Control		30.44	33.80	20.26	17.55	12.16			

[a] The calculations for Abbott's formula uses the mean value from collection time 1 week post-spray rather than pre-spray because there was an apparent increase in DFTM populations following the pre-spray sample.

In the widely spaced swath treatment, where the flight lines were 200m apart, Virtuss® was applied at 2.5×10^{11} PIB/ha in 9.4 L/ha on the treated swaths, representing a treatment of approximately 26 ha within the 260-ha plot. The infection was highest directly under the flight lines in the weeks following the treatment, then spread into the untreated areas and gradually increased over time. Population reduction on some sample lines in the area treated with the widely spaced swaths 8 weeks after treatment was over 90% based on larval counts (Table 5). In comparison, population reduction 8 weeks after treatment in 1992 was 94 and 95% in the two DFTM-infested stands given the "blanket" treatment. Population reduction

could not be corrected for natural mortality because all of the infested stands were treated, therefore none could be used as an untreated control. By the time of the last larval collection, 8 weeks after treatment, it was difficult to collect larvae from directly under the flight lines and practically all the larvae collected, irrespective of the location where they were collected from within the plot, were infected with OpNPV, and they either died as larvae in partially formed cocoons, or died as pupae. It should be noted, however, that the results of the widely spaced swath treatment are based on 1 year's data and from one, though large, plot. It is highly desirable to replicate this widely spaced swath treatment in several plots to confirm the results obtained in 1992.

Table 5. Population reduction for experimental application of OpNPV in widely spaced swath treatment of DFTM in the Kamloops Forest Region, 1992

		DFTM per m^2 at biweekly sampling times						Populaton
Treatment	Line	0	1	2	3	4	5	reduction[a]
Sample Trees	A	34.55	1.56	15.44	13.58	5.14	1.70	95.1
under flight	B	23.36	18.37	33.87	17.97	2.03	0.43	98.2
lines	C	50.33	18.76	32.38	48.23	7.27	12.30	75.6
	D	27.30	35.37	24.67	31.63	1.40	0.00	100.0
	Avg.	32.64	20.28	26.77	27.62	3.59	3.06	90.6
Sample trees	A	58.71	39.76	56.86	45.29	19.47	2.52	95.7
between flight	B	32.32	52.32	21.49	50.27	1.48	1.07	96.7
lines	C	120.59	179.70	174.04	75.36	11.12	4.86	96.0
	D	60.71	102.05	47.66	27.72	7.47	0.29	99.5
	Avg.	70.18	90.13	77.03	50.15	8.82	2.15	96.9
All sample trees	A	44.90	26.07	33.19	27.17	11.28	2.05	95.4
(both under and	B	27.61	29.14	27.68	34.12	1.76	0.75	97.3
between flight	C	89.36	60.78	111.08	63.30	9.41	8.17	90.9
lines)	D	42.48	54.52	35.12	29.77	4.16	0.13	99.7
	Avg.	50.63	43.80	51.22	38.73	6.14	2.62	94.8

[a] No untreated check ares were available and population reductions are not corrected for natural mortality.

Egg-mass surveys conducted in the fall, after treatment, showed no new egg masses on sample trees which had an average of about 21 egg masses per tree the fall prior to treatment. In the previous fall, no visible defoliation was forecast for 1992 in any of the treated stands in 1991, and Forest Insect and Disease Survey evaluations in 1993 confirmed this prediction.

In 1993, the B.C. Ministry of Forests treated all stands infested with DFTM, totalling about 440 ha, with either Virtuss® or TM BioControl-1®. Unfortunately, no areas were reserved to repeat the widely spaced swath application. Virtuss® was used on ca. 210 ha of the 440 ha at full dosage and TM BioControl-1® on 230 ha at full dosage (Table 6). Population reduction was about 95% by both of these products on the 440 ha treated at the full dose ($2.5x10^{11}$ PIB/ha). An additional 150 ha was treated with Virtuss® at about 2/3 of the recommended dosage and 25 ha with TM BioControl-1®, also at 2/3 of the recommended dosage. TM BioControl-1® applied at 2/3 of the recommended dose gave an acceptable population reduction of 64%, but in the stand treated with Virtuss® at 2/3 of the full dose,

DFTM population reduction was only 14% (Table 6). No explanation is offered for the low population reduction in these stands.

Table 6. Operational treatment of Douglas-fir tussock moth infested stands in the Kamloops Forest Region, 1993

Treatment	ha	Dosage	% Population Reduction[a]
Virtuss®	100	full	89
	110	full	98
	150	2/3	14
TM BioControl-1®	130	full	90
	100	full	98
	25	2/3	64

[a] No untreated check plots were available and population reduction was not corrected for natural mortality.

Conclusion

The results of the experiments with pheromone traps and OpNPV application over the past number of years indicate that DFTM outbreaks can be prevented by a single application of virus at the early phase of an outbreak. However, foliage protection may be negligible in the year of application, but acceptable in the following years. Tree mortality was prevented when the treatment was applied early enough in the outbreak cycle, and on early instar larvae. A virus application at widely spaced swaths makes it economically more acceptable and gives forest managers a cost-effective and practical alternative to the use of chemical insecticides in controlling DFTM. The operational testing of the management system developed for the DFTM was successful and tree mortality was minimal in stands treated with OpNPV because early infection prevented the development of full-blown outbreaks in treated stands.

It is hoped that the DFTM pest management system will serve as a prototype for the development of pest management systems for other defoliating forest pests. Work has been initiated on the western hemlock looper, *Lambdina fiscellaria lugubrosa* Hulst, and it is hoped that a similar management technique can be developed for this insect.

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Ultra-Low-Volume Aerial Application in Forest Protection

MILAN ŠVESTKA[1], JÚLIUS NOVOTNÝ[2] AND PAVEL SOKOL[3]

[1]Forestry and Game Management Research Institute, Jílovište-Strnady, Dvorakova 21, 66902 Znojmo, Czech Republic
[2]Forest Research Institute, Lesnicka 11, 96923 Banská Štiavnica, Slovak Republic
[3]Rovniankova 20, 85102 Bratislava, Slovak Republic

ABSTRACT The Canadian-Czechoslovak ultra-low-volume (ULV) air-application technology project was conducted from 1991-92. The goals of the project were transfer and modification of Canadian technology and experiences with ULV aerial application of microbial and chemical insecticides for leaf eating insect control into the former Czechoslovakia forest protection program. Two experimental field applications were carried out in spruce and oak forests during 1992. The total sprayed area was 800 ha and experts from both sides participated in these trials. The experimental and practical ULV technology spray program was used for control of *Lymantria dispar* and *L. monacha* on 41,700 ha from 1992 until 1995. A Z-37-Turbo airplane with Micronaire AU 4000 rotary atomizers was used for ULV application of Foray FC, Trebon 30 EC, Trebon 10 F, Dimilin 45 ODC and Dimilin 48 SC.

Materials and Methods

IN 1992, DEMONSTRATIONS were carried out on two experimental plots with a total area of 400 ha in spruce stands of the Forest District Telc and on two experimental plots with a total area of 400 ha in oak stands of the Forest District Lanzhot (Fig. 1). The objective of the experimental applications in spruce stands was to control *Lymantria monacha*, and in the oak stands to control *Lymantria dispar*.

The basic objective of these experimental applications was to confirm the correlation between the deposit of droplets onto spruce needles and oak leaves and the biological effectiveness of the applied preparation.

On 25 April, 1992, in spruce stands and on 2 May, 1992, in oak stands, 2.5 liter/ha (31.75 BIU/ha) of Foray FC, stained with the food colorant Rhodamin, was applied. The Z-37-T airplane was equipped with Micronaire AU 4000 rotary atomizers, a flow meter and application monitor. Important technical data about the course of the applications (time of application, dosing, speed of atomizers) were recorded by a mini-computer in the airplane. Meteorological conditions (wind force, temperature) prior to and during the application were measured with a mini-probe at the height of the airplane during application and at other height levels.

Pages 155-165 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

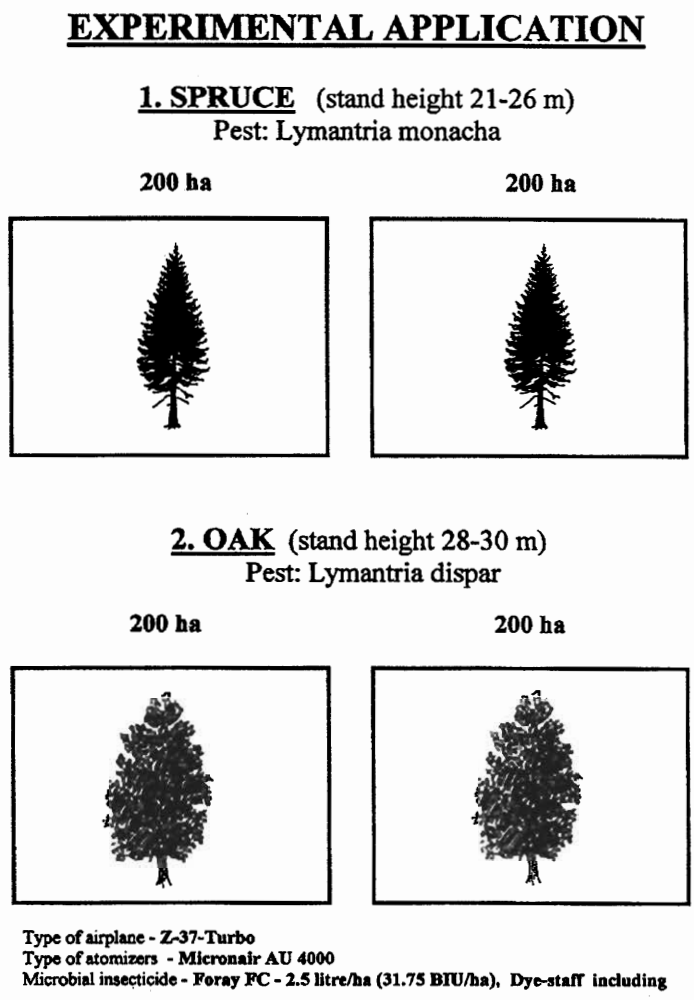


Figure 1. The basic information about experimental plots, tree species, pest, application equipment and volumt of B.t.

Great attention was devoted to studying the penetration of droplets into the stands and evaluating droplet size and the degree of coverage. Partially budded spruce and/or oak transplants were placed on 20 sample trees in each of the spruce and oak stands by means of a simple pulley fixed in the tree tops. Three transplants were placed on each sample tree, i.e. in the upper, middle and lower part of the crown. In addition, an artificial metal twig was fixed to each transplant to intercept the spray droplets (Fig. 2).

Immediately after application, the metal twigs and the needle and leaf samples from the transplants and sample trees were transported to the Department for Forest Protection laboratory of the Mendel University of Agriculture and Forestry in Brno. Droplet size and number of droplets were measured on spruce needles and oak leaves. In total, 7,200 spruce needles were examined. Droplet size in spruce stands was estimated by measuring a set of 600 drops on the artificial twigs, 600 drops on the transplant needles and 180 drops on the needles of mature trees. Droplet size in the oak stands was determined by measuring a set of 300 drops while the number of droplets was measured in 60 places, always on 10 cm^2 of both

the upper and the bottom side of the leaves. Evaluations of the spray composition, in terms of droplet size, volume and estimation of the volume mean diameter (VMD), were performed on a computer according to the respective program.

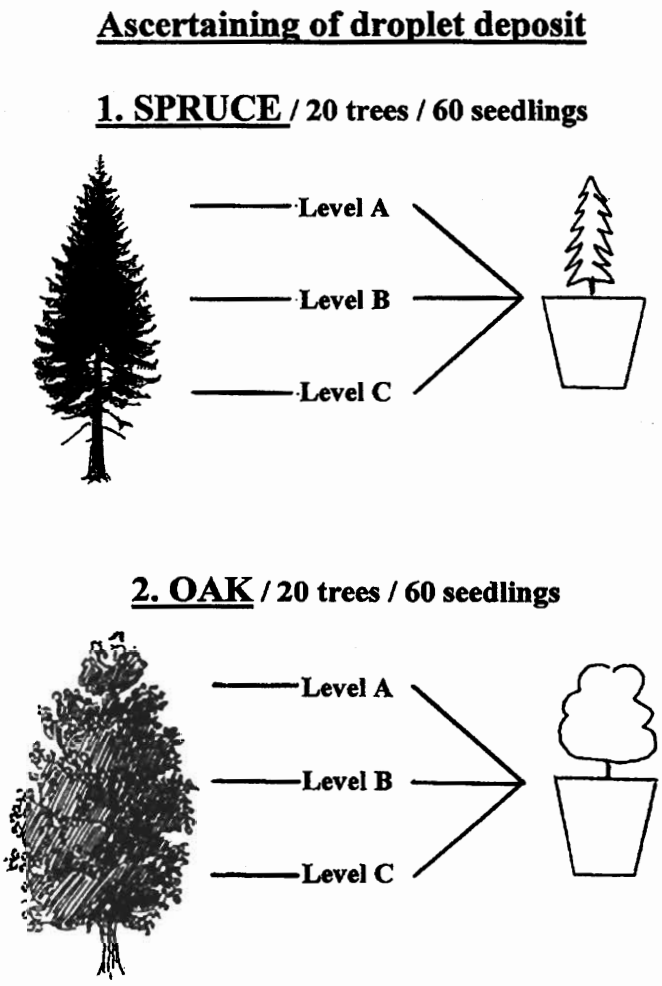


Figure 2. The basic information about tree species, number of control trees and seedlings and placement of seedlings containers during experiments concerning on ascertaining of droplet deposit.

Evaluations of the biological efficiency were based on the mortality of *Orgyia antiqua* caterpillars (2nd instar) and *Lymantria dispar* (3rd and 4th instar) released on the spruce and oak transplants. Following application, 60 spruce and 60 oak transplants in containers were taken down from the tree tops and 10 *Orgyia antiqua*, and/or *Lymantria dispar* caterpillars, covered with monofil, were placed on each transplant. Mortality was evaluated at 5-day intervals for 15 days following treatment under field conditions. A control series was simultaneously established where the caterpillars were released onto untreated transplants.

In 1992 and the following years, pilot and operational aerial ULV applications were carried out based on information obtained from these demonstration applications. In 1992,

pilot applications were made on 100 ha in the LHC Cifáre and on 50 ha in the Forest District Hodonín. Here, the bioinsecticide Foray FC was applied against outbreaks of gypsy moth, *Lymantria dispar.* The following operations in 1993 and 1994 in South Moravia were aimed against the same pest using the same preparation on 5,580 ha, and in 1994-1995 in Slovakia against *Lymantria dispar* and looper moths on 8,420 ha. During the outbreak period of *Lymantria monacha* in the Czech Republic in 1994 and 1995, the ULV technology of application was dominant and was applied on ca 98% of the total area of 28,234 ha. Although Foray FC (i.e. 5 liters/ha) and Trebon 30 EC (and/or Trebon 10 F) were used more frequently, Dimilin 45 ODC (and/or Dimilin 48 SC) in a volume dose of insecticide mixture of 10 liters/ha were used to a lesser extent.

Results

Demonstration applications. Technical data on the ULV demonstration applications are given in Table 1. The table shows that on 25 April, 1992, the flight of the airplane during the treatment of 400 ha of spruce stands, with 94 operational transits, lasted 2 hours and 30 minutes, including departure from and arrival to the advanced airfield 4 km away. The treatment of oak stands of the same area, involving 103 operational transits, lasted 2 hours and 6 minutes.

Table 1. Summary of spray emission parameters recorded by onboard datalogger

Parameters	Conifer sprays	First oak spray	Second oak spray
Start	06:49	08:28	18:30
End	10:18	09:15	19:49
Break	08:21 - 09:22	-	-
Total swaths	94	48	55
Mean flow± s.d. (l/min.)	10,89 ± 2,29	10,93 ± 6,39	16,41 ± 6,43
Mean atomiser speed ± s.d. (r.p.m)			
Outer starboard	9427 ± 699	8795 ± 613	8680 ± 613
Outer port	9708 ± 616	8780 ± 582	8929 ± 613
Inner port	8131 ± 531	7685 ± 525	7718 ± 628

Measurements of the wind force and temperature using a minioprobe (Tables 2 and 3) showed that the wind force at the airplane level at the time of the treatment of spruce stands fluctuated from 2 to 4 m/sec and the temperature ranged from 7 to 11°C. The average rate of flow of the six atomizers at the time of application was 10.89 ± 2.29 litres/min and the average speed of the atomizers ranged from 8,131 ± 531 to 9,708 ± 616 revolutions/min. The wind force at the airplane level at the time of the treatment of oak stands ranged ca from 1.4 to 3.8 m/sec and the temperature ranged between 14 and 17°C. The average rate of flow of the six atomizers at the time of application was 10.93 ± 6.39 to 16.41± 6.43 liters/min and

the average speed of the atomizers ranged between 7,685 ± 525 and 8,929 ± 613 revolutions/min.

Table 2 Minisonde data, No. 1 test site, near Telc (Saturday, April 25, 1992)

Elevation (m)				Wind vel. (m/s)				Wind direction (deg., mag.)				Temperature (°C)			
1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th
0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	6.4	3.4	9.1	12.5
7.9	52.7	12.9	9.6	0.8	2.0	0.7	0.9	150.0	160.0	164.0	163.8	7.0	8.0	10.3	11.7
35.4	79.4	56.3	75.3	4.6	2.1	4.6	2.9	159.4	189.2	176.4	188.3	9.0	10.0	11.9	12.3
69.7	130.1	104.2	157.2	6.2	4.9	5.1	4.0	185.5	198.8	205.5	194.4	10.2	10.4	12.2	13.9
112.6	179.0	166.1	234.7	2.5	2.8	4.1	5.6	257.4	219.8	226.0	200.2	10.0	10.9	12.3	14.5
158.8	226.6	223.7	311.2	0.8	3.2	3.3	9.5	314.1	219.7	216.1	206.6	9.8	11.0	12.1	13.9
189.2	271.7		445.4	0.6	3.6		16.1	281.1	223.4		212.8	9.5	10.9		13.6
211.8	309.8			0.8	3.1			286.2	221.0			9.7	10.9		
226.5	348.9			0.9	2.2			335.3	208.8			9.7	11.0		

Release Times: 1st = 6.10 a.m., 2nd = no data, 3rd = 7.59 a.m., 4th = 9.01 a.m.

Table 3. Minisonde data, No.2 test site, near Zidlochovice (May 2,1992)

Elevation (m)			Wind vel. (m/s)			Wind dir. (deg., mag.)			Temperature (°C)		
1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
0.0	0.0	0.0	-	-	-	-	-	-	14.4	16.0	17.6
53.1	50.0	139.8	3.8	1.4	9.8	149.0	145.1	123.8	14.1	14.8	17.1
79.9	104.8	188.3	6.0	2.8	2.8	148.5	130.8	143.6	14.0	13.4	16.7
151.0	257.9	284.8	8.0	9.2	9.5	151.5	136.9	145.4	13.6	13.2	16.5
196.6	284.2	436.9	8.2	9.4	16.8	149.2	139.0	149.8	13.4	12.8	15.9
218.8	303.1	512.0	4.3	4.9	9.7	147.3	140.5	159.2	12.8	12.4	15.6
250.3	353.4	594.6	2.8	6.9	10.3	147.0	142.0	160.4	12.4	11.8	15.2
263.5			3.0			148.3			12.2		
261.0			2.7			150.0			11.8		

Release Times: 1st = 7.56 a.m., 2nd = 8.34 a.m., 3rd = 9.04 a.m.

Table 4 gives the number of droplets on spruce needles, artificial twigs and oak leaves. The average length of spruce transplant needles was 9.6 mm, and 14.9 mm for mature trees. On the oak leaves, 75% of the droplets were found on the upper side and 25% on the bottom side of the leaves.

Table 4. Number of droplets on the spruce needles (per needle) and oak leaves (per cm^2)

Tree species	Tree crown levels			
	Top	Middle	Bottom	Average
Foliage simulators (needles)	2.58	3.62	2.99	3.06
Spruce- seedling needles	0.20	0.37	0.29	0.29
Spruce- tree needles	0.90	0.36	0.32	0.53
Oak leaves	0.95	0.86	0.63	0.81

Tables 5, 6 and 7 show the results of evaluations of droplet size at the respective heights. Table 8 gives a survey of results of evaluations of the efficiency (mortality) of *Orgyia antiqua* and *Lymantria dispar* caterpillars released on the treated transplants.

Table 5. Magnitude of droplets on the spruce needles and oak leaves (average in µm)

Tree species	Tree crown levels		
	Top	Middle	Bottom
Foliage simulators (needles)	87.1	168.3	93.5
Spruce- seedling needles	95.0	84.8	76.0
Spruce- tree needles	80.9	81.5	76.5
Oak leaves	197.8	229.0	141.5

Table 6. Percentage of droplets by droplet size categories

Tree species	Tree crown levels								
	Top (A)			Middle (B)			Bottom (C)		
	Droplet size categories (µm)								
	0-50	51-150	over 150	0-50	51-150	over 150	0-50	51-150	over 150
Foliage simulators	44.6	54.4	1.0	41.8	53.4	4.8	39.3	59.6	1.1
Spruce- seedling needles	52.9	45.7	1.4	47.8	51.1	1.1	45.3	54.7	0.0
Spruce- tree needles	43.1	56.9	0.0	42.6	57.4	0.0	52.9	47.1	0.0
Oak leaves	21.0	68.5	10.5	24.3	61.6	14.1	33.9	59.3	6.8

Table 7. Percentage of spray volume by droplet size categories

Tree species	Tree crown levels: Top (A) Droplet size categories (μm) 0-50	Top (A) 51-150	Top (A) over 150	Middle (B) 0-50	Middle (B) 51-150	Middle (B) over 150	Bottom (C) 0-50	Bottom (C) 51-150	Bottom (C) over 150
Foliage simulators	5.6	77.7	16.7	2.3	38.5	59.2	3.8	82.9	13.3
Spruce- seedling needles	4.8	73.4	21.8	6.3	73.9	19.8	6.6	93.4	0.0
Spruce- tree needles	6.9	93.1	0.0	6.4	93.6	0.0	9.9	90.1	0.0
Oak leaves	0.5	30.7	68.8	0.4	22.8	76.8	1.5	53.1	45.4

Table 8. *B.t.* efficacy on spruce and oak seedlings (Czechoslovakia 1992)

Plot	Mean % survival
Control (spruce)	39.33 ± 11.43
Spruce (Level A+B+C)	9.17 ± 7.71
Spruce (Level A)	9.50 ± 8.26
Spruce (Level B)	7.50 ± 9.11
Spruce (Level C)	10.50 ± 12.76
Corrected larval mortality (A+B+C): 76.69 ± 19.61	
Control (oak)	70.00 ± 13.65
Oak (Level A+B+C)	22.63 ± 15.84
Oak (Level A)	22.11 ± 15.84
Oak (Level B)	27.89 ± 17.82
Oak (Level C)	17.89 ± 15.12

Corrected larval mortality (A+B+C): 67.67 ± 11.73

The survey of the above results confirms that the demonstration treatments of spruce and oak stands were carried out under favorable meteorological conditions. The flow rate of the individual atomizers was less than 2 liters per minute, which is one of the prerequisites for producing the desired spectrum of droplets. Due to the operating speed of the airplane and maximal angle of blades, the number of revolutions of the atomizers was on the very limit of the operational maximum (i.e., 9,000 - 10,000 revolutions); the required optimal value would be 12,000 revolutions/min. This influenced the size of the droplets bioinsecticide produced, which was within the range required for this method of application. However, a spectrum of smaller droplets would have been optimal. This was again associated with the coverage of drops, which was indeed very balanced over the whole profile of spruce and oak crowns;

however, the observed values were closer to the limit of the required minimum. In spite of this fact, the biological efficiency against the vapourer moth and the gypsy moth was relatively good.

Small technical defects that occurred during both applications, were accurately identified and explained thanks to the computer data collected during the course of the experiment. These included a defect in the functioning of the flow meter and an error in the control of the application equipment.

The entire program of the project has been accomplished. The possibilities of aerial ULV applications were demonstrated under our conditions and all the participants were provided with information about all the circumstances necessary to apply this technology in practice.

Pilot and operational application. The biological efficiency of ULV applications (4 liters/ha) was compared with classical applications (100 litres of mixture/ha) and its time dynamics were simultaneously studied in detail when applying the Foray FC biopreparation against populations of *Lymantria dispar* (Table 9). No substantial differences were observed when comparing classical and ULV applications. In the first 7, days the efficiency of ULV applications was higher than 95%, sufficiently protecting the leaf area. A similar result was also reached after conventional applications by spraying.

Table 9. Efficacy comparison of LV (100 l/ha) and ULV (4 l/ha) aerial application of FORAY 48B against gypsy math larvae (L2)

	Spray applicators	Efficacy in % (Abbott formula)	
Plot (locality)	and spray volume	after 7 days	after 14 days
Bykaret (LV)	Tee-jet (100 l/ha)	93.9	97.3
Mortality on control plot (locality Tajná)		2.6	9.3
Šenkvice (ULV)	Micronair 4000 (4 l/ha)	95.7	97.0
Mortality on control plot (locality Senec)		3.1	5.4

Evaluations of the time dynamics were interesting (Fig. 4) and showed that during the first 5 days after treatment, the efficiency exceeded 90%. The mass mortality of caterpillars occurred between the 3rd and 5th days. Between the 5th and 14th days after application, the efficiency of the Foray FC bioinsecticide did not increase more than 5%. The efficiency of application ULV treatments was found to be optimal, i.e., within 48 hours the population of the pest was infected and within 120 hours mass mortality occurred. This course guarantees that feeding will stop in time to protect the assimilation and reproductive capacity of the host tree.

The results of ULV applications of three different doses of the bioinsecticide Foray FC (Fig. 5) indicated that the doses per hectare of strong concentrations of *B.t.* preparations against *Lymantria dispar* could be reduced. At the same time, they showed that it would be possible to model the per hectare doses of the preparation dependent upon the vitality of the pest and on other conditions to be applied after treatment.

Even after operational applications using Foray FC bioinsecticide against *Lymantria dispar* caterpillars, the effect was altogether quick, particularly against 1st and 2nd instars. In favorable weather conditions, the feeding of the pest stopped within the first two days of the treatment. If the pests were very numerous, or if the applications were carried out later, (i.e., during the 2nd and 3rd instars), and in less favorable weather conditions, part of the caterpillar population survived and the population was not completely destroyed until immediately before pupation.

In 1994 and 1995, the results of aerial ULV treatment against *Lymantria monacha* caterpillars were different; in this case, three types of preparations were used. In the most seriously infested localities, with as much as several thousand caterpillars on one tree, the preparation Trebon 30 EC was used, i.e., 0.2 liter/ha dispersed in 9.8 liter/ha of Petropal oil carrier. The effect of this combination was very quick and effective, with 80-100% mortality. Similarly, the results of Dimilin 45 ODC, applied at a rate of 0.2 liter/ha in the same dose of oil carrier, were somewhat slower, but they were reliable and there was no pest feeding in the treated areas. In 1994, 5 liters/ha of the Foray FC biopreparation were applied to some areas heavily infested with pests to protect drinking water. The weather conditions became worse (cold, rain) immediately after application and the effect of the preparation decreased to 30-50% mortality, so that in places with critical amounts of pests, heavy foci of feeding appeared.

On the contrary, when warm and dry weather prevailed in 1995 after the application of the same preparation in the same dose, the efficiency of the bioinsecticide was on the same level as Trebon (almost 100%).

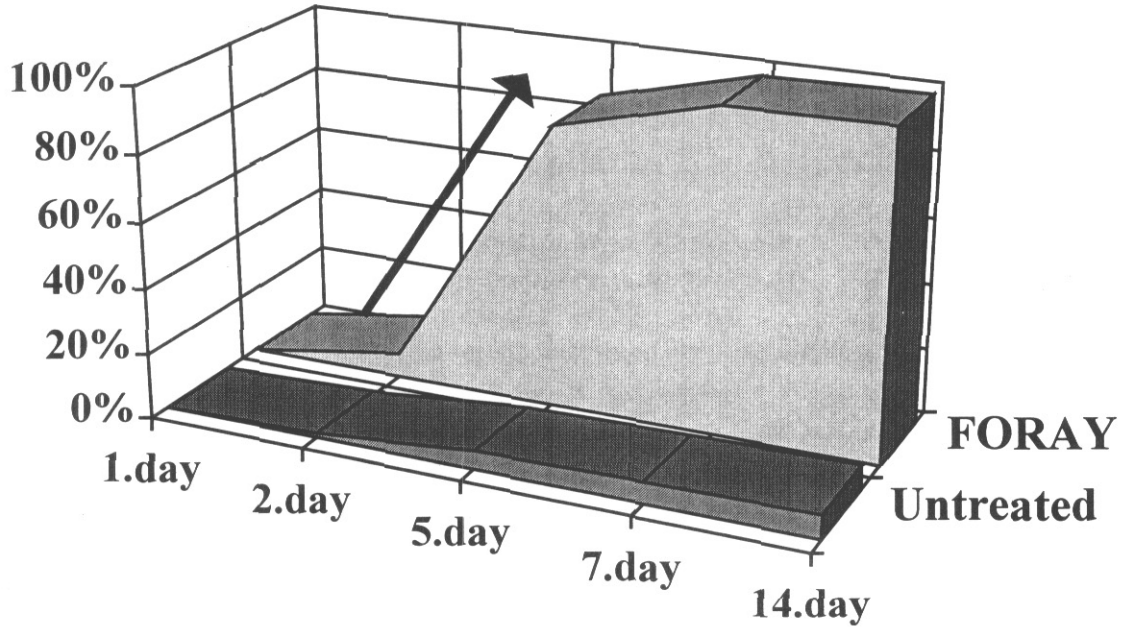


Figure 4. The distribution over time of ULV aerial application efficacy of *Bacillus thuringiensis* (gypsy moth larvae L2).

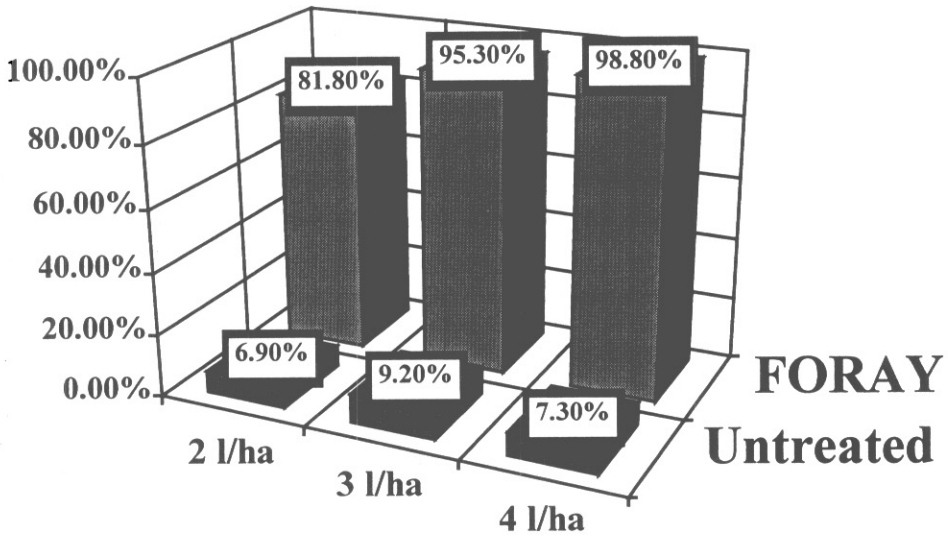


Figure 5. The efficacy of ULV aerial application of *Bacillus thuringiensis* against gypsy moth larvae (L2).

Conclusion

Technology transfer of ULV air-application of microbial and chemical insecticides from Canada into Czech Republic and Slovak Republic was made during 1991-92 based on common research program fulfillment and modifications for Central European conditions to provide an economic method of insect pest control.

The experimental, demonstration and routine ULV applications between 1992-95 have produced the following experience and knowledge about factors limiting the use of ULV technology in the Czech and Slovak Republics. These conditions include:

Suitable type of airplane	Z-37-Turbo
Suitable type of atomizers	Micronair AU 4000
Rotor blade of rotary atomizers	elongated
Optimal hectare dosage	3-5 liters
Fly-speed of aircraft	160 km per our
Optimal flow (1 atomizer)	2 liters per minute
Optimal flow (6 atomizer)	12 liters per minute
Optimal speed of atomizers	10 000 - 12 000 rotations per minute
Swath	20-30 m
Optimal size of droplets (coniferous forests)	15-60 μm
Optimal size of droplets (deciduous forests)	50-150 μm
Optimal number of droplets per	2 per needle
	0.6-1.0 per 1 cm^2 of leaf
Wind speed limit	3 m per sec.
Optimal wind speed	1-2 m per sec.
Wind direction	into treated area

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Atta texana, Texas Leaf-cutting Ant, on Typic Quartzipsamments: Ecological Considerations

D.L. KULHAVY, W.G. ROSS AND R.R. CAHAL III

Arthur Temple College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas 75962 USA

ABSTRACT Pine plantations on Typic Quartzipsamments in East Texas are difficult to establish. Forest management options following clearcutting are limited. An 8-year regeneration study of the growth and survival of loblolly, *Pinus taeda*, L. shortleaf, *P. echinata* Mill., slash, *P. elliotii* Engelm and longleaf pines *P. palustris* Mill. was conducted to determine optimum tree species and treatments for reforestation, and to recommend practical alternative land uses and management strategies for Typic Quartzipsamments. Successful regeneration provides new opportunities for insects and pathogens. Impacts of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), the Deodar weevil, *Pissodes nemorensis*, Germar, Annosus root rot, *Heterobasidion annosum* (Fr: Fr) Bref, fusiform rust, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. fusiforme (hedge and N. Hunt) Burdsall and G. Snow and the Texas leaf-cutting ant, *Atta texana*, (Buckley) will be discussed in the context of droughty site management.

IN THE UPPER Gulf coastal plains of East Texas, sandhills are droughty where alluvial and marine deposits of relatively recent geological origin occur (Burns and Hebb 1972). These droughty sites occur on broad, slightly convex interstream divides at elevations ranging from 100 to 250 meters above sea level and range in depths from 2 to 9 meters. In Nacogdoches and Rusk counties, these sandhills are characterized by Quartzipsamments developed on outcrops of the Carrizo formation, continental stream deposits formed during the Eocene series of the Tertiary system. The Tonkawa soil series is classified as thermic coated Typic Quartzipsamments, and accounts for approximately 5000 ha in Nacogdoches, Rusk, Panola and San Augustine counties (Dolezel 1980). These soils are characterized by low fertility, rapid permeability and extreme acid reaction.

The original vegetation on the sandhills was an association of longleaf pine (*Pinus palustris* Mill.), turkey oak (*Quercus laevis* Walt.) and bluejack oak (*Quercus incana* Bartr.), commonly called scrub oaks, and pineland three-awn (*Aristida stricta* Michx.), commonly known as wiregrass (Hebb 1957). The primary land use on Tonkawa soils today is woodlands (site index averages 55 at 50 years for shortleaf pine, *Pinus echinata* Mill.), 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. Sandhills are resistant to erosion and are considered important ground water recharge areas.

From 1973 to 1975, approximately 1400 ha on Tonkawa were clearcut, followed by extensive site preparation. Removal of all organic matter and surface litter from the site exposed the bare mineral soil to the sun and wind, which greatly decreased the moisture holding capacity of the soil and increased surface temperatures (Kroll et al. 1985). Repeated attempts were made to regenerate the area without success. Intensive management on this sensitive site provided incentive for a regeneration study.

Pages 166-173 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

From 1983 to 1990, a study was conducted (Tracey et al. 1991) on the site to determine the survival and growth of seven species/treatment combinations. These included: 1) untreated loblolly pine, *Pinus taeda* L., 2) Terra-Sorb-treated loblolly pine, 3) kaolin clay slurry-treated loblolly pine, 4) untreated slash pine, *P. elliotii* Engelm, 5) Terra-Sorb-treated slash pine, 6) kaolin clay slurry-treated slash pine, and 7) containerized longleaf pine. The objectives of this study were to determine optimum tree species and treatments for reforestation, and to recommend practical alternative land uses and management strategies for Typic Quartzipsamments.

Containerized longleaf pine yielded the highest survival (> 50%) throughout the study, followed by Terra-Sorb-treated loblolly pine (38%); all other treatments were unacceptable (below 30% by the end of the eighth year). Tracey et al. (1991) recommended: 1) Encourage harvest systems that minimize site exposure and leave residual overstory; underplant pine; avoid clearcutting. 2) Site preparation on previously clearcut sites must be accomplished with minimal site disturbance and topsoil displacement. 3) Reforest droughty sites in East Texas with longleaf pine using container grown seedlings or loblolly pine treated with Terra-Sorb. 4) Manage for non-timber resources, including wildlife, limited recreation and groundwater protection.

Successful regeneration provides new opportunities for insects and pathogens. Artificial monocrop systems in forestry are of recent origin and their effects on the emergence of new pests and diseases are more likely to be the direct result of environmental change (Way 1981). Heavy winter and spring precipitation followed by periods of drought during the summer for the past two years, in combination with soil characteristics have caused undue stress to trees. Minor impacts caused by insects and pathogens on the Tonkawa series include the Nantucket pine tip moth (NPTM), *Rhyacionia frustrana*, (Comstock), the deodar weevil, *Pissodes nemorensis* Germar, annosus root rot *Heterobasidion annosusm* (Fr: Fr) Bref, and fusiform rust, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* (Hedge and N. Hunt) Burdsall and G. Snow.

Slash pine found scattered throughout the study area grows well on low lying soils with characteristics of Aquic Quartzipsamments. The moisture content of these soils ensured excellent regeneration. Pathogens associated with slash pine, such as Annosus root rot and fusiform rust, are problematic.

The deodar weevil is a minor insect pest on the Tonkawa soil series. The weevil is found throughout the study area in low lying areas. The life cycle of this weevil differs from others in that oviposition occurs in the fall and the larvae feed on terminals during the winter. Adults emerge in the spring and remain inactive during the summer. Adult weevils feed on the inner bark, often girdling a stem or twig. Weevil damage to terminals and the main stem of planted 4-5-year-old loblolly pines was documented in areas of increased surface moisture due to record precipitation throughout the Tonkawa study site.

The Nantucket pine tip moth (NPTM) is widely distributed throughout the eastern and southern United States. NPTM is a larval feeder on the meristematic tissue of young pines, causing significant damage, particularly in areas where forest regeneration practices favor its proliferation (Yates et al. 1981). Larval feeding severs the conductive tissue in the tip, causing it to turn brown and die. Infestations can result in growth loss, excessive branching, multiple terminals and deformed bushy trees and is of primary importance in even-age management of loblolly and shortleaf pines. While NPTM is a major forest insect pest in

pine plantation management, on the Tonkawa study site it is a secondary pest compared to the impacts caused by the Texas leaf-cutting ant, *Atta texana* (Buckley).

Atta texana, confined to Texas and Louisiana, is the northernmost representative of this most specialized genus of Attini, a New World tribe of fungus-growing myrmicine ants. The range of the ant occupies much of the area of Texas and Louisiana lying between 92.5 and 101 degrees of longitude. In Texas, the range extends from near the Oklahoma border to the extreme southern border, with an extension into northeastern Mexico as far south as Vera Cruz.

Atta 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). These 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 25 feet (Moser 1967, 1984). *Atta texana* overturns the soil when excavating tunnels and chambers. In building these tunnels and chambers, materials transported to the surface by ants are mixed with body fluids to form uniform pellets of soil (Weber 1966). The tunnels and chambers that *A. texana* constructs in the soil are numerous and extend deeper than those of vertebrate animals. The nest area is usually marked by crescent-shaped mounds about 15 to 30 cm in height and about 30 cm in diameter. Nests are conspicuous and abundant, reach sizes of 15 to 25 m across, and have a decided impact on the forest landscape.

Atta texana shows a decided preference for grasses, weeds and hardwood leaves. These leaf parts are gathered and used to cultivate their fungus. They prune the vegetation, stimulate new plant growth, break down vegetable material rapidly and in turn enrich the soil (Hölldobler and Wilson 1990). *Atta texana* is a forest pest because it cuts the needles from both natural and planted pine seedlings. The pines usually escape destruction as long as there is other green vegetation, but in the winter pine needles satisfy the ants' need for green plant material (Moser 1967). Spatial distribution of *A. texana* is based on suitable habitat availability. The clearcutting disturbance of the study site quickly became a matrix (the most extensive and most connected landscape element type present, which plays the dominant role in landscape functioning) of ideal ant habitat. Ant densities are normally higher in secondary than in primary vegetation (Haines 1978). Nest dimensions are significantly correlated with distances foraged by various species of leafcutters (Fowler and Robinson 1979). *Atta* foraging patterns are influenced by the availability and locations of preferred plant species in its territory (Waller 1982). Adaptations in their pattern of the nest distribution enable ants to use the food available in the habitat more effectively and to reduce the unfavorable results of competition among societies, which limit their reproduction and numbers (Cherrett 1968).

Objectives

The objectives are to:

1. Determine the overall effects of *Atta texana* on soil texture and organic matter within the mound and adjacent areas;
2. Estimate the landscape area affected by *Atta texana* on different sites within an area on the Tonkawa soil series of thermic coated Typic Quartzipsamments; and
3. Discuss educational activities associated with *A. texana.*

Methods

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. Distribution of the known nesting areas of *A. texana* was examined on this ecosystem. This study area encompasses many sandy soils and loams that are capable of sustaining *A. texana*. *Atta texana* shows a decided propensity for the Tonkawa soil series of thermic coated Typic Quartzipsamments for their mounds.

Soil samples were collected from 30 *A. texana* mounds found on the Tonkawa soil series. Samples were taken on the surface and at depths of 15 and 50 cm on the *A. texana* mounds (an area currently being impacted by *A. texana*). This procedure was replicated on the inter-mound area (an area once affected by *A. texana*) and from a control area of similar physical characteristics away from the area of influence for a total of nine samples per mound. All soil samples were catalogued, oven dried, and sifted with a 10-gauge soil sieve. Loss on ignition methodology of each soil sample was processed in a muffle furnace at a temperature of 500° C. This determines the percentage of organic matter lost to the nearest 0.01%. Bouyoucos analysis (Bouyoucos 1962) was performed on 100 grams of each soil sample to determine the percent clay, percent silt and percent sand.

Using aerial photographs and ground truthing, all mounds and foraging openings were located in the regeneration study area. All nesting mounds and created forage openings were measured in the four cardinal directions (north, south, east and west). This was done to measure the overall impacts of the nesting and foraging territories on the forest landscapes.

Results and Discussion

Atta texana, by overturning the soil when excavating tunnels and chambers, has a profound effect upon organic matter and texture of the Tonkawa soil series. The tunnels and chambers that *A. texana* constructs in the soil are numerous and extend deeper than those of any vertebrate animals. Materials transported to the surface during tunnel and chamber building by ants are mixed with body fluids to form uniform pellets of soil.

Using Bouyoucos analysis to determine soil texture, it was found that *Atta texana* significantly increases the percent clay. The percent clay in the pellets of nest mound craters was statistically more significant than at the inter-mound surface and the control surface (Table 1) at the $\alpha = .05$ level. In comparing percent clay by depth, the mound surface was statistically more significant than the 15-or 50-cm depths at the $\alpha = .05$ level.

Soil brought to the mound surface by *A. texana* is significantly lower in percent organic matter than the percent organic matter present in the soil at the inter-mound and control surfaces (Table 2). Organic matter for the mound at 15-cm and 50-cm is statistically higher than the same depths in the inter-mound and the control areas at $\alpha = .05$ confidence interval.

Atta texana utilized created openings and disturbances (an event or events that cause a significant change from the normal pattern in an ecological system, Forman and Godron 1986) to create nesting areas and benefit from the use of corridors (a narrow strip of land that

differs from the matrix on either side) in their expansion. *Atta texana* is found along the FM 1087 road corridor and along the edges of stream side corridors. In the regeneration areas, *Atta texana* reacted to the monocultural habitat and dispersed in all directions, causing massive destruction to the loblolly plantation in the area.

Table 1. One-way analysis of variance for mean texture percents of Tonkawa soils (Typic Quartzipsamments) tested by site and depth (means ± standard deviations) using the Bouyoucos method

Site	N	Sand	Silt	Clay
Pellets of Nest Mound Craters	30	90.7 ± 3.7	3.7 ± 1.3	5.6 ± 3.0 a
50 cm Beneath Nest Mound Surface	30	92.0 ± 2.4	4.1 ± 1.8	3.9 ± 1.0 b
Internest Surface	30	91.9 ± 2.5	4.4 ± 1.8	3.6 ± 1.2 b

Currently, there are 52 openings found throughout the study area. The total area of the study is 78 ha, or 78,000 sq. m. Total defoliation attributed to *A. texana* accounts for 16,380 square m or 21.5% of the total landscape area. The immediate nesting areas or mounds account for 1.25% of the total area affected by *A. texana*. Not all disturbance areas contain mounds due to natural mound mortality or chemical treatment with methyl bromide.

Table 2. One-way analysis of variance for mean percent organic matter of Tonkawa (Typic Quartzipsamments) tested by site and depth (means ± standard deviations)

Site	Tonkawa Soils (n = 30 sites)
Pellets of Nest Mound Craters	0.92 ± 0.49 de
15 cm Beneath Nest Mound Craters	1.48 ± 0.68 ab
50 cm Beneath Nest Mound Craters	0.89 ± 0.39 e
Nest Mound Surface	1.45 ± 0.66 b
15 cm Beneath Nest Mound Surface	1.27 ± 0.51 bc
50 cm Beneath Nest Mound Craters	0.71 ± 0.29 e
Internest Surface	1.72 ± 0.61 a
15 cm Beneath Internest Surface	1.14 ± 0.50 cd
50 cm Beneath Internest Surface	0.71 ± 0.28 e

Within columns, means followed by the same letter are not significantly different ($P<0.05$) using Duncan's multiple range test.

Current research includes color infrared photographic coverage at a scale of 1:5000 over a 36 by 36 km area to estimate both numbers of mounds present and percentage of the area defoliated by *A. texana*. The photography includes 60 percent end lap and 30 percent side lap for use as stereo pairs. 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. Educational activities for the area include its use in teaching forest entomology,

landscape ecology, environmental science and teacher education in environmental science. Evaluation of the influence of *A. texana* on the landscape includes using the components of structure, function and change to evaluate corridors, patch dynamics and the influence on the forest matrix in long-term evaluation of a droughty landscape. The measurement of change on the forest matrix by *A. texana* gives a graphic example of the influence of social insects on the landscape. Critical thinking skills are honed by evaluating the influence of both soils and openings on the landscape as sculpted by the ants.

Recognition that soil color is indicative of soil texture change and perhaps nutrition raises questions of why the pellets are concentrated in the central nest mound area and what are the influences on the ecology of the landscape? The structure of the ant mound, with its integral tunnels and precise angles of these tunnels to both the surface and to the central nest mound (Moser 1984), add to the overall examination of the impact of *A. texana* on the landscape. Questions arise as to why the central nest mound is large (15 to 25 m across with a depth of 15 to 50 cm of soil deposited on the mound surface). Environmental education and natural history interpretation of the site lead to development of education modules and educational sequences that both intrigue and fascinate all ages and levels of education. As an educator, it is imperative that we stimulate those we are entrusted to teach.

Conclusions

While most consider *Atta texana* an economic pest, in nature they are of fundamental ecological importance. *Atta texana* serves an important ecological function of soil amelioration and increases biodiversity, especially on the very sensitive ecosystem of the Tonkawa study area. Its soil-enriching capabilities outweigh its pest status. *Atta texana* is unique with regard to soil preference, its nesting mounds, foraging areas and spatial distribution.

Plantation forestry, particularly pines on droughty sites, is adversely affected by *Atta* defoliation (Cherrett 1986). They are well-adapted for attacking monocultures (Vilela and Howse 1986) and the most disastrous outbreak of *Atta* can be attributed to the introduction of monoculture systems (Hölldobler and Wilson 1990). Repeated efforts at regeneration and control of *Atta texana* in certain areas of the study area have failed. Low site productivity makes intensive forest silvicultural practices unprofitable. Therefore, our recommendations are that: 1) native vegetation be allowed to grow in the openings created by *Atta texana,* 2) the area be managed for wildlife and limited recreation, 3) *Atta texana* be allowed to continue its biological function of soil improvement and 4) the area be utilized as an important teaching aid for forest pest management and forest entomology laboratories because of the unique nature of the area with regard to the presence of pathogens and insects.

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Pathomorphology of Lepidopteran Chorion during Transgeneration Pathogen Transmission

A.Y. BARANOV AND M.A. GOLOSOVA

Moscow Forest University, Moscow, Russia

ABSTRACT The objectives of this work were (1) to study one of the factors influencing the dynamics of forest phytophagous insects, particularly the transgeneration transmission of entomopathogens, and (2) to study the feasibility of forecasting entomopathogen activity in nature based on their influence on morphological characters of the egg stage. For this purpose we compared the morphological characters of the chorion of intact eggs of forest insects with pathological changes in the chorion of infected insects. Scanning electron microscopy was used to study pathological changes on the surface of the chorion. Practically all changes in the structure of the chorion were of a destructive nature and included closed micropyles or total absence of micropylar canals, closed aeropyle, distortions in the orientation of the rib system, alterations in the polygon structure, and specific "wounds". Data from these studies allowed us to propose a method for estimating the activity of entomopathogens within insect populations by examining the external morphology of eggs. This information would be most important in cultivating insects in the laboratory or when estimating the level of infection caused by entomopathogens in the population dynamics of forest-pest *Lepidoptera.*

FORECASTING PEST POPULATION dynamics is one of the key factors required to determine whether control measures will be necessary to protect agricultural crops. This forecast is based on estimating potential fodder base, weather conditions, natural enemies, and infectious diseases. Each of the above factors is vitally important, and each of them may contribute to the decline of a particular species in the ecosystem.

This is particularly important in the case of entomopathogenic microorganisms. The variety of entomopathogen species and the way they affect host populations vary from almost complete collapse of the population (epizootics), to regulating the abundance of pests for longer durations (i.e., chronic diseases).

The objectives of this study were to determine the factors influencing the dynamics of forest phytophagous insects, particularly the transgenerational transmission of entomopathogens, and to study the possibility of forecasting entomopathogen activity in nature based on their influence on the morphological characters of the chorion in the egg stage. For this purpose, we compared morphological characters and changes in the chorion of eggs of certain forest pests from both healthy and the pathological and infected individuals.

Materials and Methods

Cultivation of Insects. Egg masses of several species of Lepidoptera were collected in nature *(Lymantria dispar, Dendrolimus sibiricus, A. apiformis, P. bucephala, Lymantria monacha, Orgyia antiqua*). Insects from laboratory cultures (*Lymantria salicis, L. dispar, Hyphantria cunea, Bombyx mori*) were cultivated on artificial nutrient media.

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Obtaining Infected Progeny. For all experiments, the later larval stages of the target insects were selected. The larvae were infected by applying entomopathogens to the artificial nutrient media or to the leaf surface. Infected insects were stored in containers or in petri dishes (10 insects per dish) until they pupated.

Activating Latent Viruses and Microsporidioses. We attempted to stress the larvae by altering the air temperature or their feeding, by increasing the density of larvae in their containers and by infecting larvae with pathogens that possessed a long incubation period (e.g., CPV).

Estimating Pathogen Influence. We determined the presence of pathogens and their level of activity by assessing:

- the level of mortality of eggs and larvae.
- the presence of the pathogen in the excrement and meconium of insects.
- the pathological changes in the chorion.

We determined the species of pathogens by using transmission and scanning electron microscopy to observe morphological characters of the microorganisms in the affected tissues of the host.

Electron Microscopy. For studying detailed characteristics of *Lepidoptera* chorion and for identifying pathogens, we used ultrathin sections and negative-stained preparations of purified pathogen microstructures.

We surface sterilized the eggs with Triton-X-100 (Serva) followed by subsequent ultrasonic treatment. The eggs were fixed with 2.5% glutaraldehyde in 0.2 M cacodylate or phosphate buffer (pH 7.2 - 7.4) at 0 to 4°C until eggs settled at the bottom of the vessel (sometimes up to 20 -30 days). We dehydrated the samples by using a series of increasing concentrations of ethanol (from 20% to 100%) followed by 100% acetone. Fixed samples were critical point dried in CO_2 using a Hitachi HCP-2 critical point dryer. Samples of insect eggs with strong chorions (*L. dispar, L. salicis, B. mori*) or dry eggs were not fixed. The samples were partially lyophilized. We used hexamethyldisilazane to prevent shrinking of the samples during air drying (Nation 1983). Dry material was used to prepare fractures of the chorion. Gold, gold and carbon, and platinum shadowing was done in a Jeol JFC-1100 ion sputter. The samples were examined with scanning electron microscopes (Hitachi S 405-A Jeol JSM-50A, S-840, Cambridge Stereo Scan) and in a transmission electron microscope (TEM 200-CX).

Results and Discussion

In classical insect pathology the following characteristics are used to diagnose disease in the egg stage of insects: alteration of color, abnormal size, abnormal shape, inability to hatch, traumas and scars, lack of embryonation, and presence of parasites and infections by microorganisms. The condition of the chorion and its pathological changes were not studied in species of Lepidoptera. The infection of eggs with microorganisms is closely related to the transmission of the pathogens between generations. It appears that the only reason for chorion pathological changes is transmission of entomopathogens from the parent generation to the daughter generation. Such transgenerational transmission of pathogens and symbionts was reported previously by several authors. The transmission of the infection may be either

transspermal (Afzelius et al. 1989, Yefimenko 1989,), or transovarial and transoval (Al-Khalifa 1984, Brooks 1968, Hamm and Young 1974, Kitajima et al. 1985, Nair and Jacob 1985).

Data published previously show that transmission of symbiotic microorganisms in insect females takes place in the early stages of the oocyte formation, in germarium, and that infection by pathogens takes place in vitellarium. In cases of severe infection of germarium, development of oocytes normally does not proceed; therefore, eggs are not laid at all or their quantity decreases significantly.

The influence of entomopathogens on morphological characters of the chorion was studied during transovarial transmission of nuclear polyhedrosis virus and microsporidiosis (*Nosema muscularis* W., *Nosema* sp.) in *H. cunea, Euproctis chrysorrhoea, B. mori, L. dispar, O. antiqua, Mamestra suasa, M. brassicae* and *Agrotis segetum.*

Scanning electron microscopy was used to study pathological changes on the surface of the chorion. Practically all changes were of a destructive nature: closed micropyle or total absence of micropylar canals (Fig. 1), closed aeropyle, distortions in the orientation of the rib system, (Fig. 2), alterations in the polygon structure, and specific "sores." The explanation for these damages may be that the transmission of entomopathogenic viruses (their active form) and protozoa takes place during contact of the follicular epithelium with the oocyte during formation of the chorion. Thus, infection of the cells synthesizing the chorion protein leads to interruption of their functions and, as a result, to formation of distortions on the surface of chorion (Fig. 3).

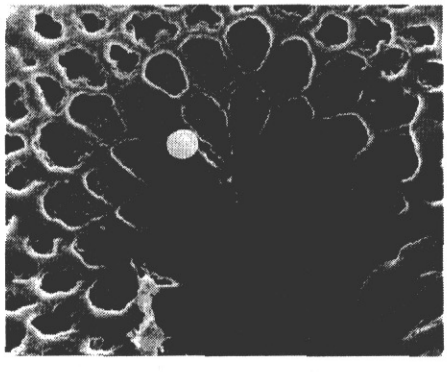


Figure 1. Destroyed micropyle in *Orgyia antiqua* chorion affected by NPV.

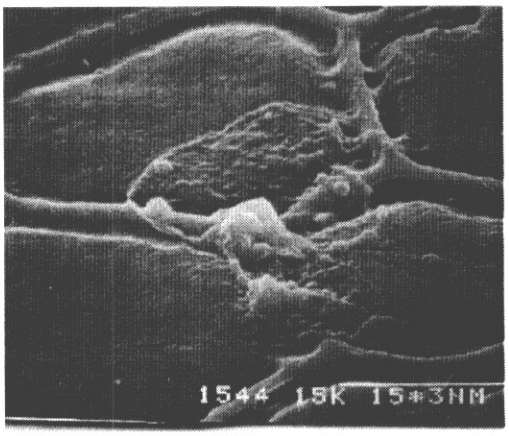


Figure 2. Distortion in the rib system orientation in *Euproctis chrysorrhoea* affected by microsporidia.

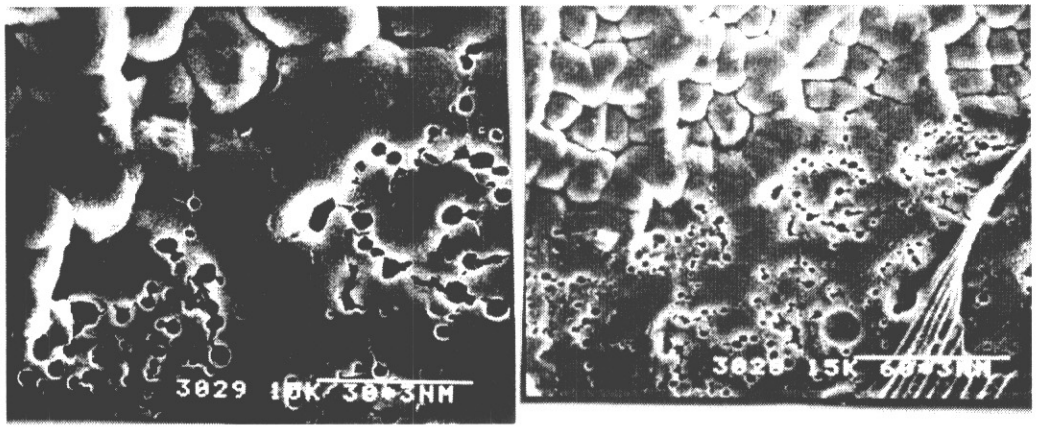


Figure 3. Distortion of chorion of *Bombyx mori* affected by NPV.

Using the scheme of choriogenesis of the silkmoth proposed by Mazur and coworkers (Mazur et al. 1980), we could assume that the most severe changes in practically all chorion structures are associated with heavy infections of the ovariola at III-IV larval stages; the presence of a closed aeropyle may be explained by a comparatively weak influence of the pathogen that leads to formation of "plugs" that did not separate from the top of the aeropyle at the stages Xa – Xd (Fig. 4). To some extent, the above suggestion is confirmed by results obtained during experimental infection of *B. mori* pupae with preparations containing virions of the nuclear polyhedrosis virus.

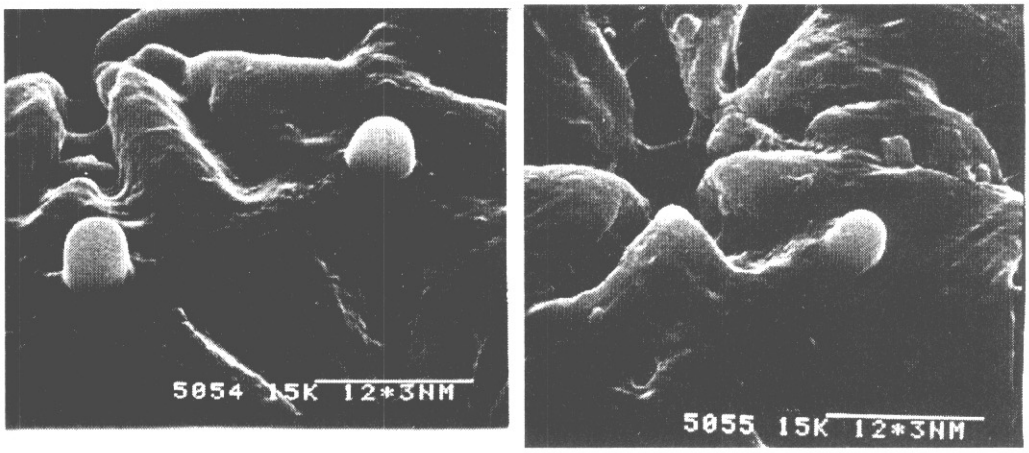


Figure 4. "Plugs" on the aeropyle in *Orgyia antiqua* chorion affected by NPV.

The destructive influence of the pathogen on the follicular epithelium cells and also distortion of vitellogenesis and chorion formation processes were demonstrated (Smith-Johannsen et al. 1986). The pathogen particles were present on the egg surface in 50% of the cases studied, which suggests that there is a coordination between transoval and transovarial pathways of transmission of entomopathogens. The regularity of occurrence that we found may be used to aid in taxonomic descriptions of insects based on the stage of the egg. The data from this experiment allow us to propose a method for identifying the influence of entomopathogens on the egg stage. This is most important in cultivating insects in the laboratory or when estimating the level of infection for use in forecasting the population dynamics of forest-pest Lepidoptera.

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The Effect of Foliage Damage on Transmission of Gypsy Moth Nuclear Polyhedrosis Virus

VINCENT D'AMICO[1,2], JOSEPH S. ELKINTON[1], GREG DWYER[1], RAYMOND B. WILLIS[2] ANDLLIS[1] AND MICHAEL E. MONTGOMERY[2]

[1]Department of Entomology, University of Massachusetts, Amherst MA 01003, USA
[2]NE Research Station, NE Center for Forest Health Research, Hamden CT 06514, USA

ABSTRACT Results of published studies suggest that gypsy moth defoliation may cause elevated tannin levels in trees, which in turn results in reduced larvae mortality caused by the nuclearpolyhedrosis virus (NPV). In a series of field experiments, we tested the hypothesis that gypsy moth defoliation of oaks leads to reduced virus transmission rates. In each of three years, we measured virus transmission rates in gypsy moths feeding on oaks, and tannin levels in oak leaves, with and without experimental defoliation in oak forests with almost no naturally-occurring gypsy moths or virus. In our experiments, we found that there was no effect of gypsy moth defoliation on tannin levels, and consequently virus transmission both in the field and in the lab was unaffected by defoliation. Our results suggest that gypsy moth defoliation does not affect tannin levels early enough in the larval season to have a measurable effect on the interaction between gypsy moth and its nuclear polyhedrosis virus.

NUMEROUS STUDIES HAVE shown that foliage that has been damaged by herbivores changes in ways that can influence herbivore growth or survival (Karban and Myers 1988). One of the more prominent examples of such induced responses is provided by changes in the levels of secondary compounds of oaks following herbivory by the gypsy moth, *Lymantria dispar* (L.). Leaves on red oak (*Quercus rubra*) trees that have experienced significant defoliation contain higher levels of hydrolyzable tannins (Schultz and Baldwin 1982, Rossiter et al. 1988), and these high tannin levels lead to reduced gypsy moth growth rates (Rossiter et al. 1988). More recently, however, this classic story has been complicated by evidence that tannins have an effect on disease transmission by reducing infection rates of the gypsy moth nucleopolyhedrosis virus (NPV), which is consumed with oak foliage (Keating et al. 1988).

Because defoliation can affect oak tannin levels, and oak tannin levels can affect virus transmission, the effect of gypsy moth defoliation on virus transmission has been cited as evidence for a tritrophic interaction among gypsy moths, oaks, and virus (Schultz and Keating 1991). Such an effect would be especially important in gypsy moth population dynamics because the virus has been the most factor causing the collapse of gypsy moth outbreak populations (Elkinton and Liebhold 1990). If defoliation does reduce virus transmission, however, the induced foliage changes in oak could effectively prevent the virus from causing gypsy moth populations to collapse. The possibility of this kind of tritrophic interaction is therefore of great significance for gypsy moth population dynamics. The evidence for this effect is based entirely on either lab data or field observations, therefore the

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objective of our research was to conduct studies to elucidate the effect of gypsy moth defoliation of oaks on the transmission of virus within gypsy moth populations in the field.

Materials and Methods

In our field experiments initited in 1993, we mimicked the natural process virus transmission by placing infected first-instar larvae on oak foliage inside mesh bags along with uninfected third instar larvae (which we refer to as test larvae). After a week, the test larvae were removed and placed in individual cups of artificial diet in the lab. Because the virus requires about 10-14 days to kill larvae in the field, this protocol ensures that only one round of virus transmission occurs. Test larvae that died were autopsied under a light microscope to verify the presence of the virus (Woods and Elkinton 1987). In previous work, we demonstrated that transmission in these experiments is only slightly affected by rainfall (D'Amico and Elkinton 1995), and that the mesh bags have no measurable effect on the concentration of phenolics or hydrolyzable tannins in the confined foliage (Rossiter et al. 1988, Hunter and Schultz 1993).

Study Site. We used mature black oak trees (*Quercus velutina*) in a forest composed of black oak, white oak (*Quercus alba*) and pitch pine (*Pinus rigida*), located on grounds of the Otis Air National Guard Base, Falmouth, MA, USA. In 1994 and 1995, we used 4-6m high red oak saplings in a forest composed primarily of red oak *(Q. rubra*) and red maple (*Acer rubrum*) located in the Cadwell Memorial Forest, Pelham, MA. Neither forest had experienced significant defoliation since gypsy moth outbreaks in the early to mid 1980's. (Otis ANGB - 1986, Cadwell - 1981). In 1993, the trees that we used were part of the canopy, while in 1994 and 1995, the trees that we used were typically in full sunlight along clearings or next to a logging road.

Manipulating Levels of Defoliation. The experiments that we report here consisted of manipulating the extent and timing of defoliation experienced by the trees on which the larvae fed, in order to ascertain how defoliation affects virus transmission. 1993 we used black oaks, for our study while in 1994 and 1995 we used red oak, which is the tree species on which most previous research work has been reported. The timing of our experiments varied slightly from year to year, although all of the experiments took place at that time of the season when virus transmission occurs in natural populations of gypsy moth larvae (see Table 1 for dates). In all of these experiments, we used test larvae that were in the same larval stage as larvae in adjacent natural populations. (1993 - 3rd instars; 1994 and 1995 2nd instars). New trees were used in each year; we were only concerned with quantifying within-season effects.

Because larvae must consume the virus on foliage in order to become infected, defoliation is an intrinsic part of the transmission process. In order to manipulate defoliation levels, we therefore imposed additional defoliation above and beyond what occurred during virus transmission. To accomplish this, in each experiment we established a "damaged" treatment, and an "undamaged" treatment, such that trees in the damaged treatment were exposed to defoliation not just from those larvae that were used to measure virus transmission, but from larvae that were added to effect defoliation (we refer to these as defoliating larvae). The difference in virus transmission rates between the two treatments is a measure of the effects of defoliation on transmission.

The most important differences among experiments were in the extent of defoliation and in the timing of defoliation relative to transmission. In 1993, we infliected defoliation only at the level of the individual branch (about 50% defoliation *within* bags). In 1994 we defoliated both at the level of the individual branch and at the level of the entire tree (30-50% defoliation *inside and outside* the virus-treatment bags). Finally, in 1995 we caused defoliation only at the level of the entire tree (30-50% of tree defoliated *outside* the virus-treatment bags). Hereafter we refer to these experiments as the branch-level, branch- and tree-level, and tree-level experiments, respectively. In the first two experiments, we inflicted defoliation only for the two days before transmission began, but in the third experiment we began defoliation five days before transmission and continued throughout the transmission period. Because defoliation occurred over a longer period in the third year than in the second year, the overall effect was that we increased overall defoliation from experiment to experiment. In other words, as we accumulated negative evidence for any effects of defoliation on transmission, we inflicted increasingly higher levels of defoliation in an attempt to demonstrate a positive effect.

To effect defoliation at the level of individual branches, we added larvae only to the virus transmission bags. Specifically, we added 40 fourth instar larvae to the bags on the damage treatment trees after the initially infected larvae had died. These larvae were removed and discarded after two days, and then test larvae were added to the bags. Because larvae do not avoid virus-contaminated oak foliage (D'Amico unpublished data), the defoliating larvae did not affect the density of virus in bags in the damage treatment. To impose defoliation at the level of the entire tree, we added additional bags that contained only healthy larvae to the trees in the damage treatment (40 fourth instars, no virus, no transmission larvae). To analyze the data from these experiments, we performed one-way ANOVAs on the arc-sine square-root transformed virus mortality.

Laboratory Bioassays. In order to compare better our results to the original published work, which demonstrated the effects of tannins on virus bioassays in the laboratory, we performed a bioassay in conjunction with both the tree-level and branch- and tree-level defoliation experimenst. At the end of the period of transmission in these defoliation experiments, we took samples of some of the unconsumed foliage from the virus-test bags and used them to measure larval infection rates with known doses. First, we surface-sterilized the foliage samples from the two treatments (rinsing thoroughly with distilled water after the bleach treatment), and then added 5 ml of virus (10^6 occlusion bodies per ml) to small (8mm diam) disks from these samples. Each disk was then fed to an uninfected, starved, third-instar larva. To ensure the efficacy of the bleach treatment, we also fed control larvae disks with 5 ml of distilled water instead of bleach. To ensure that all larvae received the same total amount of virus, any larva that did not consume the entire leaf disk after 36 hrs was discarded. The remaining larvae were reared on artificial diet for two weeks to assess levels of infection (Bell et al. 1981). We also assayed foliage from trees from outside of each experimental area which had not experienced defoliation. Finally, in the branch- and tree-level experiments, we looked for an extremely short-term effect of defoliation on oak foliage chemistry by assaying leaves from trees from outside the experiment that we damaged (cut in half with a scissors) 8 h before the assay.

Results

Manipulating Defoliation. No significant differences were observed between virus-caused larval mortality in the damage and no-damage treatments in any field experiment, whether defoliation occurred at the branch level, the tree level, or at both levels. Similarly, there was no effect of larval density on virus mortality in the larval density experiment, and there was no larval density times tree interaction. The results of statistical tests and the mean mortality for each experiment are given in Table 1. In several of these experiments, there was a trend (NS) toward increasing virus mortality with increasing insect density or increasing foliage damage. This is opposite of what we had anticipated since higher densities of insects cause greater levels of defoliation therefore greater induced chemistry effects, which should result in lower virus mortality.

Laboratory Bioassays. In the leaf disk bioassays, there were no significant differences in mean mortality from virus between treatments. Mean mortality and results of statistical tests are again summarized in Table 1.

Table 1. Summary of field experiments and laboratory bioassays and results. Within an experiment, means followed by the same letter are not significantly different (P > 0.05). HT = hydrolyzable tannins, TP = total phenolics

Date	Tree species	Description of leaf treatment	Fraction of larvae dying (SE)		Differences in mortality between treatments detected by ANOVA?		Differences in tannin levels?
			Field test	Leaf assay	Field test	Leaf assay	
June 1993	*Quercus velutina*	previously damaged not previously damaged	0.48 (0.05) 0.44 (0.04)		no; $F_{1,36} = 0.21$; $P = 0.65$	-	-
May 1994	*Q. rubra*	previously damaged not previously damaged foliage cut with scissors foliage cut 8 h prior	0.92 (0.02) 0.84 (0.03) - -	0.89 (0.03) 0.90 (0.03) 0.91 (0.01) 0.93 (0.02)	no; $F_{1,28} = 3.45$; $P = 0.06$	no; $F_{3,28} = 0.17$, $P = 0.92$	HT; no, $P = 0.09$ TP; no, $P = 0.48$
May 1995	*Q. rubra*	concurrently damaged not concurrently damaged induction control	0.60 (0.04) 0.64 (0.04) -	0.48 (0.03) 0.52 (0.04) 0.47 (0.02)	no; $F_{1,28} = 0.55$; $P = 0.47$	no; $F_{2,27} = 0.56$, $P = 0.57$	HT; no, $P = 0.27$ TP; no, $P = 0.22$
July 1994	*Q. rubra*	10 larvae/80 leaves 20 larvae/80 leaves 40 larvae/80 leaves 80 larvae/80 leaves 160 larvae/80 leaves	0.33 (0.08) 0.32 (0.09) 0.35 (0.05) 0.46 (0.04) 0.46 (0.06)	-	no treatment effect; $F_{1,29} = 3.78$, $P = 0.06$ no tree effect; $F_{5,29} = 0.22$; $P = 0.95$ no interaction[a]; $F_{5,29} = 2.34$ P = 0.08	-	-

[a] Because the interaction effect was not significant, to test for main effects the ANCOVA was redone with a model with no interaction term.

Discussion

Our results suggest that tannin levels are not affected by defoliation at the time when virus transmission occurs in natural gypsy moth populations. Apparently because of this lack of tannin induction, our virus transmission experiments did not show any effects of defoliation on virus-caused mortality, irrespective of the timing or intensity of defoliation,

nor was there any effect of defoliation on virus mortality in our laboratory bioassays. In fact, we were only able to demonstrate a significant effect of defoliation on tannin levels at a site that was defoliated naturally in July. Even in that case, it is not certain whether gypsy moth larvae induced higher tannin levels or simply chose to feed upon hosts with higher levels of constitutive tannin. It is likely also that larval to larvae virus transmission had ceased by the time elevated levels of tannins occurred because larvae were in the process of pupating at the time.

We emphasize that our protocols were designed to eliminate mechanisms that might obscure or counteract induced effects. First, although we are confident that the defoliating larvae did not concentrate virus in the experiments that included branch-level defoliation because larvae do not avoid virus-contaminated foliage, in the tree-wide defoliation experiment and the bioassays any such avoidance effects would be irrelevant. Secondly, although there is uncertainty in the literature as to whether induction effects will occur at the level of the individual branch or the entire tree (Hunter and Schultz 1993, Rossiter et al. 1988), by manipulating defoliation at both levels we allowed for either effect, or both. Finally, because our experiments were performed in synchrony with naturally-occurring gypsy moth populations, in adjacent areas, we believe that they accurately mimicked natural virus transmission processes.

We do not question the finding that tree species affect the susceptibility of gypsy moth larvae to viral infection (Keating and Yendol 1987), or that foliar tannin content may explain differences in virus transmission among tree species. However, our results suggest that the evidence for induction of tannins in oaks is equivocal, especially in the early part of the season (May and June) when most virus transmission occurs in gypsy moth populations. In fact, the results of previous studies have similarly reported low tannin levels in the early part of the gypsy moth season. For example Schultz and Baldwin (1982) and Hunter and Schultz (1995) reported high levels of tannins in July but not in mid-June, when most larval feeding and development occurs.

We realize that our data do not bear on the effects of defoliation between (larval seasons). Although there is a suggestion of such an effect in previous work (Hunter and Schultz 1993), our previous experience with virus transmission in this system (Woods and Elkinton 1987) leads us to suspect that such complex effects do not occur, because the first round of transmission in the gypsy moth larval season occurs on egg masses rather than on foliage.

Our finding that larval density also has no effect on transmission rates is relevant to our earlier work on mathematical models of disease transmission (Dwyer and Elkinton 1993, D'Amico et al. 1996). That is, classical mathematical disease models assume that disease transmission is a linear function of the densities of both host and pathogen. In previous experiments, we demonstrated that this assumption was incorrect, but it was not clear whether the nonlinearity was associated with larval density, virus density, or both. The larval density treatment that we report here strongly suggests that the nonlinearity is not due to host density, because transmission is not affected by larval (i.e. host) density.

In summary, gypsy moths may induce tannin responses in oaks under some conditions, but both our results and the results of others suggest that those conditions do occur at the time of year when most virus transmission takes place. We therefore suspect that

tritrophic interactions among gypsy moths, nuclear polyhedrosis virus, and oak foliage are unlikely.

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Microsporidia Affecting Forest Lepidoptera

J.V. MADDOX[1], M.L. MCMANUS[2] AND L.F. SOLTER[1]

[1]Illinois Natural History Survey and Illinois Agricultural Experiment Station. 607 E. Peabody Dr., Champaign, IL., USA
[2]USDA Forest Service, 51 Mill Pond Road, Hamden CT, USA

ABSTRACT Forest Lepidoptera are affected by many species of microsporidia which are often important naturally-occurring biological control agents. Although they do not often cause dramatic epizootics, microsporidia interact with their Lepidopteran hosts in a variety of ways. In order to illustrate some of the basic differences that exist among species of microsporidia we discuss the characteristics of three groups of microsporidia: *Nosema*, *Vairimorpha*, and *Endoreticulatus*. Species in the *Nosema* group are moderately pathogenic and are efficiently transmitted, both horizontally and vertically. Vertical transmission occurs usually by transovarial transmission. Species in the *Vairimorpha* group are very pathogenic, are less efficiently transmitted, and are not usually transmitted transovarially. Species in the *Endoreticulatus* group have low pathogenicity, infect only the midgut cells and are transmitted only via the feces. Microsporidia interact both directly and indirectly with most other natural enemies and have an important effect on the population cycles of many species of forest Lepidoptera.

ALTHOUGH MANY SPECIES of microsporidia affect forest Lepidoptera and are often important biological mortality factors, they do not cause dramatic and visible epizootics and frequently go undetected. Microsporidia are important natural enemies of many species of insects but have little if any potential for use as true microbial insecticides (Canning, 1982). Following a brief general introduction to the microsporidia we discuss 1) reports of microsporidia from species of forest Lepidoptera, 2) characteristics of three genera of microsporidia representing different "types" of host/pathogen relationships in forest Lepidoptera, 3) interactions with other biological control agents, and 4) how microsporidia affect forest Lepidoptera.

What are Microsporidia? Microsporidia are unicellular parasitic organisms formerly in the Phylum Protozoa. The Phylum Microspora was erected in 1969 to accommodate this unique group of organisms (Sprague, 1969, 1977). Although the largest number of microsporidian species infect arthropods (especially insects), most animal phyla contain at least a few species that are infected by microsporidia. Microsporidia are small intracellular parasites with an environmentally resistant spore stage characterized internally by the presence of a polar tube and one or more nuclei. Infection occurs when a susceptible insect ingests microsporidian spores. In the gut lumen of a susceptible insect host, spores extrude their hollow polar tube and the sporoplasm, consisting of the cytoplasm, nuclei and other organelles, is injected into the midgut cells of the insect. Extrusion of the spore is caused by specific chemical and environmental conditions in the gut lumen. Injection of the sporoplasm initiates the life cycle of the microsporidium and, depending on the microsporidian species, different tissues may be infected and different types of spores produced. Some species of microsporidia produce chronic infections while others may be very pathogenic and kill the host. In addition to horizontal transmission which occurs by ingestion of spores, many species of microsporidia are transmitted vertically (generation to

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generation) from an infected adult female to her offspring, either on the egg surface or within the egg. The general characteristics of microsporidia are discussed in several excellent reviews (Vavra, 1976a, 1976b).

The extent of microsporidia among species of forest Lepidoptera. Microsporidia are probably far more common among species of forest Lepidoptera than published reports indicate. Because microsporidia do not cause dramatic epizootics such as those caused by fungi and viruses, in which conspicuously large numbers of dead individuals occur, microsporidian infections often go unnoticed and their role in the population dynamics of insects is often not recognized. Nevertheless, microsporidia have been reported as important mortality factors for many species of forest Lepidoptera (Table 1). Based on the number of different microsporidia that have been isolated and/or described from the gypsy moth, *Lymantria dispar* L. (Table 2) we suggest that microsporidia might be much more prevalent in forest Lepidoptera populations than is reported in the literature. A more thorough and comprehensive paper on the systematics of microsporidia isolated from gypsy moth populations in Europe is included in this proceedings (Weiser, 1997). Readers should consult Weiser's paper for more details about the taxonomy of gypsy moth microsporidia. Gypsy moths collected from many areas of Europe have been extensively examined for the presence of insect pathogens. We suggest that many additional species of microsporidia would be recovered from other species of forest Lepidoptera if these species were more closely scrutinized.

Table 1. A partial list of forest insects from which microsporidia have been reported

Common name	Specific name	Reference
Browntail moth	*Euproctis chrysorrhoea*	Puruini and Weiser (1975)
Eastern tent caterpillar	*Malacosoma americanum*	
Fall webworm	*Hyphantria cunea*	Weiser and Veber (1975)
		Nordin and Maddox (1974)
Forest tent caterpillar	*Malacosoma disstria*	Thomson (1959)
Green tortrix	*Tortrix viridana*	Lipa (1976), Franz and Huger (1971)
Larch sawfly	*Pristiphora erichsoni*	Smirnoff (1966), Quednau (1968)
Large aspen tortrix	*Choristoneura conflictana*	Wilson and Burke (1971)
Spruce budworm	*Choristoneura fumiferana*	Thompson (1958)
Uglynest caterpillar	*Archips cerasivoranus*	Wilson and Burke (1978)
Winter moth	*Operophtera brumata*	Canning et al. (1983)

Characteristics of microsporidian genera representing three different types microsporidia/forest Lepidoptera associations. We believe that by separating the microsporidia into the three groups (*Nosema*, *Vairimorpha*, and *Endoreticulatus*), we can better illustrate some of the basic differences that exist among species of microsporidia isolated from forest Lepidoptera and demonstrate how microsporidia may interact with their hosts. Nevertheless we recognize that this separation into three groups undoubtedly represents an oversimplification of the very complex associations that often exist among microsporidia and their hosts. Some described species do not necessarily conform to all of the general features that we ascribe to each group, although they share some characteristics of that group. In addition, we anticipate that some of the species of microsporidia yet to be

described from forest Lepidoptera will not conform to any of the three groups that we have identified.

Table 2. Microsporidia isolated from the gypsy moth, *Lymantria dispar*, and the countries where infected gypsy moths were collected

Microsporidian species	Country	Reference
Nosema lymantriae	Czechoslovakia	Weiser, 1957a
Nosema lymantriae	Yugoslavia	Sidor, 1979
Nosema muscularis	Czechoslovakia	Weiser, 1957
Nosema muscularis	Spain	Romanyk, 1966
Nosema muscularis	USSR, Ukraine	Zelinskaya, 1981
Nosema serbica	Yugoslavia	Weiser, 1964
Nosema serbica	USSR, Ukraine	Zelinskaya, 1981
Thelohania disparis	Not given	Timofejeva, 1956
Thelohania similis	Czechoslovakia	Weiser, 1957a
Vavraia schubergi	Czechoslovakia	Weiser, 1964
Vavraia schubergi	USSR, Ukraine	Zelinskaya, 1981
Nosema sp.	Portugal	Cabral, 1977

Nosema group. A large percentage of the microsporidia reported and/or described from forest Lepidoptera are in the genus *Nosema*. This genus contains more species of microsporidia than any other microsporidian genus, but phylogenetic studies using rRNA sequence data have shown that some *Nosema* species from insect hosts other than Lepidoptera are phylogenetically very distant to the *Nosema* described from Lepidoptera (Baker et al. 1994). These same studies also indicate that *Nosema* species isolated from Lepidoptera are phylogenetically similar.

The genus *Nosema* is characterized by the formation of two spores from each sporont (the basic pre-spore developmental form). These spores are formed singularly and are not enclosed within an envelope. There is only one type of infectious or environmental spore and this spore contains two nuclei. The life cycle is one of the more simple and straightforward among microsporidian genera. Most host tissues are infected (midgut, salivary glands, Malpighian tubules, fat body, gonads, muscles) and these tissues are usually infected sequentially. As indicated in Figure 1, environmental spores are released from infected living hosts in the larval silk and/or frass. Spores may also be released into the environment when an infected host dies and the body disintegrates allowing spores to escape from infected tissues.

Species of *Nosema* are moderately pathogenic; relatively few spores are necessary to initiate an infection, but a large spore dose is typically necessary to produce larval mortality. Figure 1 illustrates how *Nosema*-type microsporidia are transmitted and at what stage mortality occurs. Infected larvae may develop into infected adults and infected females usually transmit microsporidian infections to their progeny. Transmission is both horizontal (from one larva to another) and vertical (generally from an infected female to her offspring via the egg). Transovarially infected larvae (microsporidium infects embryos within the egg) often exhibit a very high mortality rate, much higher than larvae which are infected by ingesting spores. Infectious spores are present in feces and/or silk of live larvae and are also released into the environment when infected larvae die. Infectious spores may overwinter in

the larval habitat (crevices in the bark of trees or in silken mats containing larval or pupal remains, but it is likely that most microsporidia of the *Nosema*-type survive from one season to the next in infected hosts.

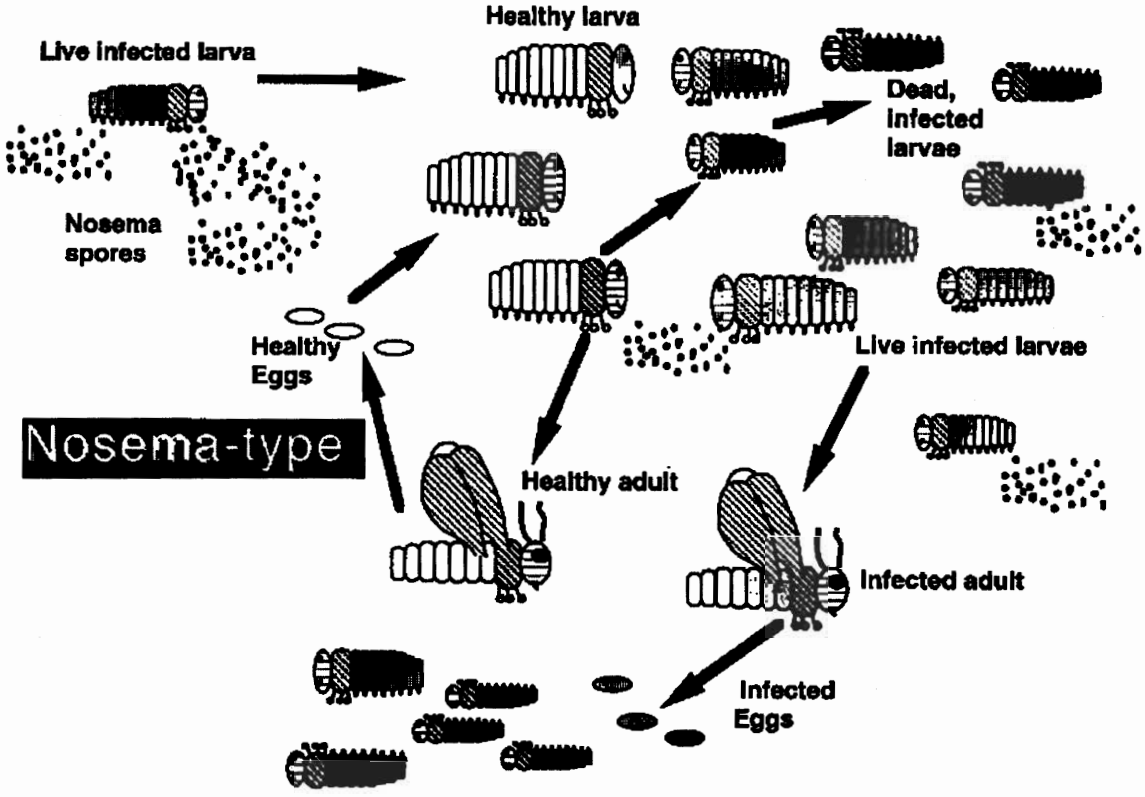


Figure 1. Diagrammatic representation of the interactions between *Nosema*-type microsporidia and their hosts. Healthy larvae become infected by ingesting microsporidian spores which are present in the feces and/or silk of infected individuals. Larvae infected by ingesting spores may die from the infection if they consume many spores at an early larval stage, but many infected larvae can develop into infected adults. Mortality may occur during pupation and emergence as adults. Much of the mortality caused by *Nosema*-type microsporidia occurs in the in the transovarially infected offspring of infected females. Transovarially-infected larvae may be heavily infected and die in early larval stadia.

Sublethal effects have been little studied, but unquestionably have a great effect on populations of many species of forest Lepidoptera (Gaugler and Brooks, 1975; Wilson, 1980). Infected larvae develop more slowly than healthy larvae which increases the time period during which they are vulnerable to additional biotic and abiotic mortality factors; behavior (movement, phototrophic responses, etc.) of both larval and adult hosts may be affected by infection. Effects on mating efficiency, attributed to behavioral differences, pheromone production, sperm production and transfer, may also occur. The total number of eggs laid, as well as the pattern of egg laying, may be affected.

Because *Nosema*-type microsporidia affect all developmental stages of their hosts, they may have an important dampening effect on their host populations; yet, because they do

not cause widespread and extraordinary mortality in any one stage, they often are not recognized as an important component of a pest's natural enemy complex. Unlike many other pathogens, the density dependent effect of microsporidia may occur in the generation following maximum horizontal transmission of the microsporidium; this is because the most significant mortality occurs in the progeny of infected females.

Vairimorpha group. Microsporidian species in the genus *Vairimorpha* are phylogenetically closely related to lepidopteran microsporidia in the genus *Nosema*, but the life cycle and host/pathogen relationships of most *Vairimorpha* species are quite different from that of most *Nosema* species (Baker et al. 1994). All species in the genus *Vairimorpha* produce two types of environmental spores. In addition to the *Nosema*-type life cycle described above, microsporidia in this genus produce an additional type of spore which contains one nucleus and is enclosed in an envelope containing 8 spores. These mononucleated octospores are probably haploid and their role in horizontal transmission is not understood.

Species in the *Vairimorpha* group are usually more pathogenic than species in either of the two other groups. Very few spores are required to initiate infections, and although the length of time required for larval mortality to occur is greatly affected by spore dose and larval age at the time they are infected, most infected individuals die as late instar larvae or prepupae; few infected larvae develop into infected adults (Maddox et al., 1981). Figure 2 illustrates how *Vairimorpha*-type microsporidia are transmitted and at what stages mortality occurs. Spores may or may not be present in silk and/or feces of infected larvae, but even when present in feces and silk, spores are less abundant than those produced in *Nosema* infected individuals. The fat body is usually the primary site of infection, and while other tissues may eventually become infected, the intensity of the infection is usually greatest in the fat body. Thus, *Vairimorpha* spores are not dispersed into the environment throughout the developmental stages of infected hosts, as is the case with *Nosema*-type infections. Rather, environmental spores are released when the host dies. Consequently, horizontal transmission is less effective in this group of microsporidia because healthy larvae are not readily exposed to environmental spores until after infected larvae die and release spores. Vertical transmission may occur, but if it occurs, the frequency of occurrence and the percent of eggs infected is usually relatively low. Thus the phenomenon whereby high rates of mortality are produced in the progeny of infected females is much less important than for the *Nosema*-type infections.

The sublethal effects, so important in the *Nosema*-type infections, have not been well documented for *Vairimorpha* species and although undoubtedly important, are probably less important for *Vairimorpha*-type microsporidia than for the *Nosema*-type microsporidia because the *Vairimorpha* species are more pathogenic.

Even though the *Vairimorpha*-group of microsporidia is more pathogenic than the *Nosema*-group, dramatic epizootics such as those observed for nuclear polyhedrosis viruses (NPV) are seldom reported. Possibly this can be explained by the behavior and gross pathology of virus-infected larvae; shortly after death, larvae literally disintegrate and polyhedra are disseminated to the foliage and other tree structures where they can be transmitted to healthy individuals. *Vairimorpha*-type microsporidia also produce large numbers of infectious propagules but the integument of dead, infected larvae does not rupture and consequently broad dissemination of infective spores does not occur. This is probably one of the major reasons *Vairimorpha* species seldom cause epizootics.

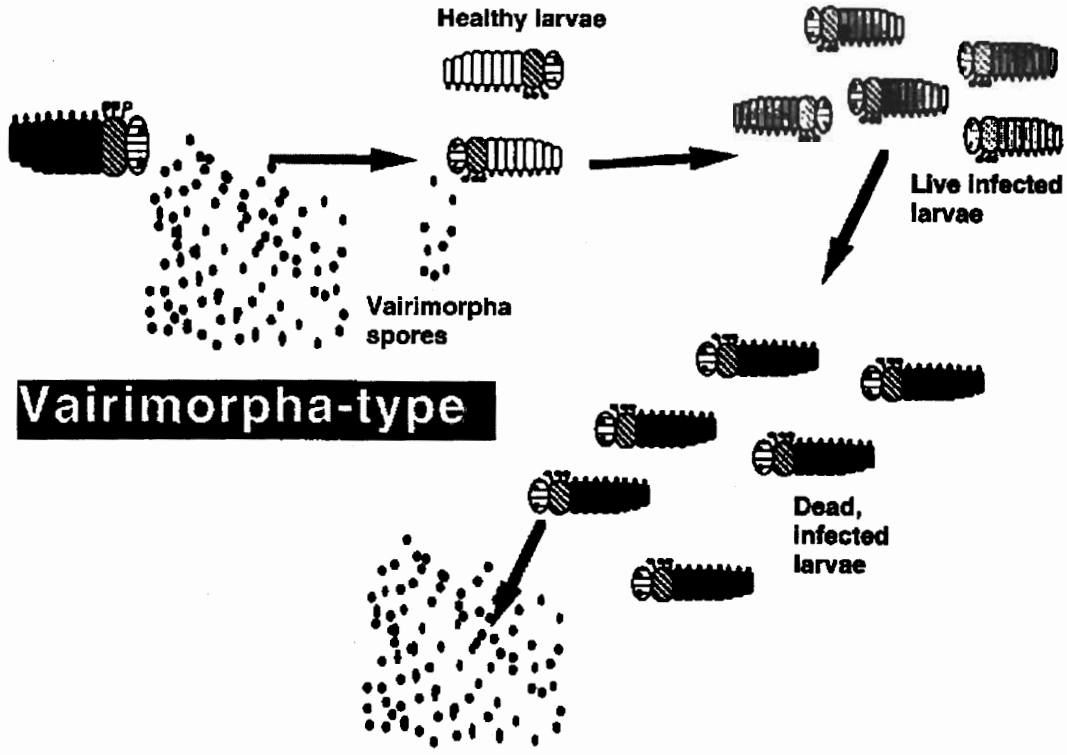


Figure 2. Diagrammatic representation of the interactions between *Vairimorpha*-type microsporidia and their hosts. Healthy larvae become infected by ingesting microsporidian spores which are released when infected larvae die and disintegrate. Spores are seldom present in the feces or silk of infected larvae. Most *Vairimorpha*-type microsporidia are very pathogenic; individuals infected during the larval stage seldom develop into infected adults. These infected individuals usually die as larvae.

Endoreticulatus group. Microsporidia in the *Endoreticulatus* group are very different from microsporidia in the *Nosema* and *Vairimorpha* groups. These differences include their phylogenetic relationships to the other two groups, life cycle, low pathogenicity, and confinement of infection to the midgut epithelial cells.

Species in the *Endoreticulatus* group produce only one type of environmental spore which contains a single nucleus. Spores are enclosed within an envelope which contains 16, 32, or more spores. *Endoreticulatus schubergi*, the species most often encountered in larval populations of forest Lepidoptera, infects only midgut epithelial cells, produces chronic infections, and is not transovarially transmitted. However, it may be transmitted on the egg surface (transovum transmission). This type of vertical transmission usually results in lower percentages of infected larvae than does vertical transmission within the egg (transovarial transmission). Figure 3 illustrates how *Endoreticulatus* -type microsporidia are transmitted and at what stages mortality occurs.

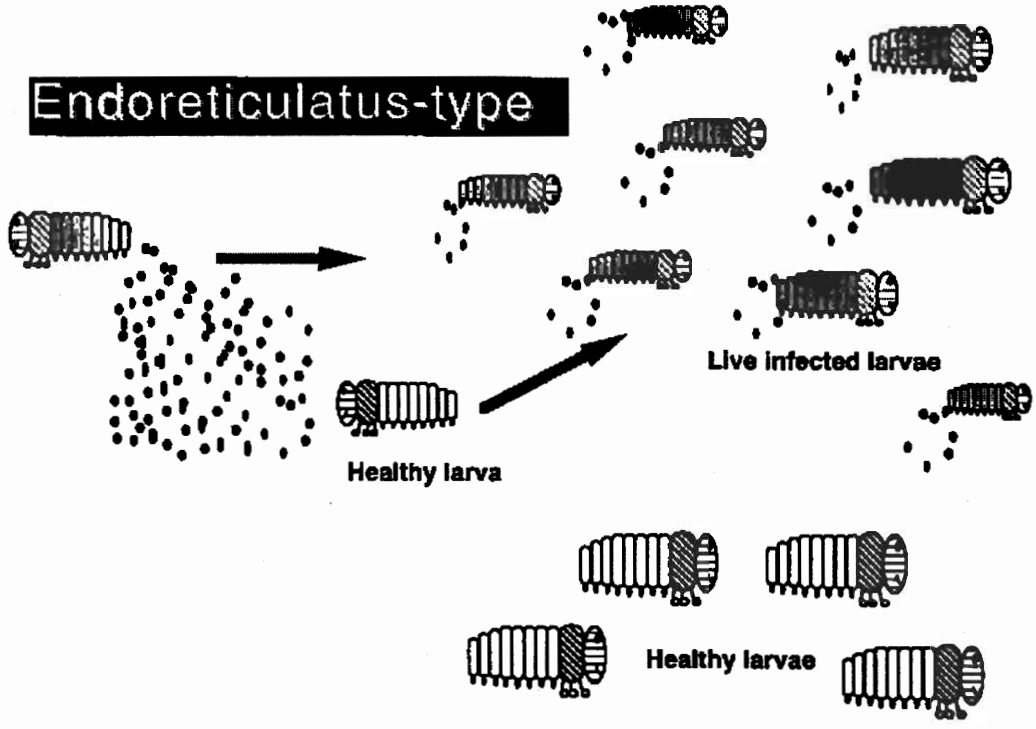


Figure 3. Diagrammatic representation of the interactions between *Endoreticulatus*-type microsporidia and their hosts. Healthy larvae become infected by ingesting microsporidian spores which are present in the feces of infected individuals. The mortality rate is very low in individuals infected with *Endoreticulatus*-type microsporidia. Infected larvae develop more slowly than healthy larvae and produce feces contaminated with spores throughout their larval development.

Endoreticulatus species are frequently recovered from many species of forest Lepidoptera but because of the chronic nature of infection, the impact this group has on insect populations is largely restricted to sublethal effects.

Interactions with other natural enemies. Microsporidia coexist with an array of other natural enemies including parasites, predators and other insect pathogens. Brooks (1993) listed eight different types of interactions that may occur within the host/parasitoid/pathogen system. The following five may apply to microsporidian infections of forest Lepidoptera; premature death of the host, diseased host is not ovipositionally attractive, host is altered nutritionally or physiologically, and direct infection of parasitoids. Parasitoids may also transmit microsporidian infections from diseased hosts to healthy hosts.

If the insect host dies from a microsporidian infection before the parasitoid completes development, the parasitoid usually dies. This has been documented for several species of Lepidoptera infected with microsporidia (Laigo and Paschke, 1968; Cossentine and Lewis, 1988) but not specifically for forest Lepidoptera infected with microsporidia. It is likely that this is also a common phenomenon in populations of forest Lepidoptera.

Insect hosts infected with microsporidia may be unattractive for oviposition by insect parasites for a variety of reasons. For example, sublethal effects of microsporidian infections frequently inhibit development and alter behavioral patterns of the infected host. Because parasitoid females prefer a host of a specific size or a specific larval stadium, any change in the age structure of the host population undoubtedly affects the proportion of the host population attacked by female parasitoids.

Parasitoids may be unable to complete development inside a microsporidian infected insect host because the indigestible microsporidian spores, present in infected host tissues, accumulate in the intestines of immature parasitoids. When this occurs the parasitoid larvae are unable to absorb sufficient nourishment and often die. There are many published examples of this type of interaction (Brooks, 1993; Cossentine and Lewis, 1988; Thomson, 1958).

Parasitoids may be directly infected by the microsporidia of their hosts and in many cases these infections cause a high rate of mortality in the parasitoids (Siegel et al., 1986; Brooks, 1973; Brooks, 1993). Although this has not been documented for any species of forest Lepidoptera, it is likely that this type of interaction occurs.

Parasitoids may also act as vectors of microsporidia. This is probably an important means of dispersing microsporidia both within and between insect populations and has been documented for lepidopteran microsporidia, but not for microsporidia of forest Lepidoptera (Siegel et al., 1986; Brooks, 1993).

Microsporidia also interact with other pathogens. It is often possible to isolate several species of insect pathogens from field populations of insects. Weiser (1987) presented information demonstrating that, over a period of years in a building gypsy moth population, microsporidia appear early in gradation followed by high prevalences of NPV and subsequent collapse of the gypsy moth population. Microsporidia could stimulate the onset of the NPV and/or decrease the rate at which the gypsy moth population increases. It has been suggested that microsporidia increase the transmission efficiency of the NPV, although the specific mechanisms by which this occurs have not been elucidated.

Many of the host/parasitoid/pathogen/microsporidian interactions that have been observed in other insect species undoubtedly occur in forest Lepidoptera. That they have not been observed reflects upon the paucity of research devoted to these topics.

How microsporidia affect forest Lepidoptera. We have discussed at a conceptual level how each of the three groups of microsporidia might affect populations of forest Lepidoptera. Unfortunately, we have relatively few extensive data sets that document the prevalence of microsporidian infections in Forest Lepidoptera over time (seasons, years, etc.) and that relate these infections to the population densities of the host (Maddox, 1987) Relatively long term data sets exist for *Nosema lymantriae* in the gypsy moth, *L. dispar* (see references in Table 1) *Nosema fumiferanae* in the spruce budworm *Choristoneura fumiferana*, (Wilson, 1973), several species of microsporidia in the winter moth, *Operophtera brumata* (Canning and Wigley, 1983), and *Nosema tortricis* in the green tortrix, *Tortrix viridana* (Lipa, 1976; Franz and Huger, 1971). Anderson and May (1980) also presented theoretical evidence that insect pathogens, including microsporidia, are responsible for the population cycles of many forest insects. Nevertheless, our field observations on most species of the microsporidia of forest Lepidoptera consist of one or two collections each year, often unaccompanied with meaningful estimates of the density of host populations. We

must accumulate better long-term data sets to fully evaluate the extent to which microsporidia affect many species of forest Lepidoptera.

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The Effects of Artificial Infections with Microsporidia on Gypsy Moth (*Lymantria dispar*) and Nun Moth (*Lymantria monacha*) - First Results

ANDREAS LINDE, CLAUDIA GENTHE AND JENS LACKER

Fachhochschule Eberswalde, Alfred-Moeller-Str. 1, 16225 Eberswalde, Germany

ABSTRACT Seven microsporidian isolates from different parts of Europe were fed to laboratory reared larvae of the gypsy moth (*Lymantria dispar*) and nun moth (*Lymantria monacha*). Infections with all isolates were achieved in gypsy moth while in nun moth, six isolates produced detectable infections. The percentage of infected larvae of both species varied significantly, indicating that differences exist in the susceptibility of the larvae to the different isolates. The pathology of infections in German gypsy moth and nun moth does not differ significantly from observations recorded in North American gypsy moths. The isolates have a diverse influence on the larval and pupal mortality. Sublethal infections with the German *Microsporidium* isolate have a significant influence on the development and pupal weight of gypsy moths.

THE GYPSY MOTH (*Lymantria dispar* L.) and nun moth (*Lymantria monacha* L.) are economically and ecologically important defoliators of deciduous and coniferous trees in European forests. Outbreaks of both insects seem to occur periodically (Schwerdtfeger 1981). Pathogens and microparasites like microsporidia are obviously involved in the generation of insect population cycles (Anderson and May 1980). Depending on the nature of the parasite involved, this interaction can also result in maintaining insect populations at a low density level, far beneath the damage threshold (Hochberg 1989). Microsporidia are present in many forest defoliating populations and are suspected to play an important role in the natural regulation of insect populations (Wilson 1981, McManus et al. 1989).

The role of microsporidia in the regulation of European gypsy moth populations is not clearly understood. Zelinskaya (1980) describes microsporidia as an important mortality factor in Russian gypsy moth populations. In addition to this, fertility and larval development are influenced by these parasites. Weiser and Novotny (1987), Novotny (1988) and David et al. (1989) report on attempts to control gypsy moth in the field by applications of microsporidia. To date, no reports on the occurrence of microsporidia in nun moth populations have been published. The objective of this study was to evaluate the potential of microsporidia in the regulation of population density of gypsy moth and nun moth. A cooperative project with the USDA Forest Service and the Illinois Natural History Survey has been established. In this paper, initial results on the susceptibility of German gypsy moth and nun moth larvae to different microsporidian isolates from gypsy moth are presented. In addition, the effects of the infection on individual larvae in the laboratory were also recorded.

Pages 198-205 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Materials And Methods

Seven microsporidian isolates collected from gypsy moth populations in different parts of Europe (Table 1) were obtained from the Illinois Natural History Survey in Champaign/Urbana and refrigerated at 4°C until they were used. The nomenclature of many of the isolates is still preliminary. Gypsy moth larvae were reared in the laboratory on artificial diet (ODell and Rollinson 1966) while nun moth larvae were reared on larch needles.

Table 1: Tissue specificity of the seven different microsporidian isolates from gypsy moth used in the infection experiments[1]

Microsporidian species: (Primary spores)	Infection of gypsy moth	Infection of nun moth
Vairimorpha lymantriae (+)	all tissues, mainly FB	all tissues
German *Microsporidium* isolate (+)	MG, MT, SG (FB)	MG, SG (FB)
Silk gland *Microsporidium* isolate (+)	SG, FB (MG, G)	SG, MG
Romanian *Microsporidium* isolate (-)	MG, FB	MG, (SG)
Endoreticulatus sp. (-)	MG	MG (FB)
Portuguese *Microsporidium* isolate (+)	MG, SG, G	MG, FB (G)
PAV *Microsporidium* isolate (?)	+	-

[1]MG = Midgut; SG = Salivary gland; MT = Malpighian tubules; G = Gonads; FB = Fat body; + = Primary spores were found; - = primary spores not detected

Third instar larvae were infected by feeding spores per os. The spore suspension was fed to individual larvae with an inoculation loop which held approximately 1µl. The concentration of all isolates was adjusted to 10^3 - 10^4 spores/ ml of suspension. For the determination of the pathogenicity of the different isolates, higher doses of spores (maximum $5x10^4$ spores/µl) were fed to gypsy moth larvae. The concentration of spores in the suspension was determined by counting spores in a Petroff-Hauser bacterial counter. A total of 40 to 50 larvae were infected with each isolate. Only larvae that consumed the entire suspension from the loop were used in the experiments.

Infected and healthy (control) larvae were individually reared at 24°C, 40%RH, and 14L:10D photoperiod. Infected and noninfected larvae were inspected every two days and their developmental stage and condition were recorded. Dead larvae, pupae or adults were dissected immediately to determine if they were infected by microsporidia. All larvae in these experiments were killed and autopsied four weeks after they were infected. Wet tissue

mounts were prepared and phase contrast light microscopy was used to confirm the presence of spores and/or vegetative stages. The following tissues were routinely examined: midgut, silk gland, fat body, Malpighian tubules, and nerve tissue.

Results and Discussion

Infectivity. Infections in German gypsy moth larvae were obtained with the following isolates: *Vairimorpha lymantriae,* the German *Microsporidium* isolate, the silk gland *Microsporidium* isolate, the Romanian *Microsporidium* isolate, *Endoreticulatus* sp., and the Portuguese *Microsporidium* isolate. Only very few infections were achieved with the PAV *Microsporidium* isolate (from Slovakia).

The highest infection rates were achieved with the German *Microsporidium* isolate (87%) and the silk gland *Microsporidium* isolate (75%), followed by *V. lymantriae* (70%) (Fig. 1). The German *Microsporidium* isolate was originally isolated from a German strain of gypsy moth in 1993 (Linde and Rappl 1994) which might explain the higher susceptibility of the larvae to this strain.

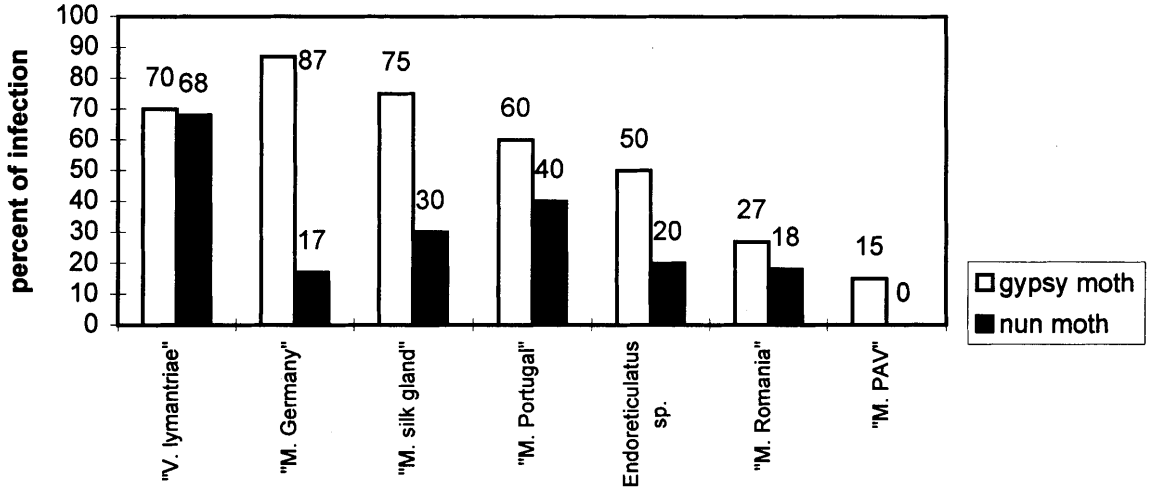


Figure 1. Results of infection experiments with gypsy moth (*Lymantria dispar*) and nun moth (*Lymantria monacha*).

Infections in nun moth larvae were obtained with the following isolates: *V. lymantriae,* the German *Microsporidium* isolate, the silk gland *Microsporidium* isolate, the Romanian *Microsporidium* isolate, *Endoreticulatus* sp., and the Portuguese *Microsporidium* isolate. No infections were achieved with the PAV *Microsporidium* isolate. The negative results with the isolate PAV *Microsporidium* suggest that the spores were not viable. Spores appeared greyish in colour under phase contrast microscopy. The highest infection rates were achieved with *V. lymantriae* (68%) and the Portuguese *Microsporidium* isolate (40%), followed by the silk gland *Microsporidium* isolate (30%) (Fig. 1). The reasons for the variation in susceptibility of the larvae to the different isolates are not yet clear and need further investigation.

The susceptibility of nun moth larvae to gypsy moth microsporidia was not anticipated. No reports on the occurrence of microsporidia in nun moth populations have been published. Gypsy moth and nun moth are taxonomically similar species, but very different in their ecology. Nun moth is more frequent in north central Europe and feeds mainly on coniferous trees, while gypsy moth reaches higher population densities only in southern Europe and mostly feeds on deciduous trees. The susceptibility of an insect to a microsporidian infection depends on the conditions in the midgut, where the spores germinate, and on the suitability of the infected cells for the development of the parasite (Linde 1990). The lower infection rates that we observed in nun moth larvae are probably due to the conditions in the gut (e.g. pH), which are different from gypsy moth as a result of the different food plants and which may inhibit the germination of spores. Nevertheless, the conditions in infected cells obviously support the development of the parasite in both insect species, indicating the close relationship between them.

Pathology. The isolates used in this study differ in their tissue specificity (Table 1). The tissue specificity of the different isolates is almost the same in nun moth, again reflecting the taxonomic similarity of these two lymantriids. *V. lymantriae* was found in all tissues of gypsy moth and nun moth larvae. Usually the fat body was hypertrophied and completely filled with spores. The Portuguese *Microsporidium* isolate was found in the midgut and salivary glands. In a few cases, spores were present in the gonads, suggesting the probability that this isolate might be transovarially transmitted. The silk gland *Microsporidium* isolate was found mostly in the salivary glands and fat body, but also in the midgut. *Endoreticulatus* sp. was found only in the midgut. Infections with the Romanian *Microsporidium* isolate were detected in the midgut and fat body.

These results correspond to those reported by Maddox et al. (1995). *V. lymantriae* and the Portuguese *Microsporidium* isolate infections were also found in the larval gonads, indicating that these isolates are transmitted transovarially as reported by Bauer et al. (1994) and Novotny and Weiser (1993).

So called "primary/early spores" (Sagers et al. 1996, Solter et al. 1993) were produced by most isolates early in the infection cycle. In fact, most infections in the midgut muscle layer were actually "primary spores," which are thought to be responsible for the transmission of the infection from one tissue to another within the insect.

Mortality. The mortality rates of gypsy moth larvae fed with a low spore dose of 10^4 spores per larva resp. (10^3 with *V. lymantriae)* did not differ significantly from the control group; only larvae infected with *V. lymantriae* showed slightly higher mortality in the first two weeks of the experiment.

In a second set of experiments, higher doses of spores ($5x10^4$ spores/µl) were fed to gypsy moth larvae. Two weeks after infection, the percentage mortality was recorded. The results are shown in Figure 2. The highest mortality was caused by *V. lymantriae* and the silk gland *Microsporidium* isolate followed by the Portuguese *Microsporidium* isolate. Much lower mortality was recorded with the German *Microsporidium* isolate (8%) and *Endoreticulatus* sp. The low mortality caused by the German *Microsporidium* isolate probably reflects the long coevolution of this German isolate with the German strain of gypsy moth. In addition to this, the German *Microsporidium* isolate only infects tissues of minor importance for the survival of the larvae (e.g. silk gland).

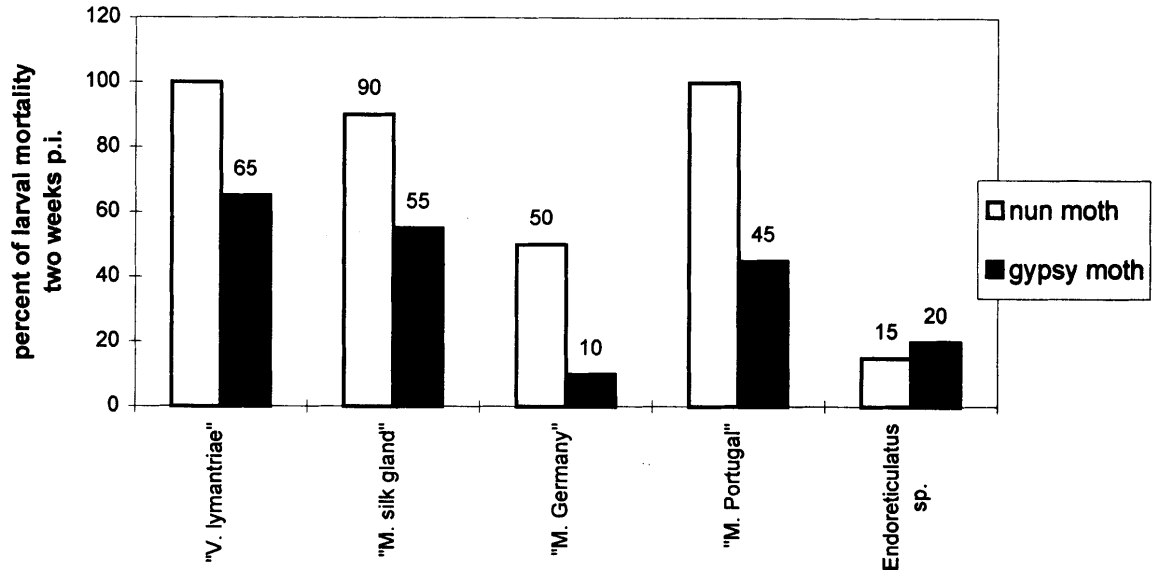


Figure 2. Mortality of gypsy moth and nun moth larvae caused by microsporidia.

The influence of different doses of the German *Microsporidium* isolate on pupal mortality and development of gypsy moth was investigated in detail. The mortality of female pupae significantly increased with the infective dose (Fig. 3). We suggest that the high spore load in the silk gland might interfere with the process of metamorphosis. The silk gland tissue is inactivated, resorbed, and probably incorporated into tissues of the adult insect. This transformation is probably disturbed when the silk gland cells are completely filled with resistant microsporidian spores.

In the nun moth, mortality rates were significantly higher. This is probably due to the fact that nun moth is not the natural host of the microsporidian isolates used in these experiments. The highest mortality rates were found with *V. lymantriae* and the Portuguese *Microsporidium* isolate followed by the silk gland *Microsporidium* isolate. Much lower mortality occurred with the German *Microsporidium* isolate and *Endoreticulatus* sp. (Fig. 2). In this respect, the results correspond to those observed with gypsy moth.

Differences in pathogenicity of microsporidian species is a well documented phenomenon (Brooks 1988). The virulence of the isolates is obviously correlated with the tissue specificity: those species which infect tissues that are important for the survival or development of the larvae (e.g. *V. lymantriae:* fat body) cause the highest mortality rates.

Development. Only few microsporidian species (e.g. *Vairimorpha necatrix*) cause high mortality in their hosts (Brooks 1988). Usually, microsporidia cause sublethal effects which are typical for a chronic disease. In this study, we investigated the influence of infections with *Endoreticulatus* sp. and the German *Microsporidium* isolate on developmental parameters (duration of development, pupal weight) of gypsy moth larvae.

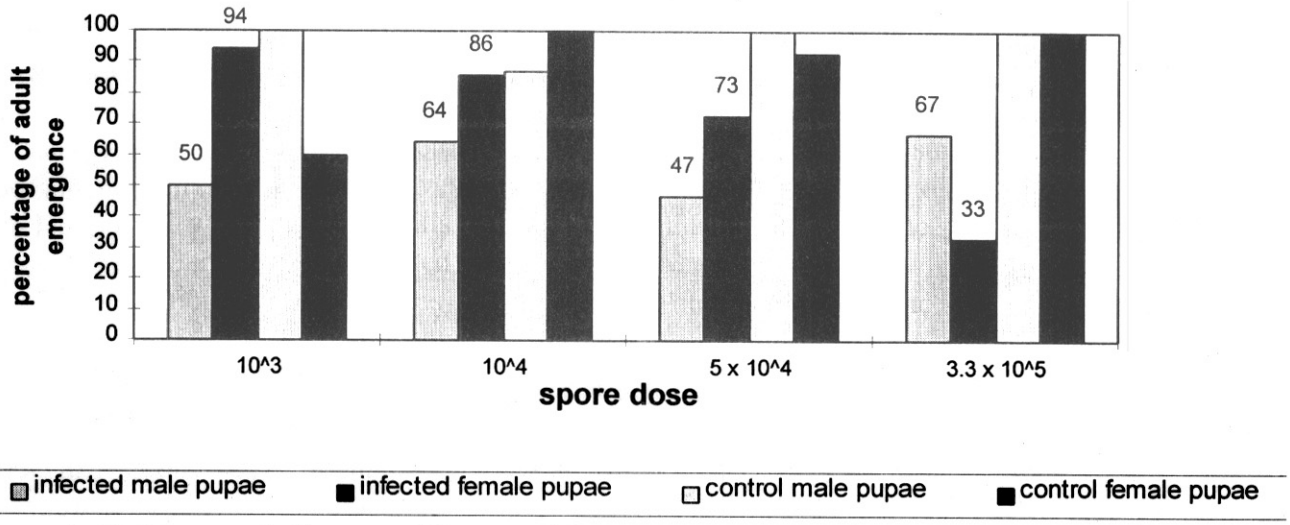


Figure 3. Influence of German *Microsporidium* isolate on the survival of gypsy moth pupae (*Lymantria dispar*).

We observed an influence of the infection on the pupal weight as well as on the development of larvae. The weight of gypsy moth male pupae infected with *Endoreticulatus* sp. was higher compared to healthy pupae (0.38gr resp. 0.35gr.). This is probably due to the prolonged development of the larvae and the heavy spore load in the infected tissues.

Larvae of gypsy moth infected with the German *Microsporidium* isolate pupated significantly later and the duration of the pupation period was prolonged. As a result, the development of infected male and female individuals from egg hatch to adult emergence was significantly longer (Fig. 4). Similar effects of microsporidian infections have been described in other species.

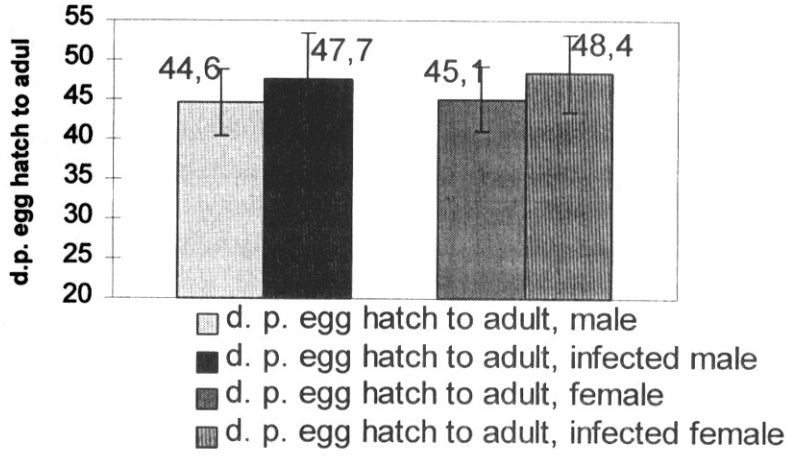


Figure 4. Influence of German *Microsporidium* isolate on the development of *Lymantria dispar*.

The results indicate that microsporidian infections may have an influence on the dynamics of an insect population. Mitchell and Cali (1994) mention the occurrence of a retarded growth and development and lower body weight of lepidopteran larvae that are infected with *V. necatrix*. Bauer and Nordin (1988) observed prolonged development in

spruce budworm infected with *Nosema fumiferanae*. Recently, Habtewold et al. (1995) demonstrated an influence of the infection of grasshoppers infected with *Nosema locustae* on the per capita reproduction and the growth of grasshopper populations.

The prolongation of the development of infected gypsy moth larvae from egg hatch to adult emergence as demonstrated in this study seems negligible, but the experiments were conducted under optimal rearing conditions in the laboratory. In the field, such effects may be enhanced by adverse weather or poor food, leading to a prolonged exposure of larvae to natural antagonists or disadvantageous abiotic conditions.

Conclusions

We were able to successfully infect a German strain of gypsy moth with seven microsporidian isolates collected from gypsy moth populations throughout Europe. In addition to this, nun moth larvae were also infected by most of the same isolates. The effects of the different isolates on the two host insects were varied and mostly sublethal. Our results present further evidence that microsporidian infections can slow down the rate of development of the larvae. Although after four weeks, most of the control larvae had pupated, there were few pupae in the group of larvae infected with *microsporidia*.

The results reported here are preliminary and should be repeated; additional research should concentrate on these long-term effects in order to obtain a realistic view of the potential of microsporidia for use in the long-term regulation of insect population dynamics.

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The Theoretical Basis for Using Baculoviruses to Control Forest Pests

EVGENIYA V. ORLOVSKAYA

Moscow Forest University, Mitishchy, Moscow Region, 141001 Russia

ABSTRACT The problems associated with using baculoviruses for classical biological control (introduction, colonization and mass release, and the application of microorganisms as an insecticide) are discussed. Based on several years of investigation, differences in the natural occurrence of virus diseases among 23 species of dendrophilous insects have been determined. The *Lepidoptera* and *Hymenoptera* have been divided into 4 groups according to differences in occurrence of viruses observed in those species. The character and intensity of epizootics caused by baculoviruses are associated with a criterion referred to as the "degree of contagion of the virus in the ecosystem." This criterion is formed from two factors that are expressed on a numerical scale (1-5): (1) the virulence and the tissues affected by the virus, and (2) the probability of contact between the feeding larvae and the virus in nature. This probability depends upon the bioecological peculiarities of each insect species. The criterion, "the degree of virus contagion in the ecosystem", is proposed as a method for selecting the best method for the use of the baculoviruses against insect species.

THE THEORETICAL BASIS of the methods for the use of viruses to control harmful insects corresponds to the main objectives of classical biological control, i.e., introduction, colonization, and mass release. The questions of introduction, colonization and the direct use of microorganisms as insecticides were discussed by Hall (1964). There are few known examples of successful introduction of viruses. The importance of sawfly viruses after their introduction from Europe to the USA and Canada was particularly significant (Bird 1953, Bird and Elgee 1957). At first, the effect was very dramatic; however, over time, the interaction between the nuclear polyhedrosis virus (NPV) and its host became more balanced. The NPV now occurs in populations of *Neodiprion sertifer* and *Diprion hercyniae* in North America. In spite of the fact that these viruses are permanent regulators of the population density of these pests in the United States and Canada, preparations of the virus are used occasionally to control these species (Podgwaite et al. 1984, Cunningham et al. 1989).

The introduction of a more virulent NPV strain (than the natural strain) from Japan into populations of *Hyphantria cunea* in Yugoslavia in 1973 caused a decrease of the population density to an insignificant level within one year (Injac 1978).

The possibilities of introducing viruses are not limited to those that are specific to an individual pest species. In 1964, we introduced the granulosis virus (GV) of *Dendrolimus sibiricus* to a Voronezh population of *D. pini*. We treated 12,000 eggs of *D. pini* with GV isolated from the thoracic region of a single butterfly. The treated eggs were placed in paper sacs on 80 pine trees in four plots. Most insects died in the pupal stage (65-80%). Within a year, the population was reduced to an insignificant level and the GV was distributed within a radius of up to 1 km. The introduction of GV into the population of *D. pini,* combined with

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activity of natural entomophages, caused a prolonged suppression (22 years) of the pest population (Orlovskaya et al. 1988).

Regarding colonization, the baculoviruses are periodically introduced only into a small portion of the insect population, after which they reproduce and are transmitted within the ecosystem. As an example of this colonization, we can point to our "ground-focus" method of introducing NPV into the populations of *Lymantria dispar* at the beginning of the gradation phase of the pest. Ten to 20 percent of the egg masses in the artificial focus were treated by NPV before larval emergence (Orlovskaya 1970). This method has been successfully utilized in Russia and some republics of the former USSR for more than 25 years (Orlovskaya 1980).

The third method of utilizing baculoviruses is the application of viral preparations as insecticides. But in this case, the use of this method is limited because of the high price of virus preparations. The spraying of a forest with a Gypchek preparation (NPV) at a rate of 1.25×10^{12} polyhedral inclusion bodies (PIB) per hectare costs $50 (Reardon and Podgwaite 1992). We have developed a virus preparation, VIRIN-ENSH, based on an experimental epizootical NPV strain, that is applied by spraying forests at the rate of 1.5×10^{11} PIB/ hectare. The price of the treatment of 1 hectare is 24,000 rubles ($5). The cost of producing VIRIN-ENSH for seasonal colonization varies from 4,800 to 14,400 rubles ($1 to $3) for every 50 hectares.

Materials and Methods

We made observations on virus diseases of insects in Estonia, Latvia, Central and Southern regions of Russia, Dagestan, Azerbaijan, Western Ukraine, Moldova, Kazakhstan and Kirghizia. Additional investigations were conducted by our colleagues in Byelorussia, Armenia, Ukraine and Siberia. Both living and dead individual larvae were investigated by means of light and electron microscopy. The susceptibility of insects to viruses, their virulence, and specificity were determined by bioassaying host insects and various species that occur in the same biocenosis (Orlovskaya 1968a). The tissue tropism was investigated by analyzing tissues of infected individuals at different periods of development of the disease. The occurrences of latent virus in populations were determined by investigating the effect of various stress factors on the insects. The duration of observations varied among different species, and the size of epizootic foci were defined by special inspections. The artificial epizootics in *L. dispar* populations were created by treating a small portion of egg masses with a virus suspension before larval emergence (Orlovskaya 1970). The active and epizootic NPV strains used for production of the virus preparation VIRIN-ENSH were obtained by adapting introduced viruses to new host insects and by direct selection using symptoms of tissue tropism (Orlovskaya 1975). The virus preparation VIRIN-ENSH was obtained by cultivating the NPV in larvae of *L. dispar* reared on special artificial media and various plant species (Orlovskaya and Shumova 1980).

Results and Discussion

Many years of research on viruses in natural populations of various insects, as well as in laboratory colonies, allowed us to determine some principles for the development of

baculoviruses in individuals and in populations. We have summarized the results of these investigations of virus diseases in 23 species of dendrophilic pest insects.

Table 1. The influence of interaction of baculoviruses with insects upon the occurrence of the viral diseases in nature and upon the methods of their use

The insect species	Virus	The occurrence of viruses in nature	The degree of contagion in the ecosystem: virulence and tissues affected by the viruses*	The degree of contagion in the ecosystem: probability of contacts of larvae with virus**	Methods of use
Lymantria dispar L.	NPV		4	5	
Lymantria monacha L.	NPV		4	5	Seasonal
Dasychira pudibunda L.	NPV	Acute	4	5	colonization
Erannis defoliaria L.	NPV	epizootics	4	5	and as an
Malacosoma neustria L.	NPV		5	4	insecticide
Hyphantria cunea Drury.	GV		5	4	
Neodiprion sertifer Geoff.	NPV		5	5	
Aporia crataegi L.	NPV		4	2	As an
Stilpnotia salicis L.	NPV	Chronic	4	2	insecticide
Selenephera lunigera Esp.	NPV	epizootics	4	3	
Euproctis chrysorrhoea L.	NPV		2	3	The use of
Dendrolimus sibiricus Tschet	GV		3	4	active strains
Diprion pini L.	NPV		3	4	for introduction
Hyponomeuta cognatella Hb.	NPV		3	3	
H. evonymella L.	NPV		4	3	As an
H. malinella Zell.	NPV	enzootics	4	3	insecticide
H. padella Z.	NPV		4	3	
Carpocapsa pomonella L.	GV		4	1	
Cocaecia crataegana Hb.	NPV		4	1	
Panolis flammea Schiff.	NPV	Rare	1	5	The use of
Dendrolimus pini L.	NPV	occurrence	1	2	active strains
Tortrix viridana L.	NPV	in a	1	1	for
Lyda nemoralis Thoms.	NPV	population	1	4	introduction

* The degree of virulence and the tissues affected.

1. The virulence is weak. Separate cells are affected, hypoderma is not.
2. The virulence is moderate. The hypoderma is affected rarely, the other tissues are affected.
3. The virulence is moderate. The various tissues and hypoderma or the gut of sawflies are affected.
4. The virulence is high. The majority of tissues are affected, the hypoderma is affected only before death.
5. The virulence is high. The majority of tissues are affected. The hypoderma or the epithelium of sawfly guts are affected before the muscles.

** The probability of contacts between the feeding larvae and the virus in nature.

1. The contacts are casual.
2. The contacts of the virus dispersed from dead prepupae and pupae with the larvae of the next generation are rare.
3. The contacts with the dead larvae inside the nests are temporary; the infection is limited within the nests.
4. The contacts of the healthy larvae and late instars with the dead larvae on the foliage are moderate.
5. The contacts between the larvae of all instars and the dead and moribund larvae on the foliage are higher.

As a result of the research on the interaction between baculoviruses and their host insects in various insect species, we have developed a table (Table 1) where insects are

grouped according to the peculiarities manifested by their virus diseases in nature. The degree of contagion is expressed by numbers according to the nature of the virus and its probability of contacting the susceptible stage of the host insect in the ecosystem. In the last column, some methods for using the baculoviruses for every insect group and every pair of "virus - host" are proposed.

The reasons for the appearance of virus epizootics in insect populations were determined by many investigators and were correlated mainly with the activation of a latent virus under conditions that were unfavorable for insects (stresses) during periods of mass reproduction of pests (Gershenson 1959, Aruga 1963, etc.). The further development of virus diseases in insects in nature varies among different species; it is connected with the main factor responsible for the epizootic, i.e. the degree of contagion. The latter is provided by pathogen virulence, tissue tropism and bioecological features such as phenology, habitat, mode of life, number of generations and dispersal activity (Orlovskaya 1968b). The investigation of the interaction between baculoviruses and their host insects in individual organisms and in the ecosystem showed that specific NPVs and GVs have different degrees of activity within different species, and that there are differences in the succession of tissues infected in various insect species. This fact has a great influence on the degree of contagion in the ecosystem.

The first group includes mainly free-living insects; their life cycle (or several cycles) is completed within one season. During this period, the highly virulent NPV or GV is accumulated quickly in the population due to intensive secondary infections. Thus, the hypoderma of *Malacosoma neustria* larvae is affected by NPV and that of *Hyphantria cunea* larvae is infected by GV before infection occurs in the muscles. Therefore, the viruses are liberated into the environment through the ruptured cuticle when the larvae are moving on the foliage, which is also where the healthy individuals are feeding. These insect species are designated "5" due to their virus characteristics, but are rated "4" based on the probability of the virus coming in contact with the susceptible larvae; the first instars of these species develop in colonies and contact with the virus occurs more frequently in the middle and later instars. Therefore, these species have a total score of "9".

The hypoderma of the majority of *Lepidoptera* species is affected last, so the viruses are liberated from the organism in the location where the death of individuals occurs; they may be larvae, pronymphs, pupae or even adults in different species. The location of the dead insects is very important for the transmission between the virus and a susceptible stage of the insect. In *Lymantria dispar, L. monacha, Dasychira pudibunda* and *Erannis defoliaria,* viruses are liberated from the dead larvae of all instars onto foliage of deciduous trees or onto the needles of conifers. Therefore, the chances of contact between the virus and healthy larvae in nature is rated a "5" and a "4" according to the activity index due to the fact that the hypoderma is infected last. In *Neodiprion sertifer,* the intestinal NPV is liberated in the feces and therefore continuously contaminates the needles; this provides a high probability for transmitting the infection to healthy larvae. This species has a total score of "10", so it has the highest degree of contagion in the ecosystem. Insects included in the first group have the highest degree of contagion of a baculovirus in the ecosystem. This fact explains the acute course of virus epizootics that occurs in these species in nature. For this group of insects, it is preferable to use the periodic seasonal colonization for introducing baculoviruses into populations. The use of virus preparations as insecticides is also possible.

The second group includes species whose life cycle is interrupted by hibernation in the larval stage. Similarly, in some species, contact of the virus with the susceptible insect stage are limited. As a result these insects (larvae of e.g. *Aporia crataegi*) very seldom die in nature. The dead pronymphs and pupae are situated mainly on branches of the tree. In 2-3 weeks, a new generation of larvae emerges from egg masses in the peripheral part of the crown and begin feeding there. These healthy individuals consume a very small dose of the virus which was dispersed passively by wind. In addition, because the second instars are preparing to hibernate, their rate of development is slow, which does not promote the rapid development of the virus within the organism. In spring, the overwintering larvae develop at low temperatures, which also doesn't promote the intensive reproduction of virus in the organism. Consequently, most mortality occurs in the pronymph and pupal stages. We have observed such a situation for many years in the western Ukraine during the period of gradation of *A. crataegi.* The infection accumulated in the population slowly, so the epizootic was chronic for 11 years (Orlovskaya 1968b). Similar epizootics have been observed in populations of *Stilpnotia salicis* and *Selenephera lunigera* (Gorochovnikov et al. 1968). In these species, there is a small possibility of contact between the virus and the feeding larvae in nature; however, the virulence of the virus is high. Such a small possibility of contact with healthy individuals (rating = "2"), even with highly virulent NPV, results in the development of a chronic viral epizootic in nature. We recommend that these baculoviruses be used only as insecticides against these species.

Some insects of this group are affected by the less virulent baculoviruses in populations (a rating of "2-3"), but there is a great potential possibility for contacts of the healthy larvae with the virus in populations of *D. sibiricus* (Lukyanchikov 1962) and *Diprion pini.* For this group of insects, the search for active strains and their introduction are necessary. In the case of *D. sibiricus,* the introduction of the cytoplasmic polyhedrosis virus (CPV) that infects the intestines is worth investigating.

The third group includes those insects whose virus diseases develop in nature locally, in the form of an enzootic, due to the isolated habitat of the larval stages. In the majority of these species, healthy larvae contact the virus only in colonies; however, the virulence of their baculovirus is very high. The dead individuals remain isolated in abandoned colonies, or in rolled leaves. The colonies of larvae that remain alive settle in new sites, escaping the external infection. In *Carpocapsa pomonella* and *Cocaecia crataegana,* contact of the larvae with the virus is very rare because the larvae develop within apples or in separately rolled leaves. These species can be controlled by using baculoviruses as an insecticide.

The fourth group includes insects that are different in their biological features, so that epizootics in nature are either extremely rare or nonexistent. The NPV isolated from all these species has a weak virulence. By artificially infecting these host species, we showed that their baculoviruses affected only separate cells and tissues. For these insect species, it will be necessary to search for active strains that can be introduced. As mentioned previously, the introduction of the Asian strain of GV, isolated from *D. sibiricus,* into European populations of *D. pini* proved to be very effective (Orlovskaya et al. 1988).

The advantage of the method of introducing very active strains over other methods is the relatively prolonged control of the pest populations (10 to 20 years); therefore, costs are low both for the virus material and for the treatment of populations.

Conclusion

The criterion "the degree of virus contagion in the ecosystem" is offered to select the most promising method for using the baculoviruses for the control of pest species. This criterion can be determined by the use of two indices, in which a scale of "1 to 5" is used for both indices. The indices of virulence and the tissues affected by the virus are included in the first scale. The second scale considers the probability of contact between the feeding larvae and the virus in nature, and takes into account the bioecological peculiarities of each insect species.

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Classical Biological Control of the Gypsy Moth, *Lymantria dispar* (L.), in North America: Prospects and New Strategies

MARC KENIS AND CARLOS LOPEZ VAAMONDE

International Institute of Biological Control, European Station, 1 Chemin des Grillons, 2800 Delémont, Switzerland

ABSTRACT On-going programs and future strategies for the biological control of the gypsy moth are reviewed. The most promising directions are: a continuation of the introduction of the two tachinid parasitoids *Blepharipa schineri* and *Ceranthia samarensis*, investigations on egg predators which are important natural enemies of the gypsy moth in eastern Europe and North Africa, studies on parasitoids specialized in low host densities, especially in poorly investigated regions in Asia, and investigations for the existence of more efficient biotypes of *Parasetigena silvestris* and *Cotesia Melanoscelus*, two parasitoid species already established in North America.

THE GYPSY MOTH has been the target of several extensive biological control programs since its introduction into North America in the 19th century. More than 60 species of natural enemies, parasitoids, predators and pathogens were introduced from 1906 to present but most failed to establish, for various reasons (Hoy 1976). Only 11 parasitoids, two predators and two pathogens became established, and among these some became major natural enemies of the gypsy moth in North America (Doane and McManus 1981, Schaefer et al. 1989, Hajek et al. 1993). The impact of these exotic natural enemies on gypsy moth populations in North America is hard to assess because of the difficulty of determining what would be the situation had these natural enemies not been introduced. Several authors claim that exotic natural enemies play an important role in regulating gypsy moth populations both at sparse densities and in outbreak situations (e.g. Clausen 1978, Berryman 1991). Nevertheless, the impact of these exotic natural enemies cannot be considered as totally satisfactory. Indeed, the gypsy moth is still the major pest of broadleaved forests in eastern North America and its distribution is expanding further west and south, despite the expensive eradication programs carried out at the edge of its present distribution.

Considering the enormous efforts made in the past to import exotic natural enemies into North America, one may conclude that everything has already been tried in the biological control of gypsy moth. However, before drawing such a conclusion, it is important to note that the gypsy moth still causes more damage in North America than in its native range and natural enemies play a more important role in the control of gypsy moth populations in Europe and Asia than in North America (see Doan and McManus 1981 for review). Furthermore, most of the introductions were done in the early days when not much was known on biological control techniques (DeBach and Rosen 1991). In view of this, and considering the low costs of biological control programs compared to the enormous losses caused by the gypsy moth in North America, and the costs of present monitoring and control

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methods, it seems reasonable to continue investigations on the importation of exotic natural enemies.

This paper reviews on-going programs and future strategies for the biological control of the gypsy moth in North America. These strategies can be categorized as follows:
(1) re-introduce natural enemies that failed to establish in previous trials but which are major components of Eurasian natural enemy complexes;
(2) introduce new natural enemies that were never considered, or seriously considered, for introduction;
(3) introduce new, better adapted biotypes of natural enemies already established in North America.

Strategies for the BioControl of Gypsy Moth

1. Re-introduction of Natural Enemies that Failed to Establish. In this section, only parasitoids will be discussed, as they represent by far the most important group of agents tested against the gypsy moth. Several European parasitoid species that failed to establish in North America are major components of the parasitoid complex of the gypsy moth in their region of origin, e.g. the two braconids *Glyptapanteles liparidis* (Bouché) and *G. porthetriae* (Muesb.). Hoy (1976) lists several reasons that could explain why these parasitoids did not establish. For the most important European parasitoids, the main reason of non-establishment appears to be the lack of alternate and/or overwintering hosts. Table 1 shows a list of the most important parasitoids established and not established in North America. The majority of the parasitoids that became established do not require an alternate host to complete their cycle. Those parasitoids established in North America that require an alternate host are extremely polyphagous, such as the tachinids *Compsilura concinnata* (Meigen) or *Exorista larvarum* (L.), which are recorded from 137 and 49 host species, respectively (Herting 1980). In contrast, all parasitoids that failed to establish despite large release programs are bi- or multivoltine and require a particular alternate host which probably does not exist in North America. Thus, releases of new individuals of the same species would probably result in the same failure. However, Fuester et al. (1988) suggested that, because all previous releases were made in New England and the gypsy moth is now spreading further north, south and west, new releases should be made in newly invaded regions where alternate hosts might be present.

2. Introduction of New Species. Despite the numerous introduction programs carried out for the last 90 years, there are still potentially important natural enemies which have never been seriously tried for introduction. The tachinid fly *Blepharipa schineri* (Mesnil) is a univoltine, oligophagous parasitoid that is a major natural enemy of the gypsy moth in Asia (Pemberton et al. 1993). In Europe, its importance has probably been largely underestimated because it has often been mistaken for the closely related species *B. pratensis* which is established in North America (Maier 1990). Recent studies in Germany showed that *B. schineri* was sometimes much more important than its congeneric species, reaching up to 96% parasitism (Maier 1990). Some individuals of *B. schineri* were already introduced in the United States at the beginning of the century, but the number of individuals released was too low to consider this a serious attempt (Hoy 1976). *B. schineri* is presently collected in

Europe by the United States Department of Agriculture and seriously considered for introduction into North America (F. Hérard, personal communication).

Table 1. Characteristics of the European and Asian parasitoids of the gypsy moth established and not established in North America

Parasitoids established in North America	Host stage attacked [b]	Host range [c]	Life cycle [d]	Alternate host required [e]
Anastatus japonicus Ashmead (=*disparis* Rushka) (Eupelmidae)	E	O	U	N
Ooencyrtus kuvanae (Howard) (Encyrtidae)	E	O	M	N
Cotesia melanoscelus Ratzeburg (Braconidae)	L	O	M	N
Phobocampe disparis (Viereck) (Ichneumonidae)	L	O	U	N
Blepharipa pratensis (Meigen) (Tachinidae)	L	O	U	N
Compsilura concinnata (Meigen) (Tachinidae)	L	P	M	Y
Exorista larvarum (L.) (Tachinidae)	L	P	M	Y
Parasetigena silvestris (Rob.-Desv.) (Tachinidae)	L	O	U	N
Monodontomerus aereus Walker (Torymidae)	P	P	M	Y
Brachymeria intermedia (Nees) (Chalcididae)	P	P	U-M	N-Y
Pimpla disparis Viereck (Ichneumonidae)	P	P	M	Y
Parasitoids released but not established [a]				
Glyptapanteles porthetriae (Muesebeck.) (Braconidae)	L	O	M	Y
Glyptapanteles liparidis (Bouché) (Braconidae)	L	O	M	Y
Meteorus pulchricornis (Wesmael) (Braconidae)	L	O	M	Y
Blondelia nigripes (Fallén) (Tachinidae)	L	P	M	Y
Carcelia separata (Rondani) (Tachinidae)	L	P	M	Y
Exorista japonica (Towsend) (Tachinidae)	L	P	M	Y
Exorista segregata (Rondani) (Tachinidae)	L	P	M	Y
Palexorista inconspicua (Meigen) (Tachinidae)	L	P	M	Y
Pimpla hypochondriaca (Retzius) (= *instigator* F.) (Ichneumonidae)	P	P	M	Y
Pimpla turionellae (L.) (Ichneumonidae)	P	P	M	Y

[a] Only common parasitoids of the gypsy moth that were released in adequate numbers are listed here (Hoy 1976).
[b] E = egg; L = larva; P = pupa.
[c] O = oligophagous; P = polyphagous (at least 10 hosts recorded in Herting 1980, 1982).
[d] U = univoltine; M = bi- or multivoltine.
[e] N = no; Y = yes.

Other important natural enemies have been neglected for other reasons. Of particular interest are the egg predators, particularly dermestid beetles. Dermestids are sometimes considered as the most important natural enemies of the gypsy moth in eastern Europe (Nonweiler 1959, Mihalache et al. 1995) and Morocco (Hérard 1979, Villemant 1995), where over 50% of the egg masses might be attacked in the declining phase of the outbreaks. In Romania, dermestids have already been used in augmentative releases as part of IPM programs (Ciornei et al. 1995). In addition to the direct effect of predation, dermestids have two other possible beneficial effects. First, they open the egg masses which are then more susceptible to egg parasitoid attack. Indeed, in the absence of egg predation, the two egg parasitoids *Ooencyrtus kuvanae* (Howard) and *Anastatus japonicus* Ashmead (= *disparis* Ruschka) have a limited effect because they can parasitize only the eggs in the top layers of the egg masses (Prota, in Brown and Cameron 1982, Hérard 1979). Second, dermestids are

supposed to play an important role in the dispersion of pathogens, particularly nucleopolyhedrosis virus, because they feed on the dead larvae before feeding on the eggs (Pirvescu 1978). In North America, egg predation by invertebrates plays a minor role in the natural control of the gypsy moth (Brown and Cameron 1982). Dermestids, or other egg predators, would therefore fill an empty niche in the natural enemy complex of the pest.

The lack of interest in dermestids as biological control agents is undoubtedly due to their reputation as pests of stored foods and fabrics. Indeed, one of the dermestids feeding on gypsy moth eggs is the famous bacon beetle *Dermestes lardarius* L.. However, the three most important dermestids found on gypsy moth in eastern Europe, *Dermestes erichsoni* Ganglbauer, *Megatoma undata* (L.) and *Megatoma ruficornis* Aub (= *pici* Kalik) (Nunweiler 1959, Mihalache et al. 1995), are not known as pests and apparently have a fairly narrow food range (Freude et al. 1979). It is strange that, until now, such important natural enemies received so little attention, and it would be of high interest to investigate in further detail their exact impact on gypsy moth populations, their role as pathogen vectors, and their food range.

Other potential biological control agents might be found in previously unexplored regions. While Europe and Japan have been extensively surveyed, large regions within the distribution range of the gypsy moth remain largely unexplored. This is particularly the case for China, eastern Russia and the Middle East, where only casual collections were made without much information on the impact of natural enemies on the local gypsy moth populations (e.g. Schaefer et al. 1984; Kolomiets 1987). In these regions, the gypsy moth, although present over large areas, is usually considered as a relatively minor pest, and it remains to be seen why damage is limited compared to North America.

Surveys should not be limited to outbreaks. It is a well known fact that parasitism is sometimes very different at high and low host densities (Mills 1990). All parasitoids introduced into North America were collected during outbreaks and other parasitoids might play an important role in limiting host populations at low density. In the 80's, the International Institute of Biological Control and the Canadian Forest Service initiated a study on low host density parasitoids using the host exposure technique (Mills 1990, Mills and Nealis 1992). Larvae were exposed on isolated trees in Switzerland, Germany and France at sites which never or rarely suffer from gypsy moth outbreaks. The main parasitoid attacking these exposed larvae was the tachinid *Ceranthia samarensis* (Villeneuve). This species was only found three times in natural populations of gypsy moth: in Austria (Fuester et al. 1983), Germany (Maier 1990), and France (M. Kenis, unpublished data). However, it was reared at 10 of the 11 sites where gypsy moth larvae were exposed (Mills and Nealis 1992, M. Kenis, unpublished data). Hence, *C. samarensis* may act as an important factor preventing the gypsy moth from producing outbreaks in regions where the pest usually stays at endemic levels.

Parasitoids attacking hosts at low density are likely to be polyphagous. Indeed, when similar host exposure experiments are made in North America, the main parasitoid reared is the polyphagous tachinid *Compsilura concinnata* (Gould et al. 1990). However, there are good indications that *C. samarensis* is not polyphagous. First, the only one other host record besides the gypsy moth is the lymantriid *Orgyia recens* Hbn. (Mihalyi 1986). Second, extensive collections of macrolepidopteran larvae at sites where *C. samarensis* was reared in high numbers from exposed gypsy moth larvae did not give rise to any *C. samarensis* (M. Kenis and C. Lopez Vaamonde, unpublished data). Finally, to test the ability of *C.*

samarensis to develop in other hosts, artificial inoculations of *C. samarensis* maggots found by dissection of mature females were made on larvae of several macrolepidopteran species. This method was successful on the gypsy moth (Quednau 1993) while on the other hosts, the maggots usually penetrated into the larvae but failed to develop further (M. Kenis, unpublished data).

Ceranthia samarensis is presently reared in Canada to augment the number of females available for release (Quednau 1993) and field cage releases started in 1991 in Ontario (V. Nealis, personal communication).

Such investigations on parasitism in low density populations should not be restricted to western Europe. Similar studies could be done in other regions where the gypsy moth usually remains at endemic levels, particularly in Asia.

3. Introduction of New Biotypes of Natural Enemies already Established in North America. The identification and characterization of biotypes in biocontrol agents is essential in a biological control program. Biotypes of parasitoids or predators are known to differ in various traits (Ruberson et al 1989, Hopper et al. 1993), and variations in traits such as developmental responses, temperature tolerance, encapsulation resistance or host preference are likely to affect the efficiency of these natural enemies as biological control agents. It is thus very important to select the biotype which is better adapted than others to the target host in the target region.

Almost all natural enemies of the gypsy moth established in North America were introduced at the beginning of the century using strains from various parts of Europe and Asia. However, it is not known which strains became established, and if these strains represent the most efficient biotypes for the region of introduction. This could explain why several parasitoids are apparently less efficient in North America than in Europe. The tachinid *Parasetigena silvestris* (Robineau-Desvoidy) is a particularly good example. This univoltine, larval parasitoid is one of the most important natural enemies of the gypsy moth all over its geographic distribution. Several European strains were introduced into North America from 1910 on and the parasitoid was recovered only 17 years later. Since then, *P. silvestris* has become a major parasitoid of the gypsy moth in North America, but parasitism is usually lower than in most European regions. Even in Europe, there are important differences in parasitism by *P. silvestris* between regions. Of particular interest is the parasitism rate observed in the Rhine Valley in France and Germany, where collections made by Maier (1990) in the 1980's and by IIBC (M. Kenis, unpublished data) in the 1990's always provided parasitism rates by *P. silvestris* of over 60% (Table 2). In this region, outbreaks are usually of short duration and we believe that *P. silvestris* is the major and the most constant factor leading to the collapse of the outbreaks. Parasitism is usually lower in other European and Asian regions, although often higher than in North America. It is not clear why *P. silvestris* is particularly dominant in the Rhine Valley. The climate in this region might be particularly favorable for the tachinid, but it is rather similar to that of regions in France and Germany where parasitism rates are lower (Fuester et al. 1983, 1988). Other environmental factors might be more important. For instance, alternative hosts are perhaps more abundant. However, *P. silvestris* is univoltine, i.e. it does not need an alternate host to complete its cycle, and is rather monophagous. Besides the gypsy moth, the only other important host is the nun moth, *Lymantria monacha* (L.), a coniferous-feeding species which is not particularly abundant in the broadleaved forests of the Rhine Valley. The high occurrence of *P. silvestris*

could also be explained by other factors, such as a low mortality due to hyperparasitoids, pathogens or predators, or good food supply for the adults, but these factors were not investigated. The possibility that the strain from the Rhine Valley represents a particularly efficient biotype is certainly worth investigating. Comparative studies could be made with different European and North American strains to determine, first, why some strains are apparently better than others, and, second, whether a European strain - that from the Rhine Valley or another region - could be more efficient in controlling North American gypsy moth populations than the introduced strain. Comparisons could be made on all traits capable of influencing the efficacy of a particular strain, i.e. fecundity, developmental responses, longevity, encapsulation resistance, host location, etc. Genetic markers could be used to determine which European biotype is established in North America and to allow the separation of the North American strain from a particular, more efficient European strain to be introduced into North America.

Table 2. Peak parasitism by *Parasetigena silvestris* observed in the Rhine Valley in France (F) and Germany (D)

Site	Year	% parasitism	
Offenburg (D)	1986	97	(Maier 1990)
Hirzfelden (F)	1992	96	(M. Kenis, unpublished data)
Mulhouse (F)	1993	63	„
Colmar (F)	1993	61	„
Offenburg (D)	1994	77	„
Bantzenheim (F)	1994	88	„
Hagenau (F)	1995	90	„

Biotypes should also be searched in the braconid *Cotesia melanoscelus* Ratzeburg, a bivoltine, solitary parasitoid which attacks first and second instars in the first generation and later instars in the second generation. It overwinters as a mature larva in a cocoon. Weseloh (1976) showed that the second generation is badly synchronized with its host because adults emerge too late, when the gypsy moth were 4th instars or larger and much less acceptable than earlier instars as hosts. The strain of *C. melanoscelus* established in North America comes from specimens collected in Sicily in 1911 (Hoy 1976). Weseloh (1976) suggests that fast developing strains could be found in other Eurasian regions and introduced into North America to improve host-parasitoid synchronization.

Conclusions

In 1989, outbreaks of the gypsy moth in seven northeastern U.S. States suddenly collapsed due to the fungal pathogen *Entomophaga maimaiga* Humber, Shimazu & Soper. In 1992, *E. maimaiga* epizootics covered most of the distribution range of the gypsy moth in North America (Hajek et al. 1993). This pathogen was first introduced from Japan to North America in 1910 and 1911 but was not recovered in the field until 1989. It is not yet clear whether the strain which recently decimated the gypsy moth populations comes from this early introduction, in which case its sudden virulence might have resulted from natural selection, or from a new, accidental introduction (Hajek et al. 1993). However, regardless of the origin of this introduction, this example shows that there is still potential for classical

biological control of the gypsy moth in North America. The most promising direction appears to be a continuation of the introduction of the parasitoids *Blepharipa schineri* and *Ceranthia samarensis*, studies on egg predators, investigations of low density parasitoids in poorly studied regions, and investigation of the existence of more efficient biotypes of natural enemies already established in North America, particularly the parasitoids *Parasetigena silvestris* and *Cotesia melanoscelus*.

Acknowledgements

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Integrated Control of Species of Geometridae in Oak Forests of Romania

CONSTANTIN CIORNEI[1] AND GHEORGHE MIHALACHE[2]

[1]Forest Research Stations Bacau, Romania
[2]Forest Research and Management Institut Bucuresti, Romania

ABSTRACT In this paper, we present results of experiments that were designed to evaluate biological and chemical approaches to control species of Geometridae in the oak forests of Romania. Our ultimate goal is to combine these tactics in an integrated system to manage this important group of defoliating insects.

SPECIES OF GEOMETRIDE, especially the winter moth, *Operophtera brumata* L., and *Erannis defoliaria* L., are present in most Romanian oak forests and frequently reach outbreak levels. Therefore, we are interested in developing an integrated approach to managing these pests that will be environmentally acceptable. A series of experiments were conducted on *Quercus petraea* and *Q. robur* forests that are typical of the hill region in northeast Romania. Heavy infestation of *O. brumata and E. defoliaria* occurred in this region in 1994.

Results and Discussion

Experiments with Foray 48B to control the winter moth. Studies were conducted in two sessile oak forests that contained a mixture of broad-leaves species (20-60 years old). Based on analysis of pupal and adult populations of *O. brumata*, we estimated that the population density was sufficient to cause 60-72% defoliation in that area. We applied Foray 48B at two doses (1.5 L/ha in 1.5 L/ water; 2.0 L/ha in 3.0 L/water) using an AN_2 aircraft equipped with micronaire nozzles (ULV application). Treatments were applied on April 25, 1994, when leaf expansion was optimal and under favorable meteorological conditions. We estimated that larval mortality was 90.8% in the low dose plot (1.5 L/ha) and 96% in the high dose plot (2.0 L/ha). Results are summarized in Table 1. As a result of these treatments, the outbreak never materialzed and minimal defoliation was recorded.

Ground application of microbial pesticides to control species of Geometridae. An experiment was conducted in a 20 year old oak stand that contained other broad-leaved species (hornbeam, ash) in the forest district Flaminzi in 1994. Although *O. brumata* and *E. defoliaria* were the species present in greatest abundance, *Tortrix viridana* and two other geometrids were also present. Projected defoliation in this area was 51%. Three dosages of a viral preparation from geometrid larvae, Virin-OB (I.P.B.P. Chisinau) and 6 doses of Dipel (Abbott Labs., USA) were applied on April 29-30, 1994. The results are summarized in Table 2. The level of control obtained with the Virin-OB preparation was comparable to that achieved with the bacterial preparations of Dipel 8L and Dipel ES.

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Table 1. Efficiency of aerial ULV treatments with the bacterial preparation Foray against the winter moth

Treatment	Area (ha)	Projected defoliation 1994 (%)	Mean efficiency (%)	Defoliation after treatment (%)	Probable defoliation 1995 (%)
1.5 L Foray + 1.5 L water	300	60.0	90.8	15-20	0
2.0 L Foray + 3.0 L water	110		95.8	10-15	0
2.0 L Foray + 3.0 L water	60	72.4	95.4	15-20	0

Table 2. Efficiency of ground applications of viral and bacterial preparations against Geometridae caterpillars in Forest district Flaminzi, forest Cosula, 1994

Treatment Variant (symbol. preparation.dose - l/ha. Polyhedron/ha)	Area treated (ha)	Mean efficiency (%) O.b.	Mean efficiency (%) E.d.	Real defoliation after treatment (%)	Probable defoliation 1995 (%)
V_{11} - VIRIN - O.B. 6 x 10^{11} pol/ha + 100 l water	20	90.9	79.1	16	0
V_{12} - VIRIN - O.B. 9 x 10^{11} pol/ha + 100 l water	10	88.9	84.7	18	4 E.d.
V_{13} - VIRIN - O.B. 12 x 10^{11} pol/ha + 100 l water	20	86.6	88.2	16	8 C.p.
V_{21} - DIPEL - 8L - 1.0 l/ha + 100 l water	10	84.5	87.9	20	4 E.d. 23 C.p.
V_{22} - DIPEL - 8L - 1.5 l/ha + 100 l water	10	86.4	92.0	11	4 E.d. 3 E.m
V_{23} - DIPEL - 8L - 2.0 l/ha + 100 l water	10	90.3	91.9	8	0
V_{31} - DIPEL - ES - 1.0 l/ha + 100 l water	10	87.6	76.1	21	0
V_{32} - DIPEL - ES - 1.5 l/ha + 100 l water	10	81.4	84.7	15	0
V_{33} - DIPEL - ES - 2.0 l/ha + 100 l water	10	87.8	82.1	12	0
M - control (untreated)	20	-	-	50	2 O.b. 8 E.d. 4 C.p.

O.b. - *Operophtera brumata,* E.m. - *Erannis marginaria*
E.d. - *Erannis defoliaria,* C. p. - *Colotois pennaria*

Aerial application of a biodegradable pyrethroid, Sumi-Alpha, for control of geometrid species. In 1994, we evaluated an aerial application of a synthetic pyrethroid, Sumi-Alpha (Sumitomo, Japan) against species of Geometridae and *T. viridana* in a 45-60 year old *Q. petraea* forest in the hill region of Romania. The population of *O. brumata* was in the eruption phase and in the second instar at the time of application; meteorological conditions were optimal. The mean efficiency of the treatment was estimated to be 99.3% and the actual defoliation realized was 8-12% (Table 3). The populations of defoliator species were greatly reduced such that no defoliation was predicted in the treated area in 1995.

Table 3. Efficiency of aerial ULV with the biodegradable insecticide Sumi - Alpha against Geometrid caterpillars, Forest district Trusesti

Dose/L insecticide 1 ha	Area treated (ha)	Projected defoliation 1994 (%)	Mean efficiency (%)				Real defoliation after treatment (%)	Probable defoliation 1995 (%)		
			O.b.	E.d.	T.v.	X_{med}		T.v.	Geom	Total
21	700	55.5	99.7	99.6	98.5	99.3	8 - 12	0.3	0.0	0.3

T.v. - *Tortrix viridana* O.b. - *Operophtera brumata*
Geom. - Geometridae E.d. - *Erannis defoliaria*
Mixed oak forest (*Q. petraea*); larval populations in L_2-L_4 at time of application (April 22, 1994).

Evaluation of measures to stimulate the abundance of insectivorous birds. In addition to food, adequate shelter is an essential limiting factor for insectivorous birds, especially those species that nest in tree cavities (hollows). Frequently, silvicultural treatments reduce the number of trees with cavities and thus have a negative effect on insectivorous species. In this situation, it is imperative to introduce artificial nests in order to maintain optimal densities of birds, especially those that are insectivorous and sedentary (Rang and Ciornei 1991).

We conducted an experiment in a 40-80 year old oak forest in the forest district Trusesti whereby we introduced 2,000 artificial nest boxes at a density of 0.5-2.7/ha in three forests: one untreated, one treated with Sumi-Alpha, and one treated with Foray (Table 4). The data in Table 4 indicate the relationship between the dependency of occupancy of nest boxes and the abundance of defoliators on three observation dates – highest in the untreated plots and lowest in the plots with the highest treatment efficiency. In August, occupancy in the untreated plot was 69.3, 30.0 in the Sumi-Alpha plot, and 46.2 in the Foray-treated plot. Reduction in the defoliator complex as a result of the treatments caused the major nesting species (*Parus major, P. caeruleus, Passet montanus*) to abandon the artificial nests.

In the summer months, birds categorized as summer guests, in addition to *Muscicapa striata* and *Ficedula hypoleuca,* occupied the nests. Another competitor, the forest mouse, *Muscardinus avellanarius*, occupied the artificial nests, especially in the Sumi-alpha treated plot (70%).

Table 4. Comparative data regarding the occupancy of artificial nests by insectivorous birds in treated and untreated oak forests in Forest district Trusesti, 1994

Treatment/ Infestation before treatment/ Treatment efficiency	Date of nest installation	Occupying species	Number/ ex/ha before treatment 8-9.04. 1994	Percentage of occupancy (%) 8 - 9 04 1994	20 - 21 06 1994	12 - 13 08 1994
		Parrus sp.	0.68	29.0	11.8	23.1
		Passer montanus	-	14.0	11.8	15.4
		Muscicapa striata	-	-	17.6	15.4
Untreated	28.03-01.04. 1994	*Ficedula hypoleuca*	-	-	5.9	7.7
(Infestation: 25%		*Sitta europaea*	0.26	-	-	7.7
Geometridae)		**TOTAL BIRDS**	**7.07**	**43.0**	**47.1**	**69.3**
		(Muscardinus) Mice	-	-	41.2	30.7
		Empty nests	-	57.0	11.7	-
		Parrus sp.	1.44	38.7	-	10.0
Sumi-Alpha 2.0 l/hec		*Passer montanus*	0.08	12.9	12.5	20.0
		Muscicapa striata	-	-	8.4	-
(Infestation: 62% Geometridae)	28.03.1994	**TOTAL BIRDS**	**6.32**	**51.6**	**20.9**	**30.0**
		(Muscardinus) Mice	-	-	45.8	70.0
Treatment efficiency:		Wasps	-	-	8.3	-
99.3%		Empty nests	-	48.4	25.0	-
Foray -		*Parrus sp.*	1.50	16.0	14.3	23.1
1.5 - 2.0 l/hec		*Passer montanus*	-	28.0	14.2	-
(Infestation: 60%		*Muscicapa striata*	-	-	4.8	23.1
Geometridae + *Tortrix viridana*)	04.04.1994	*Sitta europaea*	0.30	-	4.8	-
		TOTAL BIRDS	**5.55**	**44.0**	**38.1**	**46.2**
Treatment efficiency:		Mice (Muscardinus)	-	4.0	47.6	30.8 7.7
90.8 - 95.8%		Bats	-	-	-	
		Empty nests	-	52.0	14.3	15.3

Actions to protect and encourage species of *Formica*. An inventory of ant colonies in *Q. petraea* and mixed oak stands from the forest district Trusesti (3,168.5 ha) demonstrates the significance of species of ants, *Formica rufa* and *F. polyctena* (Hymenoptera, Formicidae). Past research has shown that there is a direct correlation between the density of ant colonies and the occurrence of winter moth outbreaks (0.6-1.4 colonies/ha for infestations of 51-55%) (Table 5). The higher density of colonies is obviously related to the abundance of host larvae in the outbreak areas to the predaceous ants.

Table 5. The density of *Formica* colonies in oak forests infested by Geometridae, Forest district Trusesti, 1994

Location	Forest type	Age (years)	Area (ha)-	Infestation with defoliators spring 1994	Total number of colonies with normal sizes	Mean number colonies/ha
Iuresti	Mixed forest with *Q. petraea*	35-60	188.3	55.0	116	0.62
Constingeni	- " -	35-60	254.5	53.0	153	060
Mascateni	- " -	35-65	300.0	7.0	98	0.32
Blindesti	- " -	40-75	279.2	51.0	40	0.14
Soldanesti	Mixed forest with *Q. petraea* *Q. robur*	30-60	205.9	51.0	24	0.12
Vinatori	Mixed forest with *Q. petraea*	35-50	161.5	6.4	19	0.12
Saulea	- " -	35-100	441.0	25.0	33	0.07
Ionaseni stat	*Q. petraea* forest	30-80	405.8	59.0	102	0.25
Biznoasa	Mixed forest with *Q. petraea* *Q. robur*	25-45	107.2	50.0	146	1.36
Zlatunoaia	- " -	40-50	124.6	41.5	72	0.58
Fundatura	Mixed forest with *Q. petraea*	35-70	365.8	51.0	129	0.35
Dracsani	- " -	35-70	333.7	20.0	27	0.08
		TOTAL	3168.5	-	959	0.30

One major cause for the decline in the density of ant colonies is the past practice of pasturing animals in the forests. This also has a negative impact on game animals and birds because the understory habitat is destroyed. Therefore, in order to sustain an optimal density of 3-4 ant colonies/ha, which is required to maintain defoliator populations at low levels, it is necessary to protect ant colonies with various kinds of shields made of wood or wire netting. In order to reach this optimal level, we frequently transfer colonies from regions where the number is high to regions where the density has declined because of pasturing (Pascovici 1961).

The use of pheromones for monitoring populations of *O. brumata*. Between 1993-1994, we conducted studies in the forest districts of Trusesti and Flaminzi to evaluate the activity of the pheromone of *O. brumata* (3Z-6Z-9Z-1, 3, 6, 9-nonadecatetratraen) that was obtained from sources in Moldavia, Italy, and Germany. As a result of these studies, we confirmed that the pheromones were efficient in discovering adults at low densities, and in better understanding the influence of climatic factors (frost, snow) in the decrease of populations at very low densities (Figs. 1 and 2).

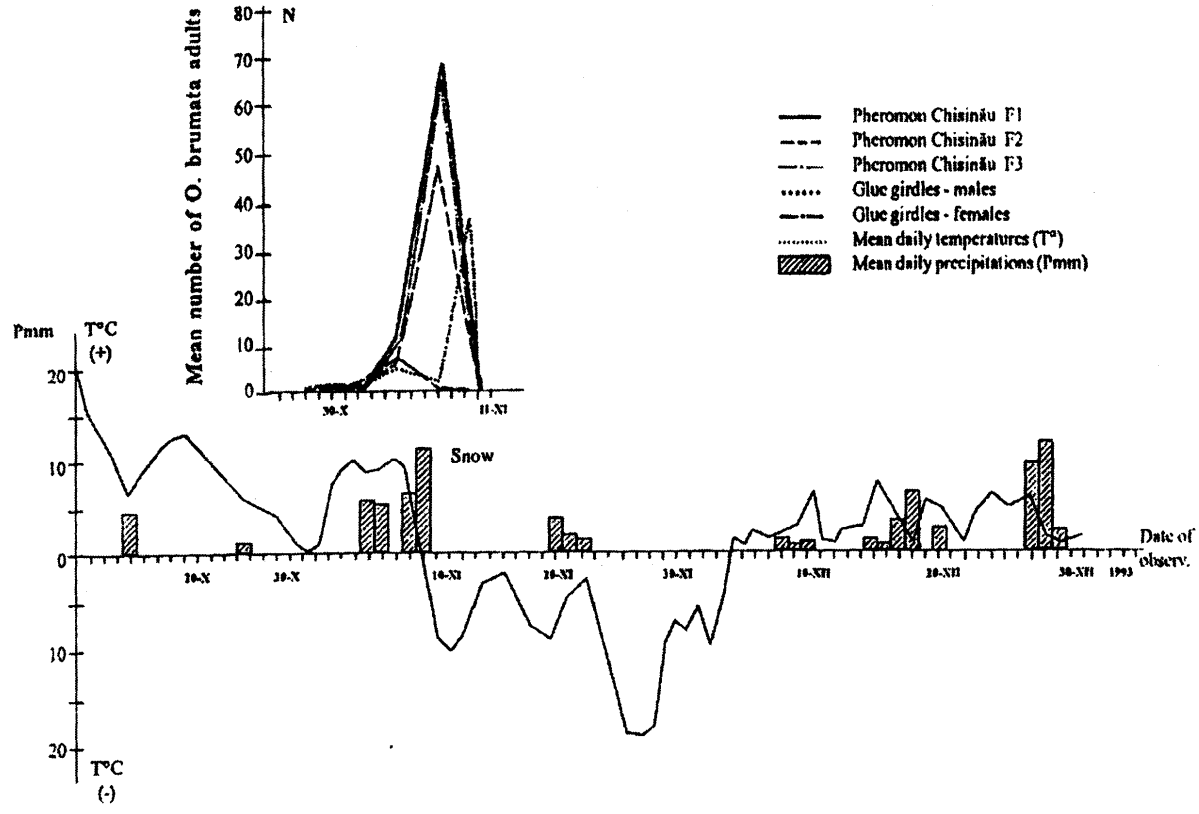


Figure 1. The flight dynamic of winter moth (O. brumata) registered by panel pheromonal traps and glue girdles correlated with the evolution of mean values of temperatures and precipitation (Forest district Trusesti, PU. III, m.u. 50A) – Meteo Station Rauseni.

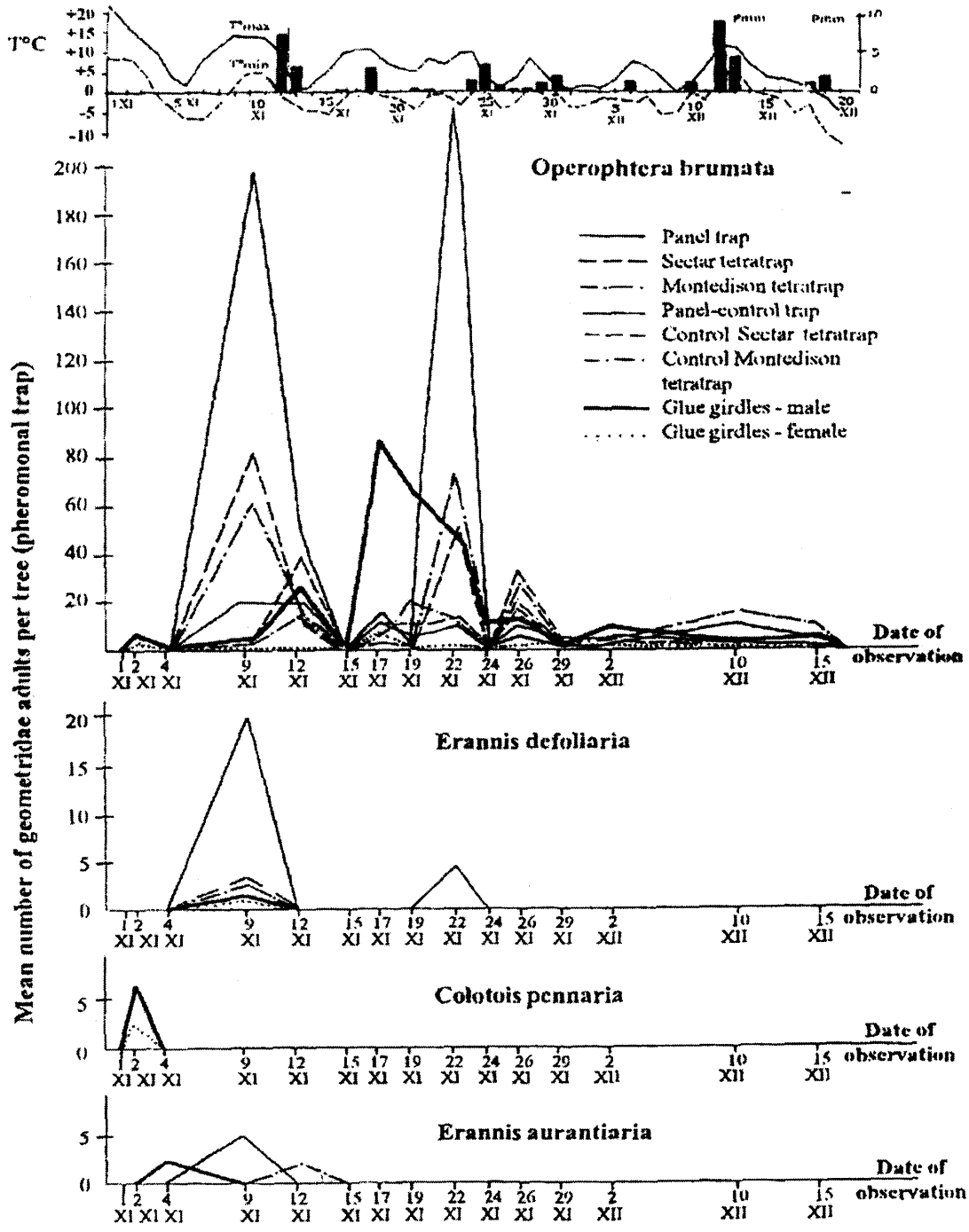


Figure 2. Flight dynamic of geometridae species using pheromonal trap and glue girdles correlated with the evolution of climatical factors (temperature; T°max T°min; precipitation – Pmm) Forest district Flaminzi – 1994.

Conclusions

The experiments that have been discussed are being integrated into a system for managing the geometrid defoliator complex in Romanian oak forests. The system has two basic components: preventive measures that apply to low-moderate density infestations, and suppressive measures that are deployed when populations are very dense and defoliation is predicted.

The preventive measures include introducing artificial nests (4-6/ha) for insectivorous birds to increase their effectiveness as predators of geometrid larvae, and protecting colonies of *Formica* in areas where pasturing is detrimental to their survival. If necessary, colonies are reintroduced from other regions in order to reach an optimum level per hectare. The use of pheromone traps for monitoring is critical to identifying areas where *O. brumata* populations are low but increasing.

When geometrid defoliator populations are high, we use aerial applications of microbial and biodegradable chemical pesticides necessary to reduce populations in the same year and prevent defoliation. We also have demonstrated the efficacy of applying ground applications of microbial pesticides such as Foray, Dipel, and Virin-OB to control geometrid populations. These methods are environmentally acceptable and fully compatible with the natural enemy complex (parasitoids, predators) that is necessary to maintain Geometrid defoliators at densities where they do not cause impacts to forest ecosystems.

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Shoot and Needle Losses in Scots Pine: Experimental Design and Techniques for Estimating Needle Biomass of Undamaged and Damaged Branches

BO LÅNGSTRÖM[1], HARALD PIENE[2], RICHARD FLEMING[3], AND CLAES HELLQVIST[1]

[1]Swedish University of Agricultural Sciences, Dept. of Entomology, P.O. Box 7044, S-775 07 Uppsala, Sweden
[2]Canadian Forest Service, Atlantic Region, P.O. Box 4000, Fredericton, N.B., Canada E3B 5P7
[3]Canadian Forest Service, Great Lakes Region, P.O. Box 490, Sault Ste Marie, Ont., Canada P6A 4C8

ABSTRACT The impact of needle and shoot losses in early and late season on growth and needle biomass of Scots pine (*Pinus sylvestris* L.) was studied in a field experiment in Central Sweden during 1991-1994. By clipping all but the current needles in June and all needles in August on 4-m trees, damage caused by the sawflies *Neodiprion sertifer* (Geoffr.) and *Diprion pini* (L.) was simulated. Parallel to that, all current shoots were clipped in early and late season to simulate shoot feeding by the common pine shoot beetle (*Tomicus piniperda* (L.)). The same treatments were applied to individual branches in whorls initiated in 1985, 1987, and 1989 of otherwise undamaged trees in the same stand. Bud formation and needle fall were recorded annually for the 300 study branches. The trees were felled in 1994, and data needed for calculations of needle weight and volume growth of stems and sample branches were recorded.

This paper describes the experimental design and techniques used to estimate the needle weights of undamaged and damaged branches at the start and end of the experiment. For most whorls, branch length explained more than 80 percent of the variation in needle biomass on undamaged sample branches. For treated branches, exponential functions were developed separately for each treatment and crown level, and these produced R^2s exceeding 0.50 in all but one case. These equations will be used to estimate needle biomass on damaged and undamaged branches at the start and end of the experiment.

KNOWLEDGE ABOUT THE impact of insect defoliation on tree growth is accumulating (for a review, see Kulman 1971, Alfaro 1991), but our understanding of the tree physiological processes involved is still far from complete, and few studies have addressed these questions (for references, see Piene and Percy 1984, Ericsson et al. 1985, Långström et al. 1990, Piene and Little 1990, Honkanen and Haukioja 1994). Understanding the links between pest population levels, the damage caused by their feeding, and the impact of the resulting defoliation on the trees, is crucial for determining proper countermeasures and forest protection strategies.

In Scandinavia, growth losses in Scots pine (*Pinus sylvestris* L.) are caused mainly by pine shoot beetles (*Tomicus piniperda* (L.) and *Tomicus minor* (Hart.); Col., Scolytidae) tunnelling the shoots or by sawfly larvae (mainly *Neodiprion sertifer* (Geoffr.) and *Diprion pini* (L.)) consuming the foliage. Shoot borers and defoliators are also found among certain groups of moths, e. g., the pine shoot moth (*Rhyacionia buoliana* (Shiff.)) and the pine looper (*Bupalus piniarius* (L.)), respectively (e. g., see Speight and Wainhouse 1989 and references therein, Eidmann and Klingström 1990). In addition, several fungal diseases cause needle

Pages 230-246 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

losses, and on young pines, moose browsing may destroy many shoots (Eidmann and Klingström 1990).

The common pine shoot beetle (*T. piniperda*) and the lesser pine shoot beetle (*T. minor*) are bark beetles which reproduce in fresh pine timber. After oviposition, the parent beetles re-emerge from the logs in early summer and fly to pine crowns where they spend the summer tunnelling out young shoots. Later in the season when they emerge, the new generation also feeds in the shoots of living pines to become sexually mature (for details regarding the life cycle of these species, see Långström 1983). At high population densities, this shoot feeding by the beetles results in severe shoot losses followed by large growth reductions, as demonstrated in several studies (Långström and Hellqvist 1991, and references therein). Recently, *T. piniperda* has become established in North America causing damage mainly in Christmas tree plantations (Haack and Lawrence 1995).

Among the defoliators, *Neodiprion sertifer* (Geoffr.), commonly known as the European pine sawfly in Europe and North America, is the most important species on Scots pine in Scandinavia where it occasionally causes severe defoliation over vast areas (Lekander 1950, Christiansen 1970, Ehnström 1985, Juutinen and Varama 1986, Virtanen et al. 1996). By comparison, outbreaks of *Diprion pini* (L.) are less frequent and more local, but it too is a major defoliator of pine in Scandinavia (Lekander 1950, Kangas 1963, Ehnström et al. 1974, Austarå et al. 1983, Ehnström 1985). *N. sertifer* larvae feed in early season on old foliage and normally leave the developing foliage of the current year untouched. In contrast, *D. pini* larvae feed on pine needles in late season and during outbreaks they typically consume all foliage, including the current needles. Both species leave the buds intact, although some feeding on the bark of young shoots may occur, at least at high larval densities (for details on the biology of the two species, see Juutinen 1967 and Geri 1988).

It is generally agreed that stem growth losses due to needle and/or shoot losses are a result of reduced availability of photosynthates for growth in the defoliated tree. The resulting growth loss may vary considerably, depending not only on the amount of foliage lost, but also on a number of other factors (e. g., tree species, defoliation history, seasonal feeding patterns, and qualitative differences between needles eaten, such as their age class and crown position). Although little evidence is available, one can assume that factors such as stand age and site productivity may also influence defoliation effects on tree growth. Recently, Honkanen et al. (1994) proposed a unifying theory based on changing sink/source-relationships over the season that could explain the variable effects of foliage losses in different situations. However, these complex patterns of interaction are poorly understood, and little research is presently directed to this important but difficult field.

Natural episodes of defoliation seldom lend themselves to detailed impact studies, because undamaged controls for comparisons are often lacking and the full defoliation history is seldom available. As Alfaro and co-workers (1991, and references therein) have demonstrated, much useful information can be derived from stem analyses using potential growth for comparison. Controlled experiments are needed, however, if full data on foliage losses and their subsequent impacts on tree growth are to be collected, as exemplified by studies on balsam fir (Piene 1989) and Scots pine (Långström et al. 1990). The enormous amount of work involved, however, limits the number of study trees. The same applies to artificial damage studies where controlled damage levels are created by artificially removing the relevant crown elements (see Långström et al. 1990). Thus, the observation that trees

have a modular structure where branches may function as more or less independent units offers the possibility of using branches as experimental units instead of whole trees (Sprugel et al. 1991, and references therein).

Project Objectives. The present study was designed to mimic the differential damage caused by shoot feeding and defoliation in early and late season, as caused by the three major pine pests mentioned above and summarized in Table 1. More specifically, we wanted to:
i) compare the impact of shoot pruning and defoliation in both early and late season on needle biomass recovery and stem growth in young Scots pines;
ii) compare the damage caused to individual branches with that of totally treated trees to ascertain if individual branches could be used to represent whole trees, and if so, which crown level was most appropriate; and
iii) measure annual needle fall to facilitate the modelling of needle dynamics on control and damaged trees (cf. Fleming and Piene 1992a,b).

Table 1. The damage patterns of the three herbivores included in this study and the treatments used to simulate their damage

Species	Feeding stage	Feeding time	Foliage Affected	Simulation Treatment	Treatment
Tomicus piniperda common pine shoot beetle	parent beetles after oviposition	June to Oct	current shoots and last year's foliage	clipping current buds and shoots in early June	EP Early Pruning
	callow adults after emergence	July to Oct	mostly current shoots	clipping current shoots in early August	LP Late Pruning
Neodiprion sertifer european pine sawfly	larvae feeding gregariously	May to July, mostly June	all foliage except the current needles	clipping all but the current needles in early June	ED Early Defoliation
Diprion pini "common pine sawfly"	larvae feeding gregariously	late July to September	all foliage	clipping all needles in early August	LD Late Defoliation

In this paper, we report on the general methodology used in the study, describe the techniques used to estimate the needle weight of undamaged and damaged branches from simple branch data, and discuss the problems involved in estimating the needle weights of branches with disturbed branch architecture.

Materials and Methods

Study Site The study was conducted at Ivantjärnsheden, Jädraås, in central Sweden, about 200 km northwest of Stockholm (61° N, 16° E, 185 m above sea level). The site was in a heath Scots pine forest, of dry dwarf shrub type, with a podzolic soil profile. For a detailed area description, see Axelsson and Bråkenhielm (1980).

Study Stand The site had been clearcut in 1971 and planted in 1972 with Scots pine seedlings of local provenance (2000 seedlings per hectare). In addition, naturally regenerated pine seedlings had developed in gaps following seedling mortality. The stand was cleaned in

1985 to ca 1500 stems per hectare, and by spring 1991, was a pure pine stand with some open patches.

Experimental Layout In 1991, *N. sertifer*, *D. pini* and *Tomicus* damage were simulated by removing all old foliage in early season, all foliage in late season, and all current shoots in both early and late season, respectively. This covered the major insect damage types causing foliage and growth losses to pine in Fennoscandia.

The study outline is based on the observation that single branches may react individually to treatments (e.g. Långström et al. 1990, Sprugel et al. 1991). By applying different damage treatments to individual branches within the same whorl (while leaving one branch as a control), the impact on branch development could be studied with less effort than the impact on whole trees. By comparing the branch development on trees with selected whorls that were artificially damaged to that of trees receiving a whole-tree treatment, the suitability of individual branches as substitutes for completely treated trees could be evaluated.

Thus, the experiment comprised the following treatments applied in 1991:

1) Control, i.e. no damage (hereafter referred to as the C-treatment);
2) Early defoliation of all needles (except the current ones developing in 1991) simulating *N. sertifer* damage (hereafter referred to as the ED-treatment);
3) Early pruning of all expanding current shoots simulating early *Tomicus* damage (hereafter referred to as the EP-treatment);
4) Late defoliation of all needles (including the current ones developing in 1991) simulating *pini* damage (hereafter referred to as the LD-treatment); and
5) Late pruning of all shoots grown out in 1991 simulating late *Tomicus* damage (hereafter referred to as the LP-treatment).

These five treatments were applied to two series of trees (Fig. 1). First, 10 trees were treated entirely with each one of the above treatments (whole-tree-treatment, hereafter referred to as the WTT series). Second, individual branches in whorls initiated in 1989, 1987 and 1985 on 10 trees were treated (branch-scale-treatment, hereafter referred to as the BST series). In the latter case, one randomly selected main branch per whorl received each one of the above treatments; the other branches on the tree were left intact.

Selection of Experimental Trees. On 21 May 1991, 75 similar looking, open-grown, experimental trees were selected in the study stand using the following criteria: DBH range of 40-60 mm (mean 52 mm ±6 mm SD), tree height 3-4 m (350 ±24 cm), "normal" height growth in 1988-90 (105 ±18 cm), 8-10 live whorls, at least 3 age classes of needles and no less than 4 main branches in the 1989, 1987 and 1985 whorls.

Of these trees, 13 trees (10 "ordinary" plus 3 "spare" trees) were randomly selected for the BST series from the 32 trees having five or more main branches in each of the 1989, 1987 and 1985 whorls. Within each of these whorls, treatments were randomly assigned to the main branches starting with the north-facing one and proceeding clockwise. Branches shorter than half the length of the well developed ones were not selected. Discarded branches on these whorls, and all other branches on these trees, were left untouched.

Of the remaining 62 trees, 50 were randomly allocated to the WTT series (10 trees per treatment) and measured for height and DBH. Another 10 trees were randomly selected for destructive needle biomass sampling.

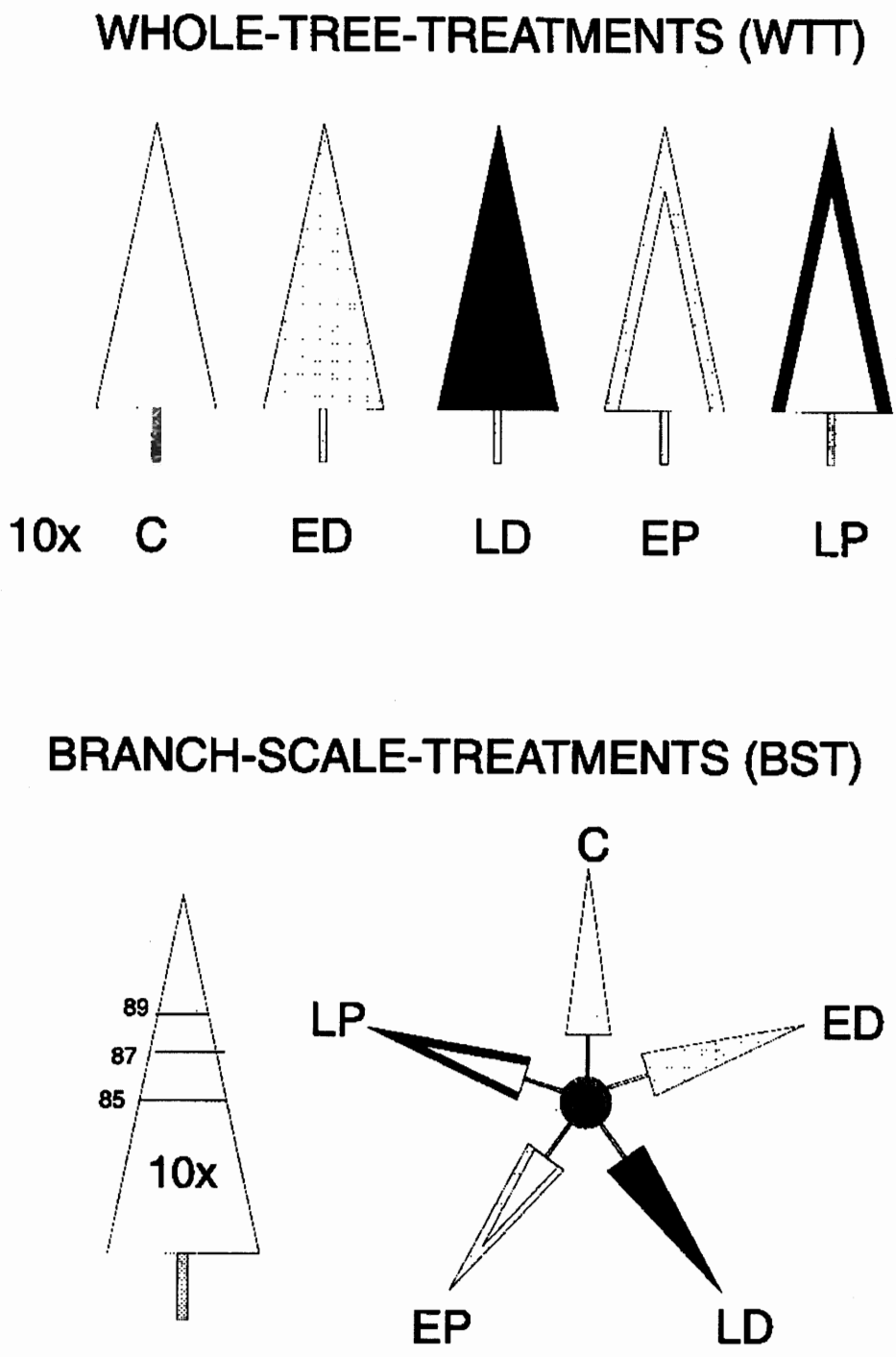


Figure 1. Schematic description of the experimental design. In the whole-tree-treatment: series, n=10 entire trees were each treated as follows: C=control; ED=early defoliation; EP=early pruning; LD=late defoliation; LP=late pruning. Individual branches in the 1989, 1987 and 1985 whorls of the 10 trees in the branch-scale-treatment series were correspondingly treated, with one main branch per whorl receiving one of the five treatments described above. The remaining branches on these trees were left unharmed.

Clipping and Pruning Starting on 2 June, all ED- and EP-trees in the whole-tree-treatment (WTT) series were pruned and/or clipped, respectively. During that week, all needles or currently expanding buds were removed in the upper crown (whorls 1990-1985) on the ED- and EP-trees, respectively. This included the needles/buds on the main stem. Needles were cut with scissors at the base of the needle pair leaving the base of the fascicle intact, and shoots were cut in the 1990 internode as close to the node as possible, i.e. within 1 cm of the bud base. The following week, all remaining needles or buds were cut in a second damage step.

The ED- and EP-branches in the branch-scale-treatment (BST) series were defoliated or clipped in a corresponding manner. During the first week, all needles or buds were taken in the outer half of the branches, i.e. from positions 1-2, 1-3 and 1-4 in the 1989, 1987 and 1985 whorls, respectively (cf. Fig. 2; see also Flower-Ellis et al. 1976, Långström 1980 for shoot labelling and branch architecture). All remaining needles or shoots were clipped in the next week.

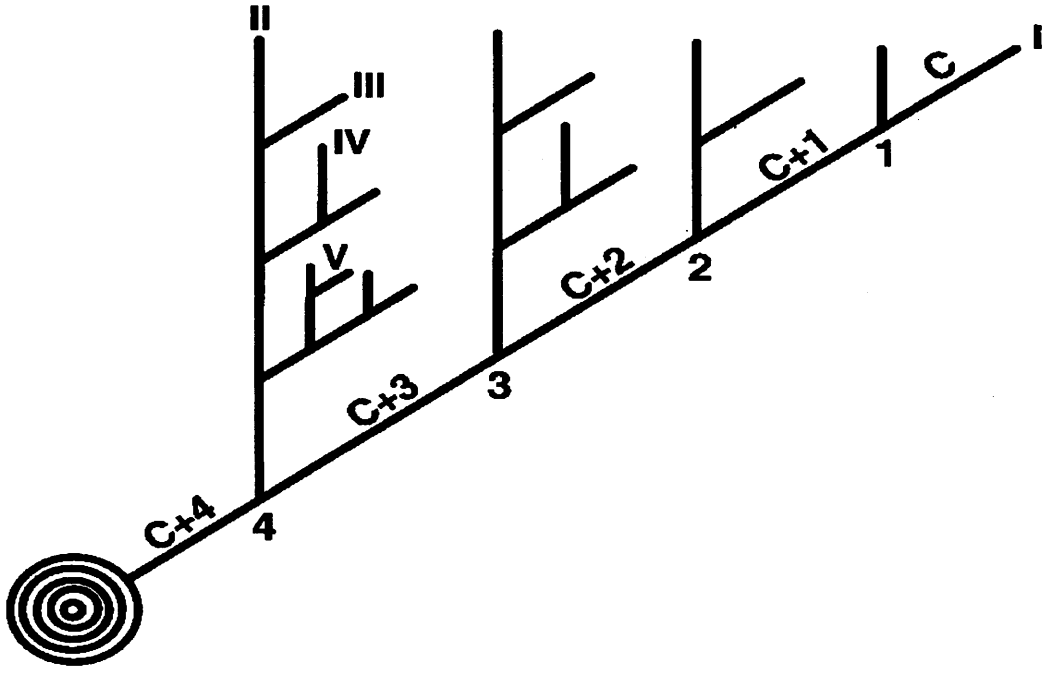


Figure 2. Schematic description of the branch architecture of a 5-yr-old Scots pine branch (Flower-Ellis et al, 1976; Långström, 1980). Roman numerals refer to the branch axis order: I=main axis or first-order branch, II=side branch or second-order branch axis, III, IV and V=third-, fourth- and fifth-order branch axes, respectively. Arabic numerals refer to the branch nodes, i.e. the forking positions on the branch axes according to the age of the side branch (measures of internodal distances equal annual shoot length increments). Shoot age is given as C for current year's growth, C+1 is last year's growth etc. The same labelling applies for needle age classes, but needles older than C+3 are rare in young Scots pine, since they normally drop after their fourth season.

The elongation of current shoots was intensive during the period of clipping and pruning, and was not completed by June 14th when the early season treatments were completed.

Similarly, starting on August 13th, the late season defoliation and/or pruning was done on the LD- and LP-branches, respectively, for both the BST and the WTT trees. Hence, needles and current shoots were cut in two steps in the late season treatments: upper crown or outer branch first, lower crown/inner branch second. At this time, shoot elongation and bud formation were completed, so the defoliation and pruning treatment included the current foliage. On August 30th, when the treatments were finished, the needle age class born in 1988 (i.e., the C+3 needles, Fig. 2), which was bound to fall that autumn, had started to turn yellow on some of the trees.

Sampling Branches for Initial Needle Weight To estimate the initial needle weight present before the treatments were applied, sample branches were taken for needle biomass estimates in late May. From the 10 trees randomly selected for this purpose, one branch in each whorl was sampled. Alternating between whorls and trees, small and large sample branches were taken in order to provide the size variation needed for computation of needle weight functions. This procedure was repeated on 19-20 August when a new branch from each tree and whorl was taken in order to estimate the needle biomass present between the 1991 needle flush and the expected needle fall in autumn. All sample branches were labelled and taken to the laboratory, and processed as explained below.

Needle Fall and Bud Mapping To estimate yearly changes in needle weights in different treatments, needle fall was estimated annually for each age class present on the study branches on the 1989, 1987 and 1985 whorls in both the BST and WTT series of trees. Altogether this was 300 branches. The technique developed by Piene (1989) was modified for Scots pine and a visual estimation of needle fall was conducted. This involved classifying needle fall as 0, 1-20, 21-40, 41-60, 61-80, 81-99 and 100 percent on selected side branches (i.e. second order branch axes) of each study branch.

Parallel with the annual needle fall estimates, we also mapped all developing buds on the 300 study branches. Beginning in spring 1991, the branch architecture of the study branches in the C-, ED- and LD-treatments of both tree series was delineated on branch maps showing the forking and the number of shoots. Each autumn, these maps and similar ones constructed for the pruning treatments in autumn 1991, were updated to include the current shoots, their buds, and notes on their health and appearance. More details on these techniques will be provided in a forthcoming paper on foliage dynamics (Piene et al. in prep.).

Tree and Branch Vitality In late September 1991, all study trees were checked for tree and branch mortality. In trees subjected to branch-scale-treatments (BST), only the experimental branches were checked. In the WTT series all branches were inspected. Dead branches were noted by whorl and marked depending on whether they had died in 1991 or were obviously dead in 1990 or earlier. Dead branches below the last green branch were ignored. We also measured the length of all branches that died in 1991 along the main axis to facilitate estimation of lost needle biomass.

In autumn 1992 and 1993, branches were distinguished according to whether they were dead, dying (no new needles, the remaining ones unhealthy and yellowish), weakened (no current buds, little but healthy foliage) or vital.

Harvesting Procedures Harvesting started on 15 August 1994, when annual growth and budsetting were completed, but before the oldest needle age class (1991) had dropped. The study branches of the 1985, 1987 and 1989 whorls were cut from the BST trees and taken to the laboratory for examination. First, all shoots and buds developed in 1994 were counted and added to the bud maps. Needle survival was then visually estimated as in previous years. Later, needle weights were determined and branches were sampled for volume estimates (see below).

The corresponding sample branches of the trees subjected to whole-tree-treatment (WTT) were treated as above. In addition, all branches in each whorl of the WTT trees were cut off and measured in the field for their annual growth in length. The current vitality status of each of these branches was then recorded as dead, dying, weakened or vital. With the exception of the control trees, one branch per whorl (and each of the entire 1985, 1987 and 1989 study whorls) was sampled for biomass determinations (see below). On whorls containing different size classes of branches, one sample branch was taken from each class.

After all branches were removed from the main stem, data for volume estimates were collected as described below. The leader needles were collected and taken to the laboratory and treated like other needle samples (see below). Field work was completed by 7 September.

Estimation of Initial and Final Needle Weights All branches collected in 1991 and 1994 for needle biomass determinations were treated as follows: First, all needle-bearing shoots (except those on the main axis) were cut and collected separately for each branch and needle age class. Then, the lengths of all internodes were measured along the main branch axes. Finally, the needles of the main axes were sorted by age class. All needle samples were dried for 24 h at 80°C, normally starting on the day of harvest. Then, the needles were separated from their shoot axes, re-dried and weighed to the nearest 0.01 g.

Using these data, relationships between branch length and needle biomass will be established for different whorls. Knowing the number of branches in each whorl and their length before shoot elongation in 1991, the total needle weight prior to treatment can be calculated for each tree in the WTT series as well as for the individual study branches in the branch-scale-treatment (BST) series. The final needle biomass present at harvest in 1994 will be reconstructed for the whole trees in a way analogous to that described above, but using the sample branches in 1994.

The reconstruction of needle weights by age class over time for the different treatments will be done by combining the initial and final needle weight estimates with the needle fall data. These procedures will be detailed in another context.

Stem and Branch Volume Estimation When all branches were removed from the main stem, the annual height growth of the stem was measured and discs were cut in the middle of each stem internode down to 1 m. Discs were also cut at DBH (i.e. 1.3 m), at 0.7 m and at the base of the stem (i.e. 0.1 m). During needle sampling discs were cut from each of the experimental branches in the 1989, 1987 and 1985 whorls of the two series of trees. These branch discs were cut in the middle of each internode along the main branch axis and at the base of the branch. All stem and branch discs were labelled, bagged and frozen immediately. All stem and branch discs were mailed to Canada by express mail, where they were kept frozen until they were analyzed.

Ring widths of the stem and branch discs were measured to the nearest 0.01 mm along two average diameters approximately perpendicular to each other. Branch and stem volumes

were calculated for each year by sectioning using annual ring widths and internode lengths according to Smalian's formula. A cone was used to estimate top volume. Further details on these procedures are given in Piene et al. (in prep.).

Statistical Methods Statistical models were developed to estimate the dry weight of all needles on treated branches at the start (1991) and end (1994) of the experiment. For brevity, this description of model development is focused on the most complex set of these models, which deals with the damaged branches in 1994. The same general approach was used in developing models for undamaged branches in 1991 and 1994.

The first step in this approach was to search for appropriate models for damaged branches. In this search, scatterplots of the total needle dry weight (g) in 1994 were plotted against branch age, length and growth. These plots suggested that, depending on the treatment, total needle dry weight was sometimes linearly and sometimes logarithmically related to branch length. Because of these logarithmic relationships, and the fact that needle weight is necessarily positive, we fitted linear models in log (Y) where Y represents the dependent or response variable, total needle dry weight.

These logarithmically transformed regression models were not used to estimate Y directly, however, because they predict geometric means. The best predictors of needle dry weight on branches where this variable was not measured are the predicted arithmetic means which tend to be under-estimated by their geometric counterparts (Sokal and Rohlf 1981). (Even back-transformation with correction can produce bias if the untransformed variable is not lognormally distributed.)

The logarithmically transformed-regression models were used to provide initial parameter estimates for fitting nonlinear models of the form,

$$E(Y) = \exp(b_0 + b_1X_1 + b_2X_2 + b_3X_3 + ...). \quad (1)$$

Here $E(Y)$ is the expected or predicted average value of Y, the total needle dry weight (g) on the branch. The b_i, $i \geq 0$, are parameters to be estimated, and the X_j, $j > 0$, are independent variables.

To reduce the potential problems associated with multicollinearity among independent variables, many of these variables were standardized (Devore 1982) by subtracting the sample average from each observed value and dividing the result by the sample standard deviation. These variables are listed in Table 2. In addition, pairs of remaining, highly correlated ($r > 0.95$), independent variables were eliminated by excluding one, usually the less recently changed, variable from the analysis. For instance, since the length of a branch at the end of the 1994 growing season (length94) was usually highly correlated with its 1993 length (length93), the latter variable was often omitted when fitting equation (1).

Technically, the process of fitting equation (1) was one of recursive model building using a pseudo Gauss-Newton algorithm for nonlinear least squares estimation (Ralston 1983). We removed parameters with estimates not significantly different from zero ($P < 0.05$) according to the partial F-test (Draper and Smith 1981) and refitted these reduced models. This procedure was continued until only parameters with statistically significant estimates remained. Residual distributions and residuals plotted against predictions were examined to verify that the regression assumptions were adequately satisfied.

Table 2. Standardized independent variables which describe branch characteristics. These variables were standardized by subtracting the sample mean from each observation and dividing the result by the sample standard deviation

Observed Variable	Unit of Measure-ment	Variable Name	Sample Size	Sample Mean	Sample Standard deviation	Sample Minimum	Sample Maximum
age	year	age	425	5.11	3.12	0	13
length in 1988	cm	length88	194	43.2	21.0	3	115
length in 1989	cm	length89	243	52.4	22.9	4	125
length in 1990	cm	length90	280	57.1	24.8	7	130
length in 1991	cm	length91	292	58.9	26.1	1	134
length in 1992	cm	length92	340	56.9	30.5	1	135
length in 1993	cm	length93	393	58.9	32.2	1	137
length in 1994	cm	length94	422	62.0	33.1	2	138
growth in 1989	cm	growth89	194	16.8	5.49	4	32
growth in 1990	cm	growth90	243	10.8	5.54	0	29
growth in 1991	cm	growth91	280	3.93	5.02	0	20
growth in 1992	cm	growth92	291	6.04	6.01	0	36
growth in 1993	cm	growth93	339	9.47	7.58	0	46
growth in 1994	cm	growth94	393	6.58	5.56	0	37

Results and Discussion

Needle Biomass of Undamaged Branches Using the sample branch data from 1991, needle biomass was regressed on branch length for each whorl as well as groups of whorls representing different crown fractions. Linear regressions explained much of the data for individual whorls or groups of whorls in the upper crown ($R^2 > 0.80$, data not shown), but were less successful in the lower part of the crown ($R^2 = 0.50 - 0.70$, data not shown). There was no difference in branch length - needle weight relationships between the two cohorts of branches taken in June and August, respectively. Hence, these cohorts were pooled. By using the experimental branches (harvested in 1994) from the 1989, 1987 and 1985 whorls of the whole-tree-treatment trees as tests, we found that the best fits occurred when using regressions derived for 3-whorl-groups in 1991 ($R^2 = 0.768$, data not shown). Thus, a satisfactory estimate of the needle biomass of any branch at the start of the experiment can be calculated.

Knowing the number of branches per whorl and their lengths, the needle biomass present on the experimental trees at the beginning of the experiment can thus be reconstructed. Similarly, these equations can also be used to calculate the needle biomass of the control trees at harvest in 1994. Thus, the estimation of the needle biomass of undamaged branches and trees is a straightforward procedure. We are currently investigating the possibility that these estimates could be further improved by fitting non-linear equations to the data (as was done for the damaged branches).

Needle Biomass of Damaged Branches Initial analyses of the data sets indicated that the equations developed for undamaged branches were not appropriate for estimating the needle weights of damaged ones. It also seemed prudent to develop different equations for each treatment.

In fitting equation (1) to the data for damaged branches, our goal was purely to derive models for estimating the 1994 needle biomass on those damaged branches which had not been sampled for this variable. At this stage, no attempt had been made to compare treatments directly in terms of their 1994 needle biomass. In fact, there are more appropriate formulations than equation (1) for making such comparisons. Nonetheless, fitting equation (1) does help to draw out trends in the data.

Figure 3, for instance, illustrates our attempt to fit equation (1) to all the data from the early pruning treatment. The result is a surface of predicted mean needle biomasses which depend on the age and length of the branch in 1994 (Fig. 3c). Because the fitted points (Fig. 3b) are drawn from this surface of predicted means, trends in the data are often clearer in the patterns of these fitted points than in the raw data (Fig. 3a). Thus, Figure 3b suggests that in the early pruning treatment, on average, needle biomass was greatest on branches of intermediate age. In addition, Figure 3b indicates that for branches of a given age, longer branches usually had greater needle biomass in this treatment.

While estimated surfaces (Fig. 3c) illustrate trends in the data, they can also be misleading. For instance, Figures 3a and b show that much of the fitted surface is extrapolated. In all treatments, the observations lie along a diagonal in the length94 x age plane: young branches are short, old branches are long. There are no old and short or young and long branches.

Parameter estimates corresponding to Figure 3 and associated statistics can be found at the top of Table 3. This table summarizes the parameter of equation (1) for estimating needle biomass on damaged branches in all treatments. The table is sectioned according to the ages of the branches being considered (age=0 represents branches initiated in 1994). The R^2 reported in the table is Kvalseth's (1985) recommended coefficient of determination. Because non-linear approximation methods were required to fit the models (Ralston 1983), the reported statistics should be viewed as asymptotic approximations (Gallant 1975).

Table 3 shows that equation (1) did not provide a good fit simultaneously to all data from the late defoliation treatment (R^2 = 0.30). One possible reason for this was that the independent variables common to all branches were limited to branch length in 1994 and branch age. This is because, by definition, branches initiated in 1994 can have no length measurements from previous years, and hence have only their age (0) and their 1994 length (or growth).

One possible solution to this difficulty was to fit equation (1) separately to branches of different ages. The last three sections of Table 3 summarize the fits using this approach. The age groupings listed (0, 1-5, and 6 and older) provided the best series of fits in terms of R^2 and SEE. There was no requirement that similar groupings apply to all treatments, so in this sense the results are noteworthy.

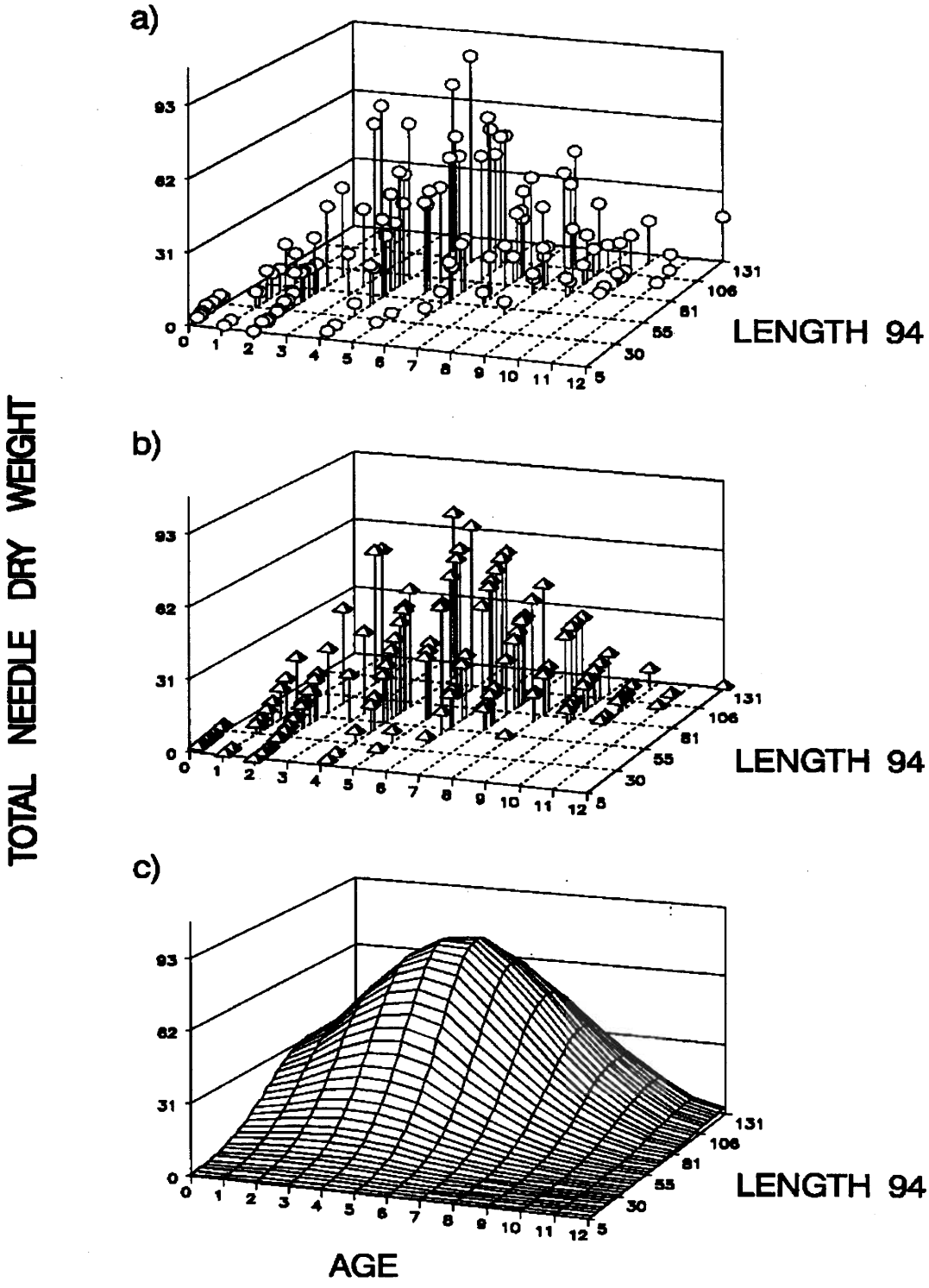


Figure 3. The relationship between total needle dry weight (g), branch length (cm), and branch age (years) in 1994 in the early pruning (EP) treatment: a) observations, b) corresponding model predictions, and c) the model's predictive surface.

Table 3. Fit statistics and parameter estimates (with standard errors, SE) for non-linear regressions of equation (1). The dependent variable is total needle dry weight (g), n is the sample size, and SEE is the standard error of the estimate. See text for further explanation

Treatment	Branch Ages	R^2	SEE	n	Independent Variables	Parameter Estimate (SE)	
early pruning	0-12	.88	7.35	128	intercept	3.27	(0.060)
					age	-0.79	(0.099)
					age^2	-0.61	(0.060)
					length94*age	0.31	(0.093)
					length94	1.51	(0.138)
					$length94^2$	-0.54	(0.087)
early defoliation	0-12	.70	9.03	100	intercept	-6.72	(0.982)
					age	-0.77	(0.098)
					age^2	-0.14	(0.071)
					ln(length94)	2.40	(0.227)
late defoliation	0-13	.30	8.22	42	intercept	-7.32	(3.207)
					age	-0.83	(0.281)
					ln(length94)	2.34	(0.749)
late pruning	0-11	.64	11.5	119	intercept	-2.36	(0.744)
					ln(age)	-0.48	(0.209)
					age^2	-0.27	(0.075)
					ln(length94)	1.56	(0.218)
early pruning	0	.54	0.90	10	intercept	-1.74	(1.087)
					ln(length94)	0.96	(0.348)
early defoliation	0	.79	0.81	10	intercept	-1.96	(0.715)
					ln(length94)	1.10	(0.240)
late defoliation	0	** insufficient data **					
late pruning	0	.90	0.47	8	intercept	5.26	(0.623)
					length94	3.18	(0.483)
early pruning	1-5	.95	5.42	65	intercept	-14.2	(2.73)
					age	-1.51	(0.418)
					ln(growth94*age)	1.44	(0.368)
					length94	-0.81	(0.272)
					ln(growth94)	-1.87	(0.448)
					ln(length94)	3.96	(0.648)
early defoliation	1-5	.85	6.70	48	intercept	-3.70	(0.716)
					growth94*age	0.90	(0.243)
					ln(growth94*age)	-0.57	(0.087)
					growth94	1.01	(0.197)
					ln(growth94)	2.18	(0.189)
late defoliation	1-5	.87	2.74	15	intercept	4.64	(0.692)
					ln(growth94*age)	-0.71	(0.230)
					length94	3.16	(0.546)
					$length94^2$	-12.6	(2.39)
					$length93^2$	12.6	(2.52)
late pruning	1-5	.89	4.76	60	intercept	13.0	(1.59)
					ln(age)	-5.55	(0.927)
					age^2	-3.46	(0.563)
					length94	0.98	(0.108)
					$length94^2$	-0.57	(0.117)

Table 3 cont'd

early pruning	6-12	.79	8.45	53	intercept	3.49	(0.179)
					growth94*age	1.39	(0.245)
					length94*age	-1.62	(0.315)
					length89*age	1.30	(0.329)
					length94	0.94	(0.175)
early defoliation	6-12	.72	8.81	42	intercept	-15.2	(2.74)
					age	-1.80	(0.303)
					ln(length94)	4.43	(0.649)
					growth90	-0.45	(0.153)
late defoliation	6-13	.56	7.68	26	intercept	-6.56	(2.067)
					ln(growth92)	4.90	(1.020)
					$growth92^2$	6.79	(2.389)
late pruning	6-11	.68	11.8	50	intercept	-7.28	(2.020)
					growth94*age	0.70	(0.148)
					length88*age	-0.40	(0.108)
					ln(length94)	2.62	(0.470)
					ln(growth93)	-0.54	(0.115)

Conclusions

Different statistical models were developed to estimate the dry weight of needles on branches subjected to various damage treatments. In some cases (e.g., early pruning) a single model provided a reasonable fit to all the data. In other cases (e.g., late defoliation) it was advantageous to develop different models for different groups of branch ages. The optimal grouping of branch ages (0, 1-5, and 6 years of age and older) was the same for all damage treatments. These models (Table 3) will be used to reconstruct the needle biomasses on damaged branches of experimental trees at the end of the experiment (i.e., in 1994). Corresponding models are in their final stages of development for reconstructing the needle biomasses of all (undamaged) branches at the start of the experiment (i.e., in 1991) and on the control trees at the end of the experiment.

The experimental design and techniques used to simulate damage caused by pine sawflies and pine shoot beetles will be discussed in detail in forthcoming papers. Here it may suffice to notice that shoot clipping produces similar growth effects as the beetle's feeding activity (Långström et al. 1990). Similarly, Lyytikäinen (1992) found no difference in larval performance when sawfly larvae were exposed to naturally and artificially defoliated trees. Thus, the defoliation and pruning treatments should fairly well represent the natural situations they are supposed to mimic. As this study was done on one site only, it is worth mentioning that another study using the same single-branch-concept was running parallel to this one during 1992-1996 in another site. Branches of Scots and lodgepole pine (*Pinus contorta* var. *latifolia)* were exposed to pruning, defoliation and both, and needle biomass and branch growth were followed over time. Thus, this second study will serve as a kind of replication in time and space to the present one.

Further exploration of the data collected includes preparation of a number of papers addressing the issues raised under the study objectives. One paper will ascertain if individual branches could be used to represent whole trees (Piene et al. in prep.); another will compare the performance of comparable branches of SBT- and WTT-trees (Långström et al. in prep.).

The main work will be to reconstruct and match needle biomass and stem growth dynamics in the different treatments. Finally, these processes will be modelled.

Acknowledgments

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Spruce Budworm Defoliation-Foliage Production: Differences Between White Spruce and Balsam Fir

HARALD PIENE

Natural Resources Canada, Canadian Forest Service - Atlantic Forestry Centre, P.O. Box 4000, Fredericton, New Brunswick, Canada, E3B 5P7

ABSTRACT Foliage production was compared between white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) following defoliation by the spruce budworm (*Choristoneura fumiferana* (Clem.)). After severe defoliation by spruce budworm, including bud destruction, both white spruce and balsam fir react with a prolific epicormic shoot production. When spruce budworm defoliation is low to moderate with no bud destruction, white spruce still react with a prolific shoot production, but no such shoot production occurs in balsam fir. The implications that this difference in shoot growth has on volume growth are discussed. Also, a hypothesis is presented which states that white spruce, balsam fir and the spruce budworm have, through evolution, developed individual adaptive strategies that ensure coexistence and future growth and survival.

MUCH ATTENTION HAS been given to the mechanisms of woody plant defenses against insect attacks (Mattson et al. 1988, Baranchikov et al. 1991). Insect feeding may reduce plant tissue quality which, in turn, may result in reduced insect performance either shortly after or in the years following the injury (induced resistance). In particular, this has been observed for deciduous species, and conifers may have a limited capacity for induced resistance (Neuvonen and Niemelä 1991). However, insect damage does not always induce resource decline (Haukioja et al. 1990). In fact, it may improve the food resource, for example, when it results in increased shoot production and foliage quality (Piene and Percy 1984, Piene 1989).

The objective of this report is to discuss shoot production in white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) in relation to their growth performance following defoliation by the spruce budworm (*Choristoneura fumiferana* (Clem.). Furthermore, it presents the hypothesis that white spruce, balsam fir and spruce budworm have, through evolution, developed individual adaptive strategies that ensure coexistence and future growth and survival.

Bud Formation. In general, there are two foliation systems in conifers: (1) the normal development of lateral buds and buds originating from the terminal bud unit; and (2) epicormic or adventitious bud development, resulting from stress or changing tree conditions that could range from improved light conditions from silvicultural operations to severe insect attacks. Epicormic shoots originate from preformed suppressed buds that are formed in continuity with the apical meristem and show the presence of a vascular trace to the primary xylem. These buds are distinguished from adventitious buds which totally lack such a trace (for a discussion see Bryan and Lanner 1981).

In balsam fir, these developing buds are epicormic in origin (Stone 1953). In white spruce, they are also most likely of epicormic origin, as adventitious buds are relatively uncommon in conifers (Stone 1953, Brown 1971).

Pages 247-252 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Shoot Production - High Spruce Budworm Densities. Although white spruce is less susceptible to spruce budworm defoliation than balsam fir (Greenbank 1963, Thomas 1983), under extremely high spruce budworm densities, bud destruction will occur. White spruce compensate for this with prolific epicormic shoot production the following year. Under normal circumstances, with no further severe insect attacks, this ensures rapid tree recovery (Piene, unpublished data).

Similarly, balsam fir responds vigorously to bud destruction with prolific epicormic shoot production. Complete defoliation of all age classes of needles of balsam fir during a 2-year period, followed by yearly protection by insecticide spraying, showed that 3 years into the recovery period, the number of shoots per centimeter of branch length was significantly higher than on undefoliated trees (Piene 1989). As a result, foliage weight per tree was similar to that of undefoliated trees (Fig. 1), although there were only three needle age classes present for the defoliated trees as opposed to the normal eight for the undefoliated ones. This rapid foliage recovery continued and 5 years after the protection started, there was no significant difference in growth rates between defoliated and undefoliated trees (Piene 1989).

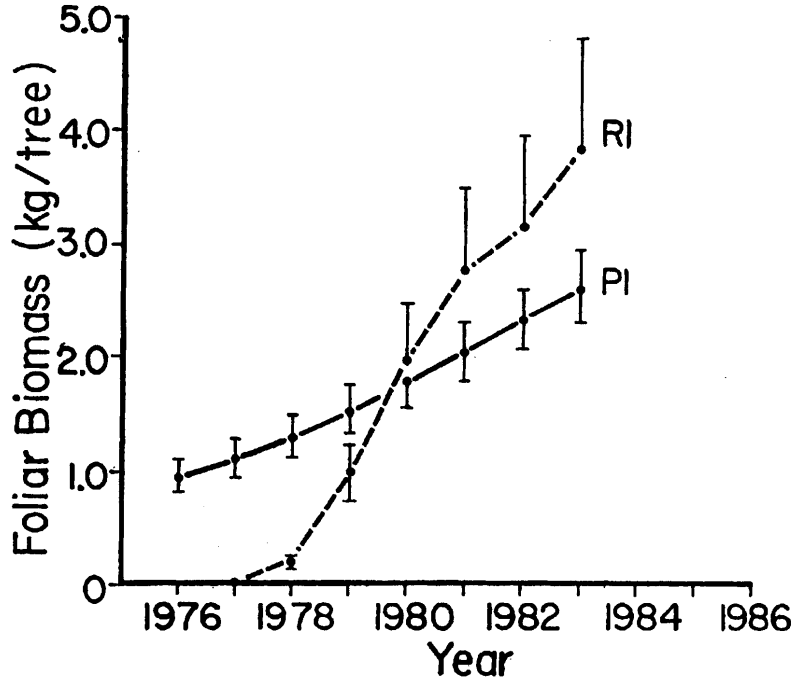


Figure 1. Changes in total foliar biomass per tree for undefoliated (P1, n=21) trees, and for trees (R1, n=16) that were completely defoliated of all age classes during 1976-77, and subsequently protected thereafter (adapted from Piene 1989). The vertical bars represent SE above and (or) below the means (p=0.05).

Based on the previous discussion, white spruce and balsam fir react similarly to severe defoliation by the spruce budworm that includes bud destruction, with prolific epicormic shoot production. Although these epicormic shoots appear mainly around the branch nodes for white spruce, they can appear anywhere along the branch for balsam fir (Piene, unpublished data).

Shoot Production - Low to Moderate Spruce Budworm Densities. When spruce budworm defoliation is relatively low and does not include bud destruction, the response to foliage loss differs dramatically between white spruce and balsam fir. White spruce does not require bud destruction to trigger the development of epicormic shoots and is extremely sensitive to losses of current-year needles. In fact, on undefoliated trees, each year there is some development of epicormic shoots (Piene, unpublished data), presumably due to changing environmental factors such as local light conditions. This extreme sensitivity to needle loss is demonstrated in an experiment where plantation white spruce were artificially defoliated. A loss of 50% of the current-year foliage resulted in an increase in shoot production of about 40%, primarily from the release of lateral buds (Piene, unpublished data). In contrast, balsam fir is not very sensitive to needle loss of current foliage when buds are not destroyed, and no significant amounts of epicormic shoots develop (Piene and Little 1990).

These differences in sensitivity to needle loss between white spruce and balsam fir when spruce budworm populations are relatively low with no bud destruction are demonstrated in Figure 2. Although a loss of about two age classes of needles during a 2-year period resulted in a growth reduction of about 20% for white spruce, the growth reduction for balsam fir was much more severe, amounting to about 50%. The white spruce compensated for the foliage loss by prolific epicormic shoot production in the second year of defoliation (Piene 1991), which reduced the growth loss in comparison to balsam fir where no such compensation occurred.

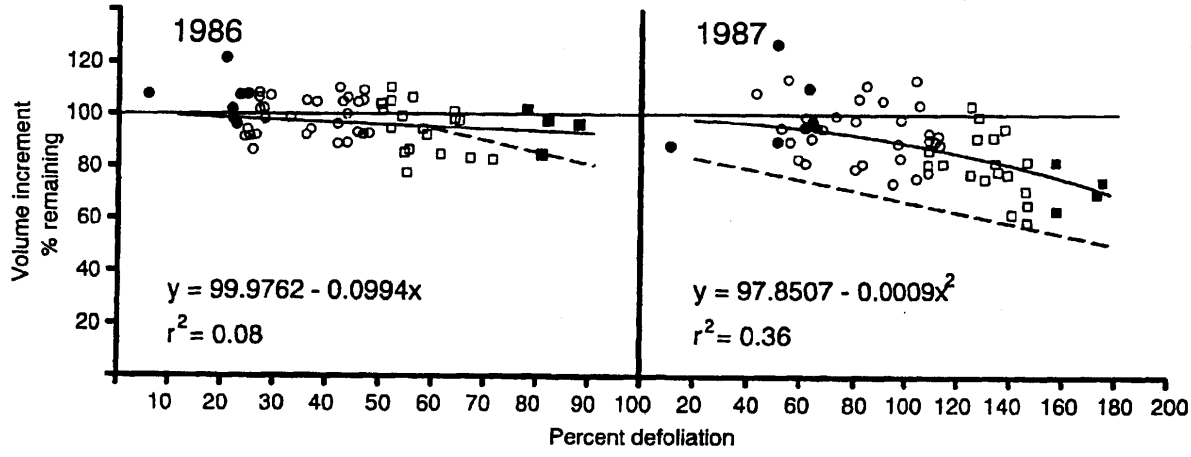


Figure 2. Relationships between percent volume increment remaining in 1986 and 1987 and percent defoliation of current-year foliage for plantation-grown white spruce. Different symbols indicate 25% classes of defoliation in 1986. Defoliation in 1987 is accumulated defoliation (defoliation in 1986 + 1987). The solid line at 100% indicates no change in volume increment. The other solid lines indicate the regression lines for white spruce, while the broken lines show the relationships for balsam fir (from Piene 1991).

Conclusion

In eastern North America, spruce in mixture with balsam fir covers large tracts of forest land, with white spruce as the most common spruce species (Gordon 1985). Periodically, the spruce budworm has severely damaged this forest, and outbreaks have been documented to have occurred since the early 1700s (Royama 1984). White spruce and balsam fir have probably been in coexistence with spruce budworm for thousands of years.

I hypothesize that white spruce, balsam fir and the spruce budworm have, through evolution, each developed individual strategies to ensure coexistence and survival. Regardless of strategy, replacing foliage lost due to defoliation is of the highest priority for a tree for future survival (Ericsson et al. 1980). During especially severe spruce budworm outbreaks, both white spruce and balsam fir experience bud destruction and, as discussed previously, both species respond with a prolific epicormic shoot production that compensates for the previous year's foliage loss. Bud destruction is also common in balsam fir, with subsequent release of epicormic buds, when spruce budworm populations are at more normal levels (Piene, unpublished). However, I contend that, for white spruce, bud destruction is relatively uncommon. Therefore, to replace lost foliage, white spruce has developed the ability to release epicormic buds even in response to small losses of current-year foliage, thus maintaining or perhaps even increasing the foliage complement (Piene, unpublished).

The spruce budworm, on the other hand, may benefit from increased nutrient levels in the needles of the epicormic shoots (Piene and Percy 1984), thus maintaining vigorous population levels (Royama 1992). As the spruce budworm outbreak continues, white spruce, balsam fir and the spruce budworm are, in a sense, benefiting from each other's existence. However, as defoliation continues, balsam fir and white spruce become weakened. This is probably due to a low shoot production, thus decreasing the amount of "food" available to the tree, in combination with a decrease in nutrient uptake caused by rootlet mortality (Redmond 1959). Eventually, the amount of "food" produced is so low that it cannot meet the requirement for tree maintenance, and the tree dies. This is particularly true for balsam fir, which is more vulnerable than white spruce (Blais 1981).

This difference is probably due to a combination of differences in foliage production and to feeding rates on older foliage. While backfeeding on older age classes is common on balsam fir, it is rarer on white spruce because the older age class foliage is almost unpalatable to the spruce budworm (Thomas 1983).

After about 6 to 10 years, the spruce budworm declines to endemic levels (Royama, pers. comm.). However, due to the difference in vulnerability between white spruce and balsam fir, a much larger percentage of the seed-bearing balsam fir than white spruce has been killed by the spruce budworm. Although balsam fir has much better seedling establishment characteristics than white spruce, the longer lived white spruce present a continued seed source that ensures a mixture of white spruce and balsam fir in the new regenerating stand.

Therefore, the spruce budworm is also an essential factor in maintaining the white spruce in the future stand (Gordon 1985). Thus, the white spruce-balsam fir ecosystem is maintained, and presents a readily available food source for the next spruce budworm outbreak.

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The Role of Parasitoids in the Population Dynamics of Forest Lepidoptera

ALAN A. BERRYMAN

Department of Entomology, Washington State University, Pullman, WA 99164 USA

ABSTRACT Using new methods of time series analysis, I show that population fluctuations of three forest caterpillar species seem to be strongly influenced, if not dominated, by interactions with insect parasitoids, and conclude that parasitoids may play a more significant role in the dynamics of forest Lepidoptera than is generally recognized.

SOME FOREST LEPIDOPTERA exhibit remarkable variations in abundance, sometimes going through 10,000-fold changes in density during population increases and decreases, (e.g., the larch budmoth, *Zeiraphera diniana*) (Baltensweiler et al. 1977, Berryman 1996). Many other forest caterpillars fluctuate with much less variability, remaining at sparse densities for indefinite periods of time.

Foliage-feeding Lepidoptera are known to be attacked by numerous insect parasitoids in the families Ichneumonidae, Braconidae, Eulophidae and Chalcidae (Hymenoptera) as well as Tachinidae and Sarcophagidae (Diptera). The larch budmoth, for example, is attacked by 94 species of parasitoids (Baltensweiler et al. 1977). The question I wish to address in this paper is: what role do parasitoids play in the fluctuations, or lack thereof, of forest caterpillar populations? I will approach this question by reference to studies on three forest defoliators.

CASE 1: The blackheaded budworm, *Acleris variana* (Tortricidae). Morris (1959) analyzed 11 years of data on the density of blackheaded budworm caterpillars and their larval parasitoids (Fig. 1), and concluded that the key factor in the population dynamics of this insect was a suite of larval parasitoids. Although key factor analysis has been discredited recently (Royama 1996), and although McNamee (1979) has proposed an alternative hypothesis for blackheaded budworm dynamics, I was forced to agree with Morris (Berryman 1986, 1991a). My conclusions are based on a reanalysis of the budworm-parasitoid data using some new methods of time series analysis (Royama 1977, 1992, Berryman 1991a, 1992, 1994, Berryman and Millstein 1994, Turchin 1990).

Time series analysis of population counts over a number of years looks for correlations between the rate of increase of the average individual, $R = \ln N_t - \ln N_{t-1}$, and population density N_{t-d}. In other words, we perform a simple regression on the model

$$R = a + bN_{t-d} \qquad (1)$$

where d is the dominant lag in the density dependent feedback response (Berryman 1992), or on the multiple regression on the model

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$$R = a + b_1 N_{t-1} + b_2 N_{t-2} + \ldots\ldots b_d N_{t-d} \quad (2)$$

where d is now the maximum dimension of the feedback structure (Turchin 1990) and densities may be transformed into logarithms (Royama 1977, 1992). The dimension is rarely greater than 2 in biological data.

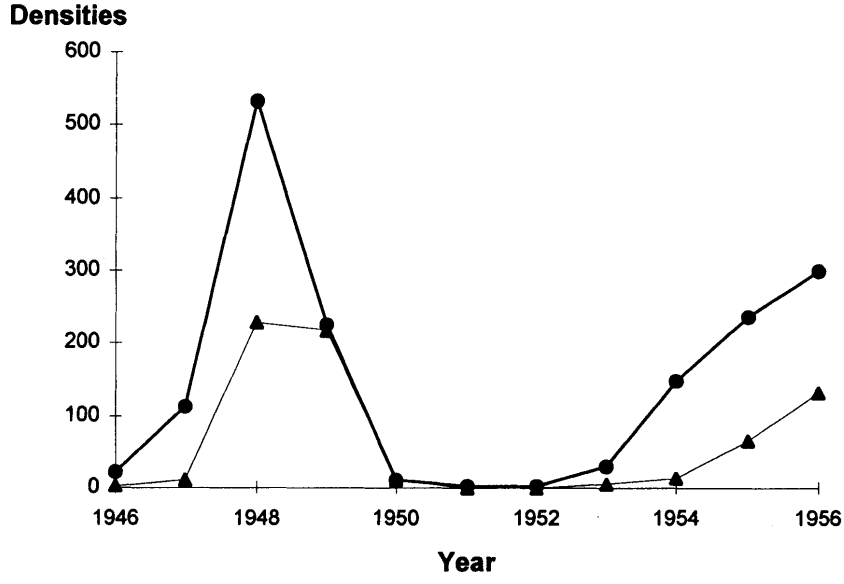


Figure 1. Numbers of blackheaded budworm larvae per 100 m^2 of balsam fir foliage; ● = total larvae, ▲ = parasitized larvae (after Morris 1959).

In the case of the blackheaded budworm, the dynamics are strongly affected by "second order" feedback (d=2), or delayed density dependence (Turchin 1990, Berryman 1986, 1991a, 1992, Berryman and Millstein 1994). What this means is that the survival and/or reproduction of the budworm in one year is dependent on larval density in the previous year. To obtain such an effect, one needs to have a negative feedback mechanism that operates with a delay of the same relative time scale as the budworm. There seem to be two plausible explanations for this second order feedback effect:

1. *A foliage effect.* Second order feedback can be created if the quality of foliage is affected by defoliation in the previous year (the "delayed induced defense" hypothesis [Haukioja et al. 1988, Baltensweiler and Fischlin 1988]) or if high caterpillar densities and/or food shortages in one year affect the survival and/or fecundity of the next generation via physiological (the "maternal effect" hypothesis [Rossiter 1994, Ginzburg and Taneyhill 1994]) or genetical (the "genetic polymorphism" hypothesis [Chitty 1967]) mechanisms. However, blackheaded budworm populations decline before the host plant (balsam fir) is seriously defoliated and food shortage becomes an important limiting factor (Morris 1959, Miller 1966). Hence, it seems unlikely that the second order feedback is due to foliage effects.

2. *A parasitoid effect.* Many parasitoids, especially those which are relatively specific, have generation spans similar to those of their lepidopteran hosts. This, together with the fact that parasitoids often exhibit strong numerical responses to host density, can give rise to delayed

negative feedback. The numerical response of parasitoids can be measured by fitting the equation (Berryman 1991a, 1994)

$$R_p = \ln P_t - \ln P_{t-1} = A_p - C_p \frac{P_{t-1}}{N_{t-1}} \tag{3}$$

to time series data, where R_p is the realized per-capita rate of change of the parasitoid population from one generation to the next, P_t is the density of the parasitoid population, N_t is the density of the host population, A_p is the maximum rate of change of the parasitoid when host density is infinitely large, and C_p is the impact of the parasitoid on its host. Fitting this model to data on the density of budworms and larval parasitoids explains 91% of the variation in R_p, demonstrating that the parasitoids have a very strong numerical response.

We can also estimate the effect of the parasitoid on the rate of change of the budworm by fitting the equation (Berryman 1992, 1994)

$$R_n = \ln N_t - \ln N_{t-1} = A_n - B_n N_{t-1} - C_n \frac{P_{t-1}}{N_{t-1}} \tag{4}$$

in which the parameters A_n and C_n have similar meaning as for the parasitoids and B_n reflects the effects of first order feedback due to competition for food, functional responses of predators, and so on. Equation (4) explains 85% of the budworm population changes and, of this, 76% is explained by parasitism alone (partial correlation 82%). Equations (3) and (4) can now be used together to simulate budworm-parasitoid dynamics, and we see that the model predicts the 6-8 year cycles of abundance seen in the data (Fig. 2). These results, together with the analyses of Morris (1959), Berryman (1986, 1991a, 1992) and Turchin (1990), strongly suggest that parasitoids are largely responsible for density fluctuations in budworm populations.

CASE 2: The spruce needleminer, *Epinotia tedella* (Tortricidae). Munster-Swendsen (1991) analyzed 20 years of data on the spruce needleminer inhabiting a Danish spruce plantation (Fig. 3), and used these data to construct a detailed simulation model of the interactions between needleminer, host-tree, parasitoids, predators, diseases and weather (Munster-Swendsen 1985). This model faithfully recreated the dynamics observed in this and other plantations. By deleting variables from his model, Munster-Swendsen found that parasitoids were the major factors regulating populations of this needleminer. This conclusion is further supported by the fact that strong second order effects are observed in spruce needleminer data, and parasitoids have a strong numerical response, with equation (3) explaining 81% of the variation in parasitoid rates of change (Berryman and Munster-Swendsen 1994).

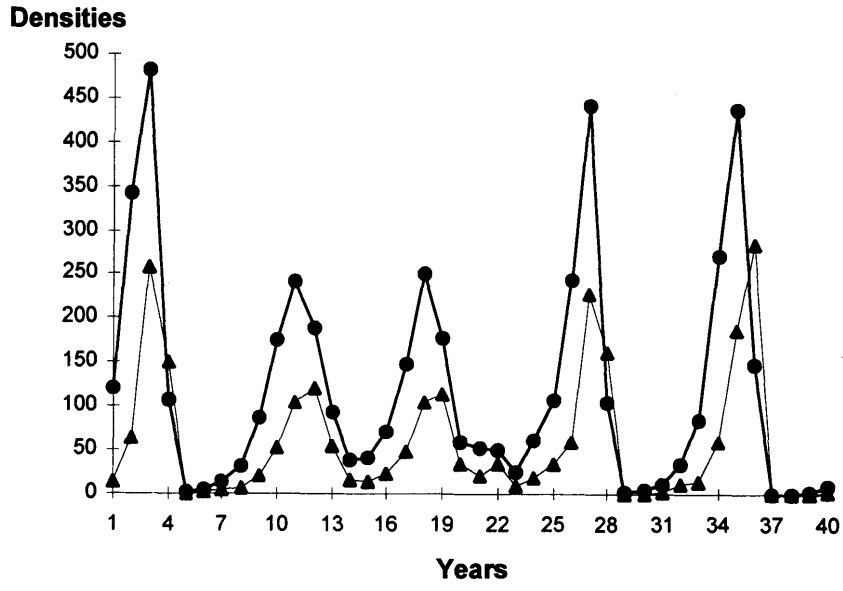


Figure 2. Simulation with the two species model [equations (3) and (4)] with parameters estimated from the data in figure 1: ● = total larvae, ▲ = parasitized larvae $A_p = 2.442, C_p = 5.535, A_n = 2.152, B_n = 0.003, C_n = 4.131,$ **with some random variability added to the computed *R*-values (after Berryman 1991a).**

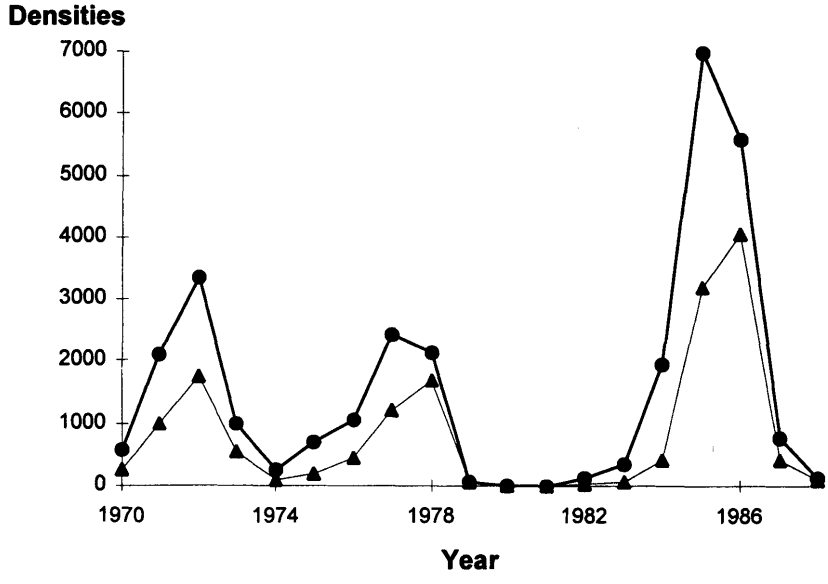


Figure 3. Numbers of spruce needleminer and parasitoid larvae per 10 m^2 of spruce foliage [from Munster-Swendsen (1991) and personal communication]. ● = total larvae, ▲ = parasitized larvae

Like the blackheaded budworm, spruce needleminers rarely cause severe defoliation to their host trees. Parasitoid density also has a strong negative effect on needleminer rates of

change, explaining 76% of the variation. Simulation experiments show that models using fits to equations (3) and (4) also recreate the 9-10 year oscillations seen in needleminer populations.

One of the interesting things that emerged from needleminer population studies was the phenomenon called pseudoparasitism (Munster-Swendsen 1994). Munster-Swendsen found that "reduction in fecundity" was a key factor in needleminer population fluctuations, and that direct mortality caused by parasitoids was insufficient to explain the decline of needleminer populations. This lead him to discover that parasitoids often sting, but fail to oviposit in their hosts, particularly when parasitoid densities were high (possibly due to interference between parasitoids). Needleminers which were pseudoparasitized developed to adults but were infertile (Brown and Kainoh 1992), thereby explaining, simultaneously, the "reduction in fecundity" effect and the strong suppressive effect of parasitoids. These results may cause us to reconsider the role that parasitoids play in the population dynamics of other forest defoliators.

CASE 3: The gypsy moth, *Lymantria dispar* (Lymantriidae). Sisojevic (1979) collected 26 years of data on the density of gypsy moths and their tachinid parasitoids in the former Yugoslavia (Fig. 4). The data show a strong second order effect (Montgomery and Wallner 1988, Turchin 1990, Berryman 1991b), but in this case defoliation of the host plant sometimes occurs. However, experimental supplementation of gypsy moth populations during the low density phase prevented defoliation, suggesting that some other factor, probably parasitoids, was able to respond and suppress the prey population before defoliation could occur (Maksimovic et al. 1970).

On the other hand, the gypsy moth dynamics are not quite so simple. Berryman (1991b) found that second order effects dominated the time series for the first 16 years but first order feedback became prevalent in the final 10 years. In addition, multivoltine generalist parasitoids were observed to be more common during this time, while univoltine specialists were most abundant during the first period (Fig. 4). This suggests that the dynamics of gypsy moth populations in southern Europe are largely determined by the relative dominance of tachinid generalists, which generate first order dynamics, and tachinid specialists which generate second order dynamics.

Berryman (1991b) also found strong second order effects in the North American gypsy moth time series following its collapse from very high densities, and concluded that gypsy moth populations had been controlled by introduced parasitoids, an idea that has generated some controversy (Liebhold and Elkinton 1991, Berryman 1991c). However, stocking experiments by Gould et al. (1990) strongly suggest that generalist tachinid parasitoids can suppress incipient gypsy moth outbreaks by rapid (first order) spatial density dependent responses. These results suggest that North American gypsy moth populations are being regulated by similar mechanisms as those in Europe.

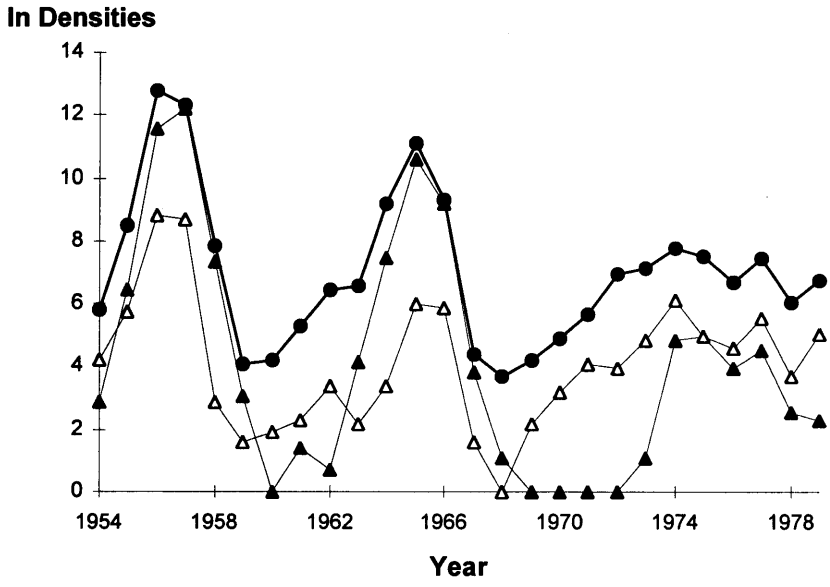


Figure 4. Numbers of gypsy moth egg masses per ha (●) and percentage parasitism by specific (▲) and general (Δ) tachinid parasitoids (after Sisojevic 1979).

Conclusions

I have discussed three cases where parasitoids seem to be a major force in the observed population fluctuations of foliage-feeding forest Lepidoptera. If time had permitted I could have included other examples and cited cases of successful biological control of forest caterpillars by parasitoids to support this contention (see, Berryman 1996). My general conclusion is that parasitoids frequently play a more significant role in the dynamics of forest Lepidoptera than they are sometimes given credit for. Of particular importance is the recent discovery of pseudoparasitism (Brown and Kainoh 1992, Munster-Swendsen 1994) which suggests that the effect of parasites on the dynamics of their hosts may be greater than is generally believed (particularly in Tortricids), and may also explain the reduction in fecundity often observed during the decline of caterpillar outbreaks. This should not be taken to mean that I believe other factors (e.g., food quantity/quality and virus epizootics) are not important in specific cases or at certain times in the examples cited above. Parasitoids, however, seem to be a more consistent and persistent force in the dynamics of many defoliator populations, regardless of the other forces that may be involved.

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Effects of Silvicultural Management on Gypsy Moth Dynamics and Impact: An Eight-Year Study

R.M. MUZIKA, A.M. LIEBHOLD, AND K.W. GOTTSCHALK

USDA Forest Service, 180 Canfield Street, Morgantown, WV 26505 USA

ABSTRACT A long-term study initiated in 1989 at the West Virginia University Forest contrasted the effects of silvicultural treatments on the development of gypsy moth (*Lymantria dispar* L.) outbreaks and their impacts. The area is a relatively susceptible *Quercus* spp./mixed hardwood forest. Egg mass densities, survivorship, and mortality from natural enemies differed little between stands that were treated silviculturally and those that were not. However, stands that were thinned had less overstory mortality than unthinned stands despite incurring comparable levels of defoliation.

THE GYPSY MOTH (*Lymantria dispar* L.) is a polyphagous insect first introduced into North America in the late 1860s. Since that time, its range has expanded steadily from the northeastern United States to large areas of commercial forests in the Appalachian Mountains. Outbreaks are likely to be intense and substantially affect forest resources in those areas. While it is possible to reduce defoliation levels by applying pesticides aerially, other approaches to managing gypsy moth are needed because of the expense and ecological impact of pesticides on the environment. Several silvicultural approaches to managing gypsy moth populations have been proposed over the last 100 years (Fiske 1913, Clement and Munro 1917, Behre 1939, Bess et al. 1947, Gottschalk 1993). All have emphasized the use of sanitation thinning to reduce or eliminate host species preferred by the gypsy moth. Theoretically, this technique would lower stand susceptibility (defoliation potential). Gottschalk (1993) also proposed the use of presalvage thinning to remove low-vigor host trees to reduce stand vulnerability (likelihood of mortality following defoliation).

Of the relatively few studies that have examined the effectiveness of silvicultural manipulations in reducing stand susceptibility and vulnerability, most have focused on the effects of thinning on gypsy moth impacts with respect to forest stand structure and composition. In addition, there is a need to understand how silvicultural manipulations may influence the dynamics of gypsy moth populations. The objectives of this study were to test the effects of both presalvage and sanitation thinning on gypsy moth dynamics. Specifically, we tested how thinnings affected changes in egg mass density, patterns of within-generation survivorship, and the amount of mortality caused by various gypsy moth parasitoids and pathogens. We also evaluated the resulting forest vegetation following thinnings and the long-term impact of gypsy moth populations.

Pages 261-268 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Materials and Methods

The study area was located at the West Virginia University Forest (WVUF) in Monongalia and Preston Counties. In 1989, 16 stands (average size 10.5 ha) that reflected a range of overstory types were established on the WVUF. Some stands were mixed hardwood, with only 15% oak (*Quercus* spp.) in the overstory, while others were mixed oak, with more than 80% of the basal area in oak species. Each stand was paired with an adjacent stand bearing similar vegetation and site characteristics. In the winter of 1989-90, one stand of each pair was selected for thinning. In stands where oak accounted for a low proportion of stand basal area (mostly less than 50%), a sanitation thinning was applied. The primary objectives when marking trees were to reduce total stand basal area and preferentially remove host-tree species preferred by the gypsy moth (Gottschalk 1993). In stands where oak accounted for a higher proportion of stand basal area (greater than 50%), presalvage thinning was applied. The principal objective was to remove trees in poor condition regardless of species or their preference by gypsy moth larvae (Gottschalk 1993).

Gypsy moth sampling. Gypsy moth populations were sampled before thinning and each year thereafter until 1996 by counting all egg masses in 0.01-ha (1/40-acre) plots in each stand (Liebhold et al. 1994). Within each stand, plots were located in a grid with 100 m between sampling points. Each stand had 10 to 19 permanent plots depending on stand size.

In stands where larval densities were sufficiently high, larvae were collected weekly to quantify mortality due to parasitism and disease. The first larval sample was timed to coincide with larval hatch and the last sample was taken when pupation began. When available, 100 larvae were collected each week at five sampling locations within each stand. Early instars were collected by sampling foliage of saplings and seedlings; late instars and pupae were collected from tree boles and also from burlap bands that were placed around trees.

Larvae were placed in individual 30 ml plastic cups containing artificial diet. The cups were placed in an outdoor insectary located on the WVUF so that temperature and phenological development were approximately the same as that for field populations. Each cup was checked weekly until eclosion. The presence of parasitoids in each cup was recorded and cadavers were inspected microscopically for viral polyocclusion bodies or fungal spores. The maximum percent mortality among collections was used as the estimate of mortality occurring for each agent in the field. Peak percentage mortality is the best measure of parasitoid and disease impact under the sampling plan used in this study (Gould et al. 1989).

Because mortality caused by various gypsy moth parasitoids and pathogens is density dependent (Elkinton and Liebhold 1990), we wanted to evaluate the effect of thinning on mortality using an analysis that accounted for variation in host density. Stepwise regression (Draper and Smith 1981) was used to model peak mortality (transformed using an arcsine-square root transformation) as a linear function of: (1) N_t, gypsy moth density [log(x+1)] at the beginning of the current generation; and (2) N_{t-1}, gypsy moth density [log(x+1)] at the beginning of the prior generation. Each of these independent variables was successively added to the model; the probability associated with the *F* statistic ($P < 0.05$) for each independent variable was used as the criterion for entering and retaining each term in the model. These selected variables were included as covariates in an analysis of variance where we assumed a randomized complete-block design (Steel and Torrie 1980). Peak percent

mortality was the response, N_t and N_{t-1} were included as covariates (only if they were significant in the stepwise regression), and treatment (thinning) and block were the effects.

Vegetation sampling. Overstory vegetation was sampled in 1989 prior to silvicultural treatments, and each year thereafter. Measurements were taken on overstory vegetation on each of 20 0.04-ha (0.1-acre) plots in the 16 stands. All overstory vegetation (dbh ≥ 6.3 cm) in each plot was identified as to species and measured. Defoliation estimates were taken on each overstory tree. The percentage of foliage removed was estimated visually and the estimates weighted by the diameter of the defoliated tree.

Results and Discussion

In this study, eight distinct causes of larval mortality were identified across all stands (Table 1). Unidentifiable causes, however, accounted for the majority of gypsy moth larval mortality in each year except 1991. Not all mortality agents were recovered in all stands.

Table 1. Peak percent mortality each year from mortality agents of gypsy moth, based on weekly collections of larvae and pupae

Item	1990	1991	1992	1993	1994
Unidentified	71.0	47.5	86.8	91.1	90.1
NPV	34.7	86.3	51.4	41.5	17.6
Entomophaga maimaiga	0	0	5.7	36.7	2.0
Parasetigena silvestris	1.1	19.8	25.2	30.3	36.2
Cotesia melanoscela	0	1.7	11.6	28.7	19.8
Blepharipa pratensis	22.7	13.4	20.3	8.4	[a]
Brachymeria intermedia	3.4	19.8	2.9	3.0	[a]
Compsilura concinnata	1.0	16.2	6.9	5.6	16.8
Phobocampe unicincta	0	0	6.8	3.0	9.2

[a] Incomplete data

The relationship between parasitism and host density varied considerably among parasitoid species (Table 2). Parasitism by *Brachymeria intermedia*, *Compsilura concinnata*, *Cotesia melanoscela*, and *Parasetigena silvestris* was positively related to density in the current generation, N_t, and parasitism by *Blepharipa pratensis* was inversely related to N_t, reflecting the delayed density dependence of these parasitoids.

Parasitism by *C. concinnata*, *C. melanoscela*, and *P. silvestris* was inversely related to host density in the previous generation, N_{t-1}. These patterns are mostly in agreement with previous studies (Elkinton and Liebhold 1990, Williams et al. 1992, 1993).

Mortality caused by the nuclearpolyhedrosis virus (NPV) was highest in 1991 but only in defoliated stands where it caused populations to decline in subsequent years. Overall, virus mortality was positively related to both density in the current and previous generation (Table 2), and generally concurs with existing knowledge of NPV epizootiology (Doane 1970, Woods et al. 1991). By contrast, *Entomophaga maimaiga* caused considerable mortality in 1993 but much less mortality in 1992 and 1994, and no mortality prior to 1992. Mortality caused by *E. maimaiga* was first discovered in North America in New England in

1989. By 1992, this pathogen apparently expanded its range to encompass nearly the entire range of the gypsy moth (Hajek et al. 1995). Thus, its absence in our samples from 1989 to 1991 can be explained by its general absence from the region during that period.

Table 2. Results of stepwise regression of peak mortality on egg mass density (N_t) and lag egg mass density (N_{t-1})

Dependent variable	Independent variable[a]	Estimate	Probability of $\alpha > F$
Blepharipa pratensis	N_t	-0.070	0.047
	N_{t-1}	0.12	0.002
Brachymeria intermedia	N_t	0.14	0.0006
Compsilura concinnata	N_t	0.12	0.0001
	N_{t-1}	-0.077	0.006
Cotesia melanoscela	N_t	0.12	0.003
	N_{t-1}	-0.20	0.0001
Phobocampe unicincta	N_{t-1}	-0.061	0.002
Parasetigena silvestris	N_t	0.10	0.012
	N_{t-1}	-0.20	0.0001
NPV	N_t	0.16	0.003
	N_{t-1}	0.13	0.009
unknown	N_{t-1}	-0.14	0.0001

[a] N_t = egg mass density at the beginning of the same generation [log(1 + egg mass/ha)], N_{t-1} = egg mass density at the beginning of the previous generation [log(1 + egg mass/ha)].

Rates of parasitism by *P. silvestris* and *C. melanoscela* generally increased from 1989 through 1994. Perhaps this is related to the increasing population densities of gypsy moth over this period. Another cause of the increase in parasitism rates is that they tend to be low in newly established populations along the expanding population front; range expansion by parasitoids tends to lag behind the expansion of host gypsy moth populations (Ticehurst et al. 1978).

When gypsy moth larval mortality between thinned and unthinned stands was compared using a paired *t*-test (Sokal and Rohlf 1981), we found parasitism by *B. intermedia* and *C. melanoscela* significantly higher in thinned stands, and mortality caused by NPV significantly lower in thinned stands (Table 3). However, the results in Table 2 indicate that mortality is often closely associated with gypsy moth densities. Therefore, the differences in mortality rates may be due to differences in gypsy moth densities between thinned and unthinned stands. As a result, it was necessary to assess the significance of thinning on mortality rates using an analysis of covariance, where gypsy moth density and/or lagged density were used as covariates. The least squares means in Table 3 adjust mortality rates based on the known relationship(s) with gypsy moth density. None of the least squares means indicated a significant effect on thinning. Thus, the adjusted analysis indicated that thinning had no effect on mortality rates.

Table 3. Unadjusted means and least squares means (adjusted for covariates listed in Table 1) for transformed peak percent mortality

Dependent variable	Unadjusted mean		Least squares mean	
	unthinned	thinned	unthinned	thinned
Blepharipa pratensis	0.291	0.306	0.270	0.327
Brachymeria intermedia	0.092	0.150*	0.088	0.154
Compsilura concinnata	0.238	0.213	0.232	0.236
Cotesia melanoscela	0.261	0.271*	0.243	0.309
Phobocampe unicincta	0.054	0.093	0.098	0.075
Parasetigena silvestris	0.334	0.385	0.357	0.370
NPV	0.631	0.549*	0.555	0.583
unknown	0.973	1.00	0.994	1.01

* Significant at $\alpha = 0.05$.

Figure 1 shows the temporal pattern of gypsy moth dynamics, defoliation, and overstory mortality for paired thinned/unthinned stands with high egg mass densities. Populations of gypsy moth increased rapidly from 1989 to 1990 and egg mass density (Fig. 1a) and defoliation (Fig. 1b) were greatest in 1991. Live basal area (Fig. 1c) began to decline in 1991 and overstory mortality was greatest between 1991 and 1992. Both egg mass density and defoliation appeared to be greater in unthinned than thinned stands, but the differences were not statistically significant. It is possible that differences were not observed because gypsy moth densities were already at outbreak levels. Following 2 years of defoliation in these stands, populations collapsed to low densities such that it probably would be difficult to detect differences in densities due to thinning (Fig. 1). However, it is also apparent that thinned stands experienced less overstory mortality than their unthinned counterparts.

Since we detected a decrease in gypsy moth densities following thinning in only two of eight thinned stands, it is difficult to conclude that thinning caused a reduction in densities. However, numerous studies have reported that outbreak frequency is closely related to the proportion of stand basal area represented by host-tree species preferred by the gypsy moth (Bess et al. 1947, Houston and Valentine 1977, Herrick and Gansner 1986). Perhaps we did not observe a more dramatic decrease in gypsy moth densities in thinned stands because the proportion of basal area in preferred species was not reduced greatly in any of the stands following thinning. Nevertheless, our results suggest that any reduction in gypsy moth density caused by thinning is most likely not the result of differential response by natural enemies but rather is due to another factor, for example, mortality occurring during dispersal and/or effects on fecundity. Despite demonstration of an apparent lack of effect on gypsy moth populations caused by thinning, there was a distinct difference in overstory mortality between the thinned and unthinned stands.

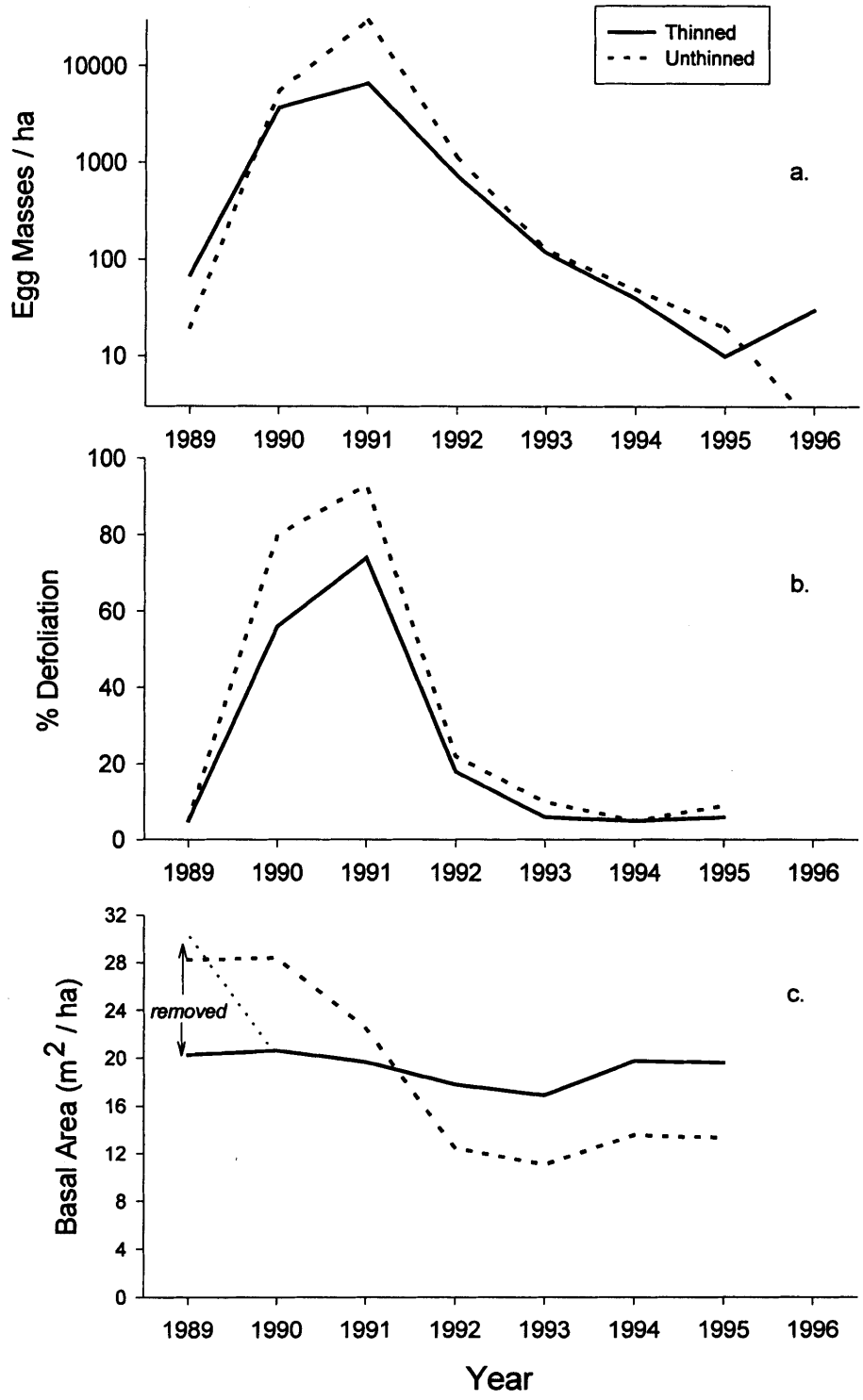


Figure 1. (a) Gypsy moth egg mass density from 1989 to 1996: (b) defoliation estimates of overstory trees from 1989 to 1995; (c) live basal area in defoliated stands; the amount of basal area removed in the silvicultural thinning is represented by the length of the arrow and small dashed line at the 1989 mark.

Conclusion

In this study we were unable to determine that thinning significantly altered rates of gypsy moth mortality caused by specific parasitoids or pathogens. Similarly, Grushecky (1995) found no effect of silvicultural thinning on predation of gypsy moth life stages. Thus, it seems unlikely that these silvicultural operations can reduce the frequency or intensity of gypsy moth outbreaks by enhancing the activity of natural enemies. However, the lack of a detectable effect of thinning on the action of these natural enemies does not preclude the feasibility of using silvicultural approaches to manage gypsy moth populations. Our data provide evidence that thinning may help to reduce mortality, though it may actually increase defoliation in certain situations.

Silvicultural manipulations are more likely to affect stand susceptibility simply by reducing the total or relative amount of host foliage (Gottschalk 1993) than by affecting gypsy moth populations directly. Moreover, silvicultural manipulations can be useful tools in gypsy moth management by removing and utilizing trees that are likely to die as a result of defoliation (i.e., those with poor crowns).

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The System of Gypsy Moth Population Regulation in the Slovak Republic

JÚLIUS NOVOTNÝ, MAREK TURCÁNI AND MILAN ZÚBRIK

Forest Research Institute, Lesnícka 11, 96923 Banská Štiavnica, Slovak Republic

ABSTRACT The gypsy moth is a very important pest in oak forests of the Slovak Republic and has a 6-8 year outbreak cycle. Frequency and abundance of pathogens, parasitoids and unknown mortality agents were observed during the last two outbreak periods. Currently, we are conducting research on the development of a pheromone monitoring system and on the use of microbial pesticides such as *Bacillus thuringiensis* and nuclearpolyhedrosis virus to augment the natural bioregulation of the gypsy moth. Using this scientific information, an experimental model of gypsy moth control was developed that emphasizes the use of ecological methods to control gypsy moth populations in Slovakia before outbreaks develop. The main objective of the new strategy is to minimize the incidence of defoliation caused by gypsy moth. The term "advance control", or "control in advance" is introduced to define actions that are taken to manage populations at a time when pest populations are low but have an increasing trend in abundance. The steps involved in this process and the parameters that were used for making decisions are discussed.

THE GYPSY MOTH, *Lymantria dispar* L., causes significant damage in the oak forests of Slovakia. The periodicity of outbreaks is 6-8 years and the area infested can vary significantly (Fig. 1). The impact of pathogens, predators and unknown mortality agents on the pest population density differs during various outbreak stages, however, the role of predators has not been examined. *Bacillus thuringiensis* (*Bt*) and nuclearpolyhedrosis virus (NPV) products were used as an artificial component of the natural bioregulation complex. The dosage and method of application was determined based on the population density of the pest. We utilized data collected from pheromone traps over a 12-year period to monitor the densities of gypsy moth populations.

The development of a strategy for regulating the abundance of defoliators such as the gypsy moth is similar to that employed in most integrated pest management (IPM) systems. The aim of the system is to utilize ecologically and economically acceptable measures during the period of progradation to maintain pest populations below an economic threshold.

This model of integrated oak protection against leaf-eating insects is based on two basic activities: (a) determine precisely when the first indication of population increase above a threshold level occurs; and (b) Take appropriate actions to maintain populations below a predetermined economic threshold. Monitoring, prognosis and population regulation are processes that are integral to the principles of forest protection.

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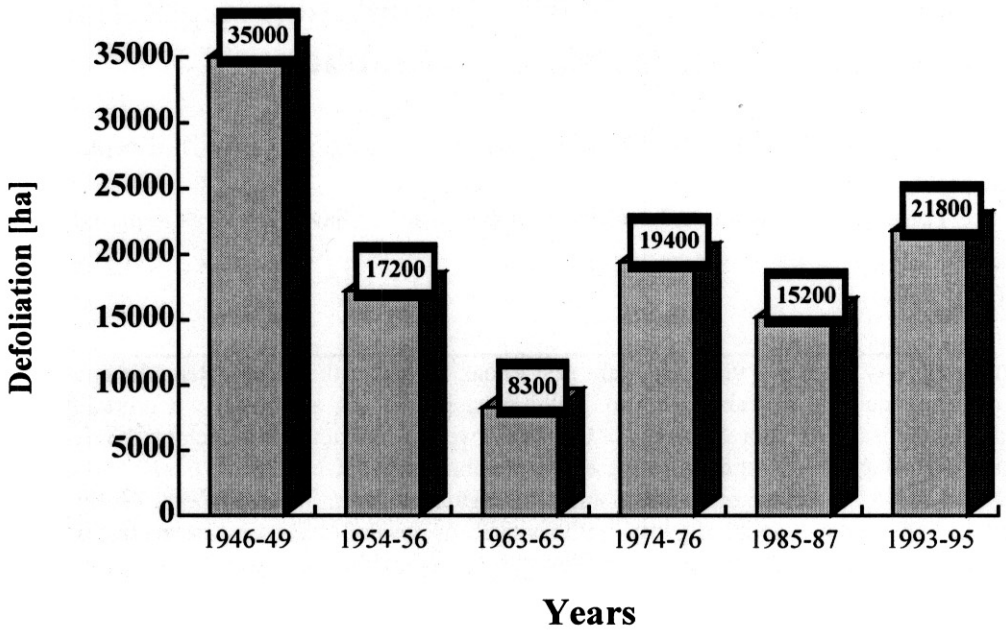


Figure 1. The area damaged by gypsy moth in the Slovak Republic during outbreak periods.

Material and Methods

In 1992 we initiated an experimental study to evaluate preventive treatments before population densities began to increase. The experimental area chosen was an oak forest in the forest district (FD) Ciáre, which is historically a primary focus for *L. dispar* outbreaks.

Within the FD, a relatively self-contained forest complex consisting of 110 ha in a locality referred to as Kovácová was used for this experiment. At that time, estimates of the density of *L. dispar* populations throughout the FD Ciáre indicated that a slight increase in trend was occurring, which is indicative of an impending mass outbreak of this species.

The experimental plot was treated with half of the normal dose of *Bacillus thuringiensis*, Foray 48 B (2 l/ha = 25 BIU), using a ULV aerial application with Micronair 4000 atomizers. For comparison, forest stands in the forest regions (FR) Mochovce, Nevidzany, and Pata, which also are primary foci for *L. dispar* outbreaks, were left untreated. During 1990-1994 the population trends of *L. dispar* were monitored using a modified Turcek method on both the experimental and comparison plots (Turcek 1956). The efficacy of the preoutbreak application of *Bt* was determined by comparing the results of monitoring *L. dispar* densities on the experimental and control plots for several years after the applications. These applications were referred to as "advance control," or "control in advance." We introduced the term "advance control" to define pro-active (preventive) measures that are initiated at a time when background populations of *L. dispar* begin to show an increasing trend, which normally indicates that an outbreak is imminent.

Results

Mortality agents affecting gypsy moth populations. During the last ten years, research activity in Slovakia has focused on entomopathogens and the complex of parasitoids that attack the gypsy moth, and their impact on population densities of the pest under Central European conditions. The results of this research are very encouraging.

Observations during periods of two gypsy moth outbreaks confirmed that the natural bioregulation complex has a major influence on gypsy moth abundance. The intensity of the effect of the natural bioregulative complex varies depending upon the phase of gradation of the pest.

Laboratory and field observations demonstrated that mortality caused by natural enemies ranged from 79.1% to 97.3% while the population was increasing, from 86.2% to 99.7% during the outbreak phase, and from 83.6% to 85.1% during the period in which the population declined. Entomopathogenic microorganisms and undetermined factors affected pest abundance most significantly. The contribution of both of these factors to overall mortality was 70.6% during the endemic period, 52.7% during increasing populations, 66.8% during the outbreak phase, and 68.3 % during the period in which the population declined. The highest mortality of gypsy moth in natural conditions was caused primarily by the nuclearpolyhedrosis virus (*Borrelina reprimens* Holmes). Several species of entomopathogenic bacteria caused mortality of early larval stages of the pest, however, presence of natural mortality caused by *Bacillus thuringiensis* was rarely observed. Several microsporidia were recovered, namely the genera *Nosema, Thelohania* and *Pleistophora.* Fungi were rarely encountered as a primary cause of natural mortality in gypsy moth populations. Mixed infections occurred very frequently and these usually consisted of virus and Microsporidia (Table 1).

Table 1. Species of gypsy moth pathogens recovered in the Slovak Republic

Family and species	Family and species
VIRUS:	**BACTERIA:**
Borrelina reprimens (Holmes)	*Bacillus thuringiensis* (Berliner)
Smithia rotunda (Bergold)	*Pseudomonas aeroginosa* (Schroeter)
PROTOZOA:	**FUNGI:**
Vairimorpha sp	*Beauveria bassiana* (Balsamo)
Nosema serbica (Weiser)	*Spicaria farinosa* (Dicks)
Thelohania disparis (Timofejeva)	
Pleistophora schubergi (Zwolfer)	

The effect of parasitoids was substantially lower, especially during advanced phases of the outbreak. The amount of gypsy moth mortality caused by parasitoids in different population phases was as follows: 29.4% (latency), 47.3% (gradation), 33.2% (culmination), and 31.7% (regression/decline). The main families of parasitoids recovered were Braconidae and Tachinidae. The Braconids were prevalent when the populations were in the endemic and outbreak phases, while the Tachinids were prevalent in all other population phases. *Cotesia melanoscelus* (Ratz.), *Glyptapanteles liparidis* (Bouche), *Parasetigena silvestris* (R.-D.) *and*

Blepharipa pratensis (Meigen) were confirmed as the principal species that were recovered (Table 2).

Table 2. Species of gypsy moth parasites observed in the Slovak Republic

Family and species	Years of outbreak		
	1972-1974	1985-1987	1992-1994
Braconidae			
Cotesia melanoscelus	x	xxx	xxx
Glyptapanteles porthetriae	xx		x
Glyptapanteles liparidis	xx	xx	xx
Meteorus versicolor			x
Ichneumonidae			
Apechtis compunctor			x
Hyposoter tricoloripes			x
Hyposoter sp.			x
Iseropus inguisitor		x	
Iseropus instigator		x	x
Iseropus turionelae		x	
Lymantrichneumon disparis			x
Phobocampe unicincta (=Hyposoter disparis)	x	x	xx
Phobocampe sp. (P. lymantriae, P. pulchella)			xx
Pimpla hypochondriaca			x
Theronia atalantae		x	x
Campoplex sp.		x	
Casinaria sp.			x
Chalcididae			
Brachymeria intermedia		x	x
Monodontomerus sp.			x
Tachinidae			
Blepharipa pratensis	xxx		xxx
Blepharipa schineri			x
Blondelia nigripes	xxx	x	
Carcelia gnava			x
Compsilura concinnata	xx	xx	x
Parasetigena silvestris	xxx	xxx	xxx
Pales pavida			x

Table 2 cont'd

Exorista larvarum			x
Zenillia libatrix	x	x	x
Drino incospicua			x
Sarcophagidae			
Agria affinis		x	
Kramerea schuetzei		x	
Muscina stabulans	x		
Pseudosarcophaga affinis	x		

x - occurrence, xx - important, xxx - very important

Bioregulation of gypsy moth population density. Before *L. dispar* populations enter the progression phase, our primary objective is to take appropriate actions necessary to suppress populations so that they will not enter the outbreak phase. We began to estimate the abundance of gypsy moth egg masses in the Kovácová area of FD Cifáre in 1990 after the pheromone monitoring system indicated that the trend in populations was increasing from latency to a base level. Based on the estimate of egg masses per tree in the fall of 1991, we initiated a program to apply *Bt* (Foray 48 FC) aerially in the spring of 1992.

We applied *Bt* at a dose of 2 liters/ha (25 BIU), which is 50% of the standard dose recommended, and achieved 79.8 % mortality within two weeks after treatment. No actions were prescribed for the other focal sites in the FRs Mochovce, Nevidzany, and Pata, where gypsy moth population densities were comparable. Observations on all populations were recorded in subsequent years.

While the population density in the experimental (treated) area of Kovácová has remained at a base level (less than 0.28 egg masses per tree), outbreaks developed in the three comparison sites. In the FR Nevidzany, the egg mass density increased from 0.29 per tree in the fall of 1992 to 3.07 per tree in the fall of 1993. It was necessary to apply chemical pesticides in both young and mature stands in order to prevent severe defoliation.

The situation in FR Mochovce was even more difficult. The number of egg masses per tree, which was similar to that found in FR Kovácová in 1991, increased dramatically to 25.24 in the fall of 1992, making it necessary for us to aerially apply pesticides over an extensive area in the spring of 1993. Despite these efforts, heavy residual populations required treatment again in 1994.

In the FR Pata, where egg mass densities were lower in 1991 than in Kovácová, the population increased to 5.64 egg masses per tree in the fall of 1992, which required that we apply pesticides in the spring of 1993 to prevent damage from occurring. Despite our efforts, severe defoliation occurred in young stands in this FR when the stands were reinvaded by windblown larvae from mature stands in the adjacent area. The changes in egg mass densities over time that occurred in these plots are summarized in Table 3.

We reached two conclusions from these results: (1) it is necessary to maintain *L. dispar* abundance at base levels to prevent serious impacts that affect the health of oak forests; and (2) this goal can be achieved by implementing an early detection system based

on the use of pheromone traps and egg mass surveys, correct diagnosis of increasing trends of *L. dispar* abundance from latency to a base level, and pre-emptive treatments to prevent the increase of populations to the progradation phase.

Table 3. Changes in the abundance of gypsy moth populations based on the mean egg masses per tree and control forest regions

Locality (FR)	Years					
	1990	1991	1992	1993	1994	1995
Kovácová ☒	0.060	0.09	0.14	0.28	0.054	0.11
Mochovce þ	0.005	0.08	25.24	1.74	0.0	0.0
Nevidzany þ	0.000	0.04	0.29	3.07	0.0	0.0
Pata þ	0.005	0.05	5.64	0.04	0.002	0.002

☒ - Locality where the model of efficient bioregulation of gypsy moth population density was used
þ - Control plots

We have referred to this process as "advance control" or "control in advance." The most critical factor in this process is the decision to take action when populations are still very low, because as demonstrated in the three comparison areas, gypsy moth populations are capable of expanding to outbreak levels in a single generation, thus there is little room for error.

The model of efficient bioregulation of gypsy moth population density. In order to maintain gypsy moth populations at endemic levels, we have developed a model for bioregulation of populations that allows us to supplement the actions of the natural enemy complex by using ecologically acceptable artificial means. The model consists of the following steps:

1) A systematic monitoring grid of pheromone traps is deployed in historically primary outbreak areas (foci) beginning in the third year after the collapse of the last outbreak. The grid consists of 16 pheromone traps spaced 50 m apart in a 4 x 4 configuration.

(a) If less than 60 male moths per trap are caught within the grid, no further action is necessary and the monitoring grid is activated again in the following year;

(b) If more than 60 moths per trap are caught within the grid, proceed to Step 2;

2) Estimates of the density of the gypsy moth population in the area are made using a modification of the Turcek method (Turcek 1956), whereby the number of egg masses are counted on the boles of 300 trees within the area of the monitoring grid.

(a) If the abundance of egg masses is estimated to be below 0.05 per tree, no action is required and the monitoring grid is activated again in the following year (Step 1).

(b) If the abundance of egg masses is estimated to be between 0.05 and 0.20 per tree, proceed to Step 3.

(c) If the density of egg masses exceeds 0.20 per tree, this indicates that the population is increasing rapidly and is beyond the point where bioregulation is feasible. This population will be scheduled for treatment in the following spring. Chemical pesticides will be applied aerially to prevent defoliation from occurring.

3) The probability of increased abundance of the gypsy moth population is estimated based on weather conditions in the preceding years.

(a) If it has been less than 4 years since the collapse of the last outbreak in the area, and hot, dry weather, which is favorable to gypsy moth populations, did not occur in the spring (April-May) of the last two years, no further action is recommended. The monitoring grid is restored in the following year (Step 1).

(b) If it has been 4 or more years since the collapse of the last outbreak, and if favorable weather (hot, dry) did occur in the spring of the two preceding years, proceed to Step 4.

4) Application of microbial pesticides and the criteria that are considered for their use.

Only two microbial pesticides are recommended for use in this pre-emptive strategy: commercial preparations of *Bt*, and the gypsy moth NPV. In most of the area designated for treatment, one-half of the standard dose of *Bt* (20-30 BIU/ha) is applied using ultra low volume (ULV) technology to reduce the density of populations to a base level. In environmentally sensitive areas, however, where rare or sensitive lepidopteran species occur, a full dose of the NPV is applied (5×10^{11} - 1×10^{12} POBs/ha).

The timing of application of both products is critical since neither *Bt* nor the NPV have a long period of residual activity. Spraying is usually conducted when larvae are in the second instar and leaves of preferred host tree species are about two-thirds expanded. Preferably, the ambient temperature should exceed 12°C, so that most larvae are actively feeding.

The selection of forest stands for treatment is based on the following criteria listed in descending order:

1) Forest stands where silvicultural treatments or reforestation efforts have occurred.
2) Oak stands where oak wilt is present.
3) Young oak stands in any condition.
4) Conifer stands.
5) Oak stands containing mast crops that require protection.
6) Stands containing other tree species that are healthy or have mast crops.
7) Any forest stand that is within 300 m of orchards or vineyards.

Discussion

This article describes a new and novel strategy for managing the gypsy moth in Slovakia whereby artificial bioregulation tactics (microbial pesticides) are prescribed when gypsy moth populations are still at a base or endemic level to prevent them from entering a progressive phase of increase. This system is referred to as "advanced control" and is dependent upon the use of an intensive monitoring network of pheromone traps in gypsy moth focal areas.

This system differs from the approach to managing gypsy moth populations that is described in Doane and McManus (1981), where pesticides are used to suppress populations when defoliation is imminent. It is important to recognize that there are differences in the status of the gypsy moth in the U.S. and in Slovakia, and in the characteristics of the forest in the two locations. In the eastern U.S., the gypsy moth is established in over 16 states, but for varying lengths of time. The insect has been present in New England forests for over 80

years, however, the gypsy moth is a relative newcomer to the states of Virginia and West Virginia to the south, and to Ohio and Michigan to the west. The gypsy moth is distributed in about 50% of the potentially susceptible oak forests of the U.S. Throughout this region, where the gypsy moth occurs, there are large areas of contiguous susceptible forests containing many species of oaks (*Quercus*). Thus, when outbreaks do develop, the potential for defoliation is massive, as exhibited in 1981 when over 5 million ha were defoliated.

In Slovakia, where the gypsy moth has existed for centuries, oak forests occur as discrete parcels that may be widely separated by farmland or conifer forests. Therefore, there are more opportunities to implement integrated management strategies on specific areas that are less than 100-200 ha. Results from early studies in Slovakia and other countries in Central Europe led us to believe that we needed a new strategy to address defoliating insects such as the gypsy moth. During the last two gypsy moth outbreaks in Slovakia, populations increased rapidly in mature oak stands and then young larvae were dispersed by wind into adjacent oak plantations or conifer stands before any control actions could be initiated. In this situation, the only practical alternative that is available is to use chemical contact pesticides in order to prevent severe impacts from occurring. We needed to develop a strategy where we could address the gypsy moth problem in a preventive manner, utilize the benefits of the extensive natural enemy complex, and minimize the undesirable utilization of chemical contact pesticides.

Our bioregulation model is based on utilization of a pheromone-based monitoring system that detects changes in the abundance of gypsy moth populations at a base level (less than 60 male moths per trap). This information triggers the need for egg mass surveys only when there are indications that populations are increasing from latency. Taking into account the estimates of population density from egg mass surveys, and our knowledge and experience with spring weather conditions that are conducive to increases in the abundance of populations, we can make decisions about the feasibility of applying microbial controls that will supplement natural bioregulation processes. The important aspect of this process is that populations are treated at very low densities, which prevents them from progressing to outbreak status.

Our recent experiences with this strategy in the FD Ciáre suggests that it has been successful in preventing outbreaks from developing. We propose to identify further forested areas that serve as gypsy moth foci so that our monitoring system can be expanded. We also suggest that this model system can be modified to address other defoliator problems that are common to Slovakia and neighboring countries.

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Pheromone Monitoring of the Larch Bud Moth, *Zeiraphera diniana*, in the Swiss Alps

WERNER BALTENSWEILER

Blumenbergstrasse 9, CH-8634 Hombrechtikon, Switzerland

ABSTRACT Pheromone monitoring helped to detect specific differences in pheromone communication, moth size and flight activity between two host races of *Zeiraphera diniana*. The host race on larch is bigger than the one on cembran pine and flies mainly at night. However, since response polymorphism of the males to pheromones was too rare in the course of the population cycle and since it was not consistently linked with the variable color polymorphism, assortative mating of the black colourmorphs cannot be the driving force of the cycle in the trough phase.

THE LARCH BUD moth is perhaps the most clear-cut case in the world of a truly cyclic moth (Ginzburg and Taneyhill 1994). Due to its regular devastation of the larch forests around the tourist resorts in the Engadine valley at 8-9 years intervals, control of this lepidopteran pest was demanded immediately after World War II. Therefore, a larval census was established in 1949 covering an area of 6000 ha of subalpine larch-cembran pine forest. Since then 5 population cycles were observed, several large-scale control operations were attempted, and more than 100 scientific papers published. The knowledge obtained led to the conclusion that control operations will be neither ecologically nor economically justifiable. In contrast, the study of the larch bud moth system revealed itself as very rewarding from a scientific point of view. It yields not only an outstanding example for ecosystem research (Baltensweiler 1996) but also an intriguing case for sympatric speciation of host races on either the deciduous larch or the evergreen conifers (Emelianov et al. 1995). Morphologically these host races are distinguishable only in their 5th larval instar, but they differ considerably in their development rates and surprisingly also in their pheromone communication (Baltensweiler et al. 1978; Guerin et al. 1984). All these traits are polymorphic and are well reflected in the offsprings of crossings between the host races. Interestingly enough, the extreme black larch form predominates at the peak of the population cycle on larch whereas intermediate colourforms prevail during the trough of the cycle (Baltensweiler 1993).

The host race on larch employs the trans-11-tetradecenyl acetate (larch form LF/ *E*11-14:Ac) whereas the host races on evergreens, i.e. cembran pine and Norway spruce, make use of the trans-9-dodecenyl acetate (AF / *E*9-12:Ac). Priesner (1979) discovered among the progeny of an AF x LF crossing F1-males which showed the same maximum EAG response to both the *E*9-12:Ac and *E*11-14:Ac. Subsequently, 'response' types were based on the relative effectiveness of the pheromone components *E*9-12:Ac vs. *E*11-14:Ac. Nine response types were distinguished, ranging from $\geq$100 / 1 to 1 / $\geq$100 and including 7 potential intermediary responses (30/1 to 1/30) (Priesner and Baltensweiler 1987a). This response polymorphism appeared to be the logical counterpart to the findings that the females produce in their glands these substances in variable ratios (Guerin et al. 1984).

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Therefore, the specificity of male attraction to synthetic sex lures and the response type of the relevant males captured, as measured by electroantennogram (EAG) measurements (Priesner and Baltensweiler 1987b), was studied by means of a standard series of 35 different lures, made up of varying combinations of the two pheromones.

In this paper the use of pheromone monitoring is exemplified with regard to the evaluation of two hypotheses, which were proposed to explain the immediate sequence of one cycle after the other:

1) The findings that the dark phenotype is an expression of a recessive gene in the homozygote (Baltensweiler 1993) and that both sexes exhibit a pheromone polymorphism led to the hypothesis that a correlation between colourmorph and pheromone type provides the basis for assortative mating between the different fitness types which occur at different stages of the cycle (Guerin et al. 1984).

2) Correlation between traits such as early emergence, large size (Stearns 1989) and black colourmorph could account for an increased fitness whereby subsequent assortative mating among the largest individuals would result in population increase.

Materials and Methods

Standard Series of Lures and Trap Model. The standard series of lures consisted of 5 doses of pure *E*11-14:Ac and *E*9-12:Ac respectively and 25 binary mixtures of these substances (Fig.1). Each lure was represented by just one trap. For the sake of interpretation, the traps were combined into three groups; two groups of 15 traps each with the predominance of either substance, and the intermediate group of 5 traps with equal doses of the two substances. In 1985 we reduced the number of lures to 8 combinations (Fig. 1), but each lure was replicated 4 or 5 times.

The synthetic pheromone substances (*E*11-14:Ac; *E*9-12:Ac) and their blends on rubber caps as well as traps were provided by H. Arn, Swiss Federal Research Station for Agriculture, CH-8820 Wädenswil, Switzerland.

The Tetra Trap (Arn et al. 1979) were hung on lower branches approx. 2 m above ground on either larch or cembran pine. The catching surface, an exchangeable sheet of carton covered with Tangle Trap (Tanglefoot Company, Grand Rapids, Michigan, USA) measured 155x90 mm.

The marking and recapture experiment. A standard series exposed in the mixed larch-cembran pine forest God god, S-chanf was used from the 23.8.-9.9.1982 to test the consistency of attraction: The tetra traps # 1, 8, 5 (Fig. 1) were not equipped with the adhesive carton, instead powdery dyes of different colours were filled into the trap to let attracted males mark themselves and leave the trap again at their will.

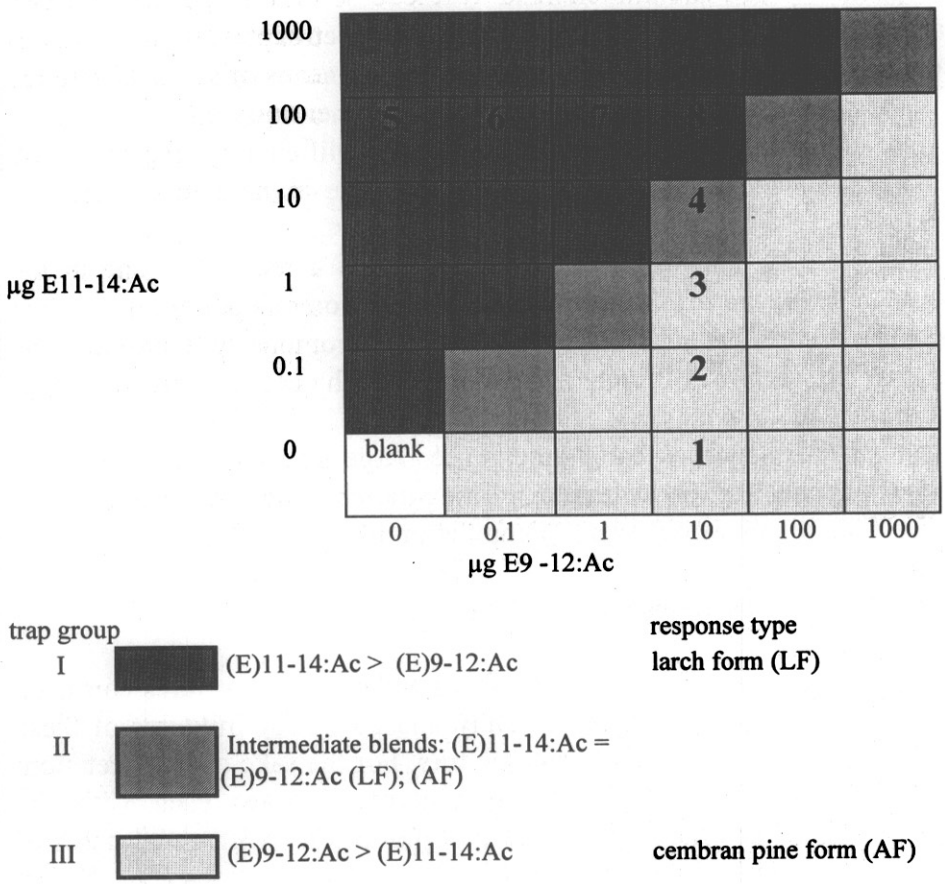


Figure 1. Trapping design 1981/1985-1989: 1 - 8.

Test sites. The test sites were chosen in the Engadine valley in either pure larch forests, mixed larch-cembran pine forests and a pure cembran pine forest:

pure larch forest:	1981:	Ardez, God San Steivan; 1500 m a.s.l.
	1982:	Sils, Crappa, 1850 m a.s.l.
pure cembran pine forest:	1981:	S-charl, Praditschöl, 2100 m a.s.l.
mixed larch-cembran pine forest:	1981:	S-chanf, God god, 2050 m a.s.l.
	1982:	Pontresina, Val Bernina, 1900 m a.s.l.

Results

Pheromone Polymorphism as measured by EAG Analysis. More than 1800 males from field populations of either pure or mixed host forests or F1-hybrids of 3 host races were analyzed (Priesner and Baltensweiler 1987a,b, Baltensweiler and Priesner 1988). Whenever feasible we ascertained also the correlation between the larval colour type and the response type.

Table 1 lists the catches for the three sites and the lure groups I-III, weighted according to the number of traps per group. The catch in Ardez clearly reflects the expectations, the small proportion of males found on lure group I is considered as being due

to accidental or disoriented attraction of LF moths. Rather a surprise was the large proportion of LF males caught in the pure cembran pine forest of S-charl on trap group III. These males are thought to be immigrants from larch forests at lower altitudes. Obviously, these data are not sufficient to allocate the catch to its proper host race, additional criteria such as the pheromone response type of the males need to be known.

Table 1. Percentage of catch for 3 groups of pheromone compounds in 3 sites (July-October 1981)

			number moths		
			Ardez	S-charl	S-chanf
group	lures µg	n traps	4720	4304	2302
I	*E*9-12:Ac > *E*11-14:Ac	15	1.72	24.88	37.05
II	*E*9-12:Ac = *E*11-14:Ac	5	24.60	28.16	47.90
III	*E*9-12:Ac < *E*11-14:Ac	15	73.68	46.96	15.90

Ardez: pure larch forest;
S-charl: pure cembran pine forest;
S-chanf: mixed larch-cembran pine forest.
(n moths weighted for 15 traps/group)

The marking and recapture experiment was considered to provide some information about the consistency of the orientation to a specific lure. The recapture of males marked in traps #1 and 4 is shown in figure 2a,b. The recaptures are rather evenly distributed all over the traps of lure group I and II, as an exception a few moths were attracted to trap *E*9-12:Ac/*E*11-14:Ac 100/1000µg in lure group III. Because there were very few males in trap 0/10µg caught and marked and only 3 recaptures in traps 0/100 and 0/1000 µg recorded, no table is provided. This poor result is considered to be due to the deterrent effect of defoliated larch trees present at the site.

In 1985 we resumed the same experimental idea, however, the number of lures was reduced to 8 (Fig. 1). and the traps were exposed in only two sites, i.e. the pure larch forest of Sils and the mixed larch-cembran pine forest of Pontresina. Among the male response types we distinguished only between 'pure' ≥100 /1 and 'pure' 1/ ≥100 responses, i.e. between AF or LF males. At that time the population cycle was at its minimum density and we continued the monitoring until 1989 when the first local defoliation in Sils signaled the beginning of the peak phase. Figures 3a, 3c show the percentage of total catch/lure (defined by trap# 1-8; Fig. 1) and Fig 3b,d represent the absolute numbers of either the AF or the LF response types per lure for the years 1986-1989 and the two sites.

0	0	0	0	7	5
0	0	0	0	22	13
0	0	0	4	20	7
0	0	1	4	12	12
0	4	6	5	15	13
0	0	4	8	21	15

dye

fig. 2a

n=198

E11-14:Ac µg	E9-12:Ac µg 0	0.1	1	10	100	1000
1000	0.00	0.00	0.00	0.00	3.54	2.83
100	0.00	0.00	0.00	0.00	11.11	6.57
10	0.00	0.00	0.00	2.02	10.10	3.54
1	0.00	0.00	0.51	2.02	6.06	6.06
0.1	0.00	2.02	3.03	2.53	7.58	6.57
0	0.00	0.00	2.02		10.61	7.58

0	0	0	0	3	3
0	0	0	0	4	4
0	0	0	2	11	6
0	0	2	4	8	8
0	1	1	0	6	5
0	0	1	6	5	1

fig. 2b

n=81

E11-14:Ac µg	E9-12:Ac µg 0	0.1	1	10	100	1000
1000	0.00	0.00	0.00	0.00	3.70	3.70
100	0.00	0.00	0.00	0.00	4.94	4.94
10	0.00	0.00	0.00		13.58	7.41
1	0.00	0.00	2.47	4.94	9.88	9.88
0.1	0.00	1.23	1.23	0.00	7.41	6.17
0	0.00	0.00	1.23	7.41	6.17	1.23

Figure 2. Mark-recapture experiment percentage recapture. Traps exposed on Cembran Pine 23.8.-9.9.1982, S-chanf, God god.

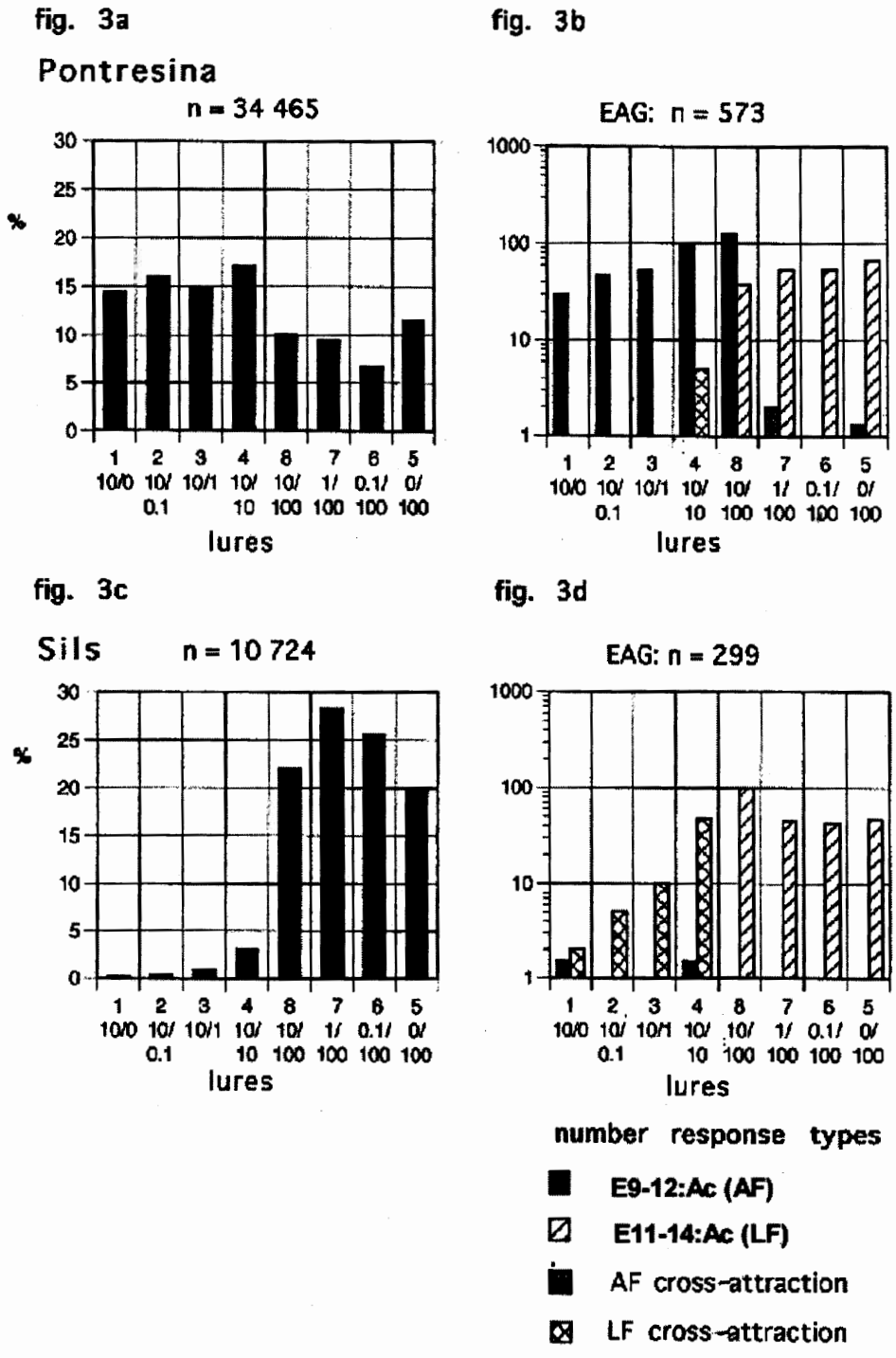


Figure 3. Percentage of total catch in 5 generations 1985-1989 per tetra trap #1-8 (Fig. 1) (Fig. 3a,c) Number of 'pure' response types per trap# 1-8 (Fig. 3b,d). (*E*9-12:Ac/*E*11-14:Ac =100/1 'pure' AF male); (*E*9-12:Ac/*E*11-14:Ac 1/=100 'pure' LF male); Fig. 3a,b: Pontresina: larch-cembran pine forest; Fig. 3c,d: Sils: pure larch forest.

In combination with the EAG response type of captured males it was found that the attraction to the single chemicals is highly selective. The pure *E*9-12:Ac source (trap 10/0 id.

trap#1) attracts almost only AF and the pure *E*11-14:Ac source (trap 0/100 id. trap #5) with one exception only LF males. Traps baited with compound mixtures, on the other hand, usually contained individuals of both host races, whereby the AF tolerated a larger amount of *E*11-14:Ac added to its own pheromone than the LF (Pontresina: trap 10/100 id. trap #8). Thus, an admixture of an equal amount of *E*9-12:Ac to *E*11-14:Ac (trap 10/10 id. trap #4) significantly reduced the attraction of LF males and higher ratios of *E*9-12:Ac/*E*11-14:Ac almost prevented attraction.

Five out of 103 EAG-analyzed moths caught in Pontresina on the 10/10 lure revealed themselves as LF males (4.8%) and none were found on traps#1-3, whereas 3 moths out of 177 analyzed individuals from the traps #5-7 were AF males (1.7%). Considering the biased collection of moths for EAG analysis from the trap 10/10 (id. trap#4), absolute cross-attraction would be even smaller.

In Sils we discovered only 2 *E*9-12:Ac response types out of a total of 299 EAG-analyses. Of the 297 LF, 64 or 21.5% were collected from the traps 1-4, however since the total catch on these traps amounted to 476 or 4.4% of the total, i.e. 10 724 moths, the bias is even more obvious. Whether this surprisingly large proportion of LF-moths being attracted to traps with greater amounts of *E*9-12:Ac represents oriented flight and should be termed 'cross-attraction' is open to speculation. Since the total catch on dummy traps amounts to 20 individuals only, i.e. approximately the same quantity as on trap #1 (id. 10/0), the increasing quantity of moths on traps #2-4 reflects the trend of increasing probability of oriented flight.

Another interesting result is seen in figure. 4, where from 1985 to 1989 the absolute number of moths per day and trap groups #1-4 and #8 is decreasing, whereas in contrast the absolute population of LF is increasing. Two interpretations are possible, either the discrimination by the LF improves or else the proportion of response types tolerating larger amounts of *E*9-12:Ac decreases. Because we did not continue the detailed analysis initiated by Priesner, this second interpretation cannot be confirmed.

The Size Criterion. Visual observation of the trap cartons revealed an obvious and consistent difference in size between the host races, the AF being ~1 mm smaller than the LF. However since size was also considered to be an important criterion for fitness within the hostrace, the length of most of the moths from the front of the head to the tip of was measured.

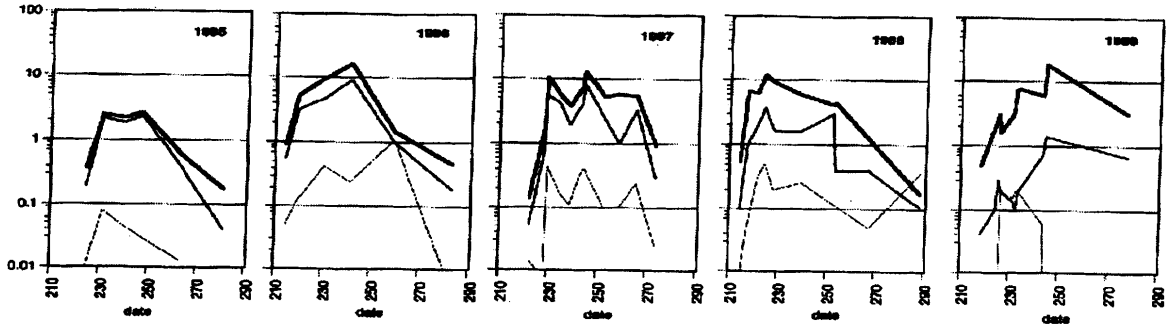


Figure 4. Density of *Z. diniana* moths per day and trap group, Sils 1985-1989.
Trap #1-4: —— 100 µE9 - 12Ac; 0-10 µE11 - 14Ac
Trap #8: ——— 10 µE9 - 12Ac; 100 µE11 - 14Ac
Trap #5-7 ▬▬ 0-1 µE9 - 12Ac; 100 µE11 - 14Ac

LF populations show in general a typical leptokurtic size distribution (Fig. 5) with a maximum falling into the two size classes 9.76-10.00 and 10.01-10.25 mm in the course of the 5 years 1985-1989. Size distributions of AF populations are of the platykurtic type, their maxima ranging from 9.01-9.25 mm to 9.51-9.75. Lure group II which attracts both host races exhibits either a platykurtic or in the extreme case, such as in 1986, a bimodal distribution.

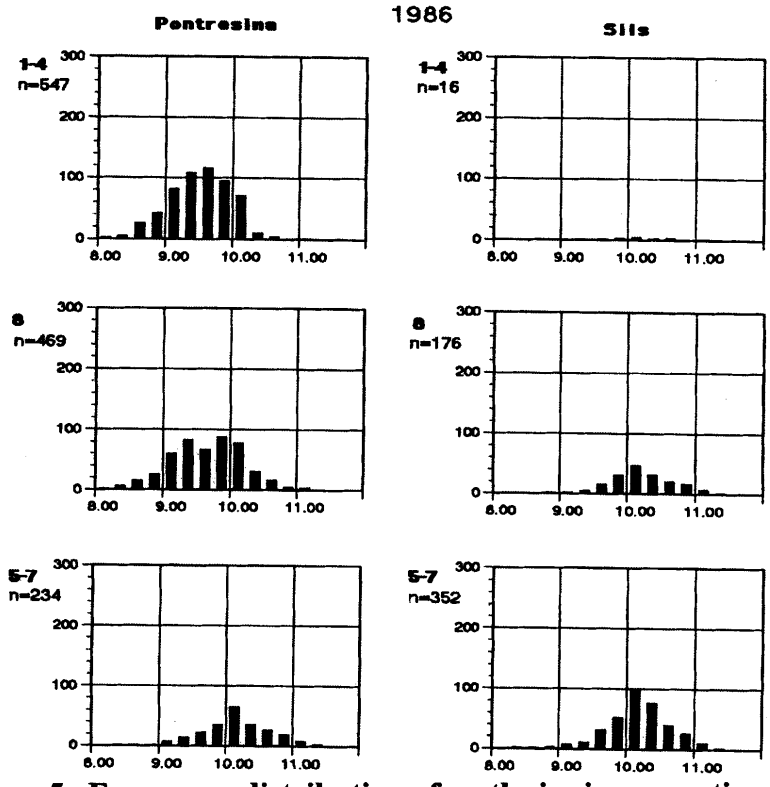


Figure 5. Frequency distribution of moth size in generation 1986.
trap groups #1-4, 8, 5-7, (class size: 0.25 mm)
Pontresina: larch-cembran pine forest
Sils: pure larch forest

Diurnal Flight Activity. In 1982 the standard series design was used in the mixed larch-cembran pine forest God god to evaluate the flight behaviour of the two host races. Between August 12th. and September 9th the traps were inspected intermittently at 12 hour intervals. In order to account for the activity threshold of the moths at approx. 7°C, the nights were grouped according to their temperature (weather station Bever):

day, n= 16;	1300:17.52 ±0.88 °C;
warm night, n=7:	1900:14.51 ±0.77 °C; 0001: 8.20 ±0.88 °C,
cold night, n=7:	1900:11.63 ±0.75 °C; 0001: 4.40 ±0.99 °C

Figure 6 clearly reveals the differences in diurnal flight behaviour but also a seasonal trend in the moth flight. At the beginning of the flight season moths of both host races fly mainly during warm nights, but in the middle of the flight season, the cembran pine form is, in contrast to the larch form, mainly day-active. This behaviour, however, is rather variable since also the LF may become day-active after cold nights or towards the end of the flight season in October.

Discussion and Conclusions

The efforts involved to determine male pheromone polymorphism with EAG analysis is considerable. When we realized that the response polymorphism proved to be too rare in field populations that it could be of any importance at the level of population dynamics (Baltensweiler and Priesner 1988), we restricted the analysis 1985-1989 to the determination of either the 'pure' $\geq$100 /1 or the 'pure' 1/ $\geq$100 response type, i.e. the correctness of attraction. Because of the rareness of male polymorphism and the fact that colour morphs and response types were not consistently correlated, led us to accept that hypothesis 1, i.e. assortative mating among black fitness types mediated by pheromone communication cannot not be valid.

As to hypothesis 2, it is postulated that fast development, which leads to early emergence and large size, are important criteria for superior fitness. These criteria, which all apply to the dark LF, would then cause synchronisation and, hence, favour assortative mating among them. This reasoning should express itself by the catch of the largest moths at the beginning of the annual moth flight of the 4 generations 1985-1988 which lead up to the peak of a cycle in 1989. It does not, however, necessarily presuppose a pheromone polymorphism.

Figure 7 shows the variation of moth size in the Sils population for the lure groups I-III, which all are made up of LF response types (Fig. 3b). Obviously the trend of decreasing moth size in the course of the annual moth flight is not confirmed. This postulated decrease in size, however, is reflected by the course of moth size on lure 10/100 (id. trap#8) in Pontresina (Fig. 8). But this trend stems from the fact that both host races are attracted to this trap, the large LF as well as the smaller and later emerging AF, which is well disclosed by its bimodal size distribution (Fig. 5). Hypothesis 2 could only be accepted if this phenomenon would be corroborated for the population attracted to lure group I, which is not the case.

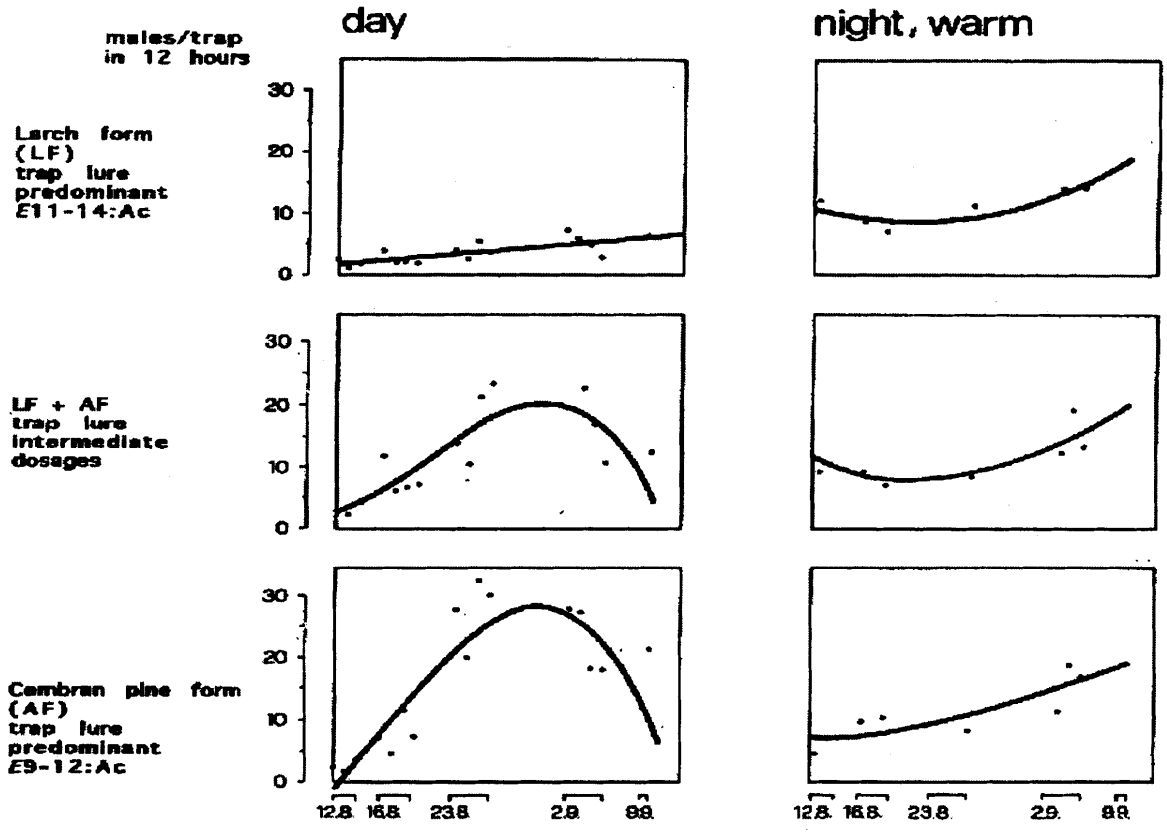


Figure 6. Flight behaviour of the two host races of *Z. diniana* as revealed by their attraction to parapheromone blends. S-chanf God god: 12.8.-9.9. 1982. traps exposed on cembran pine

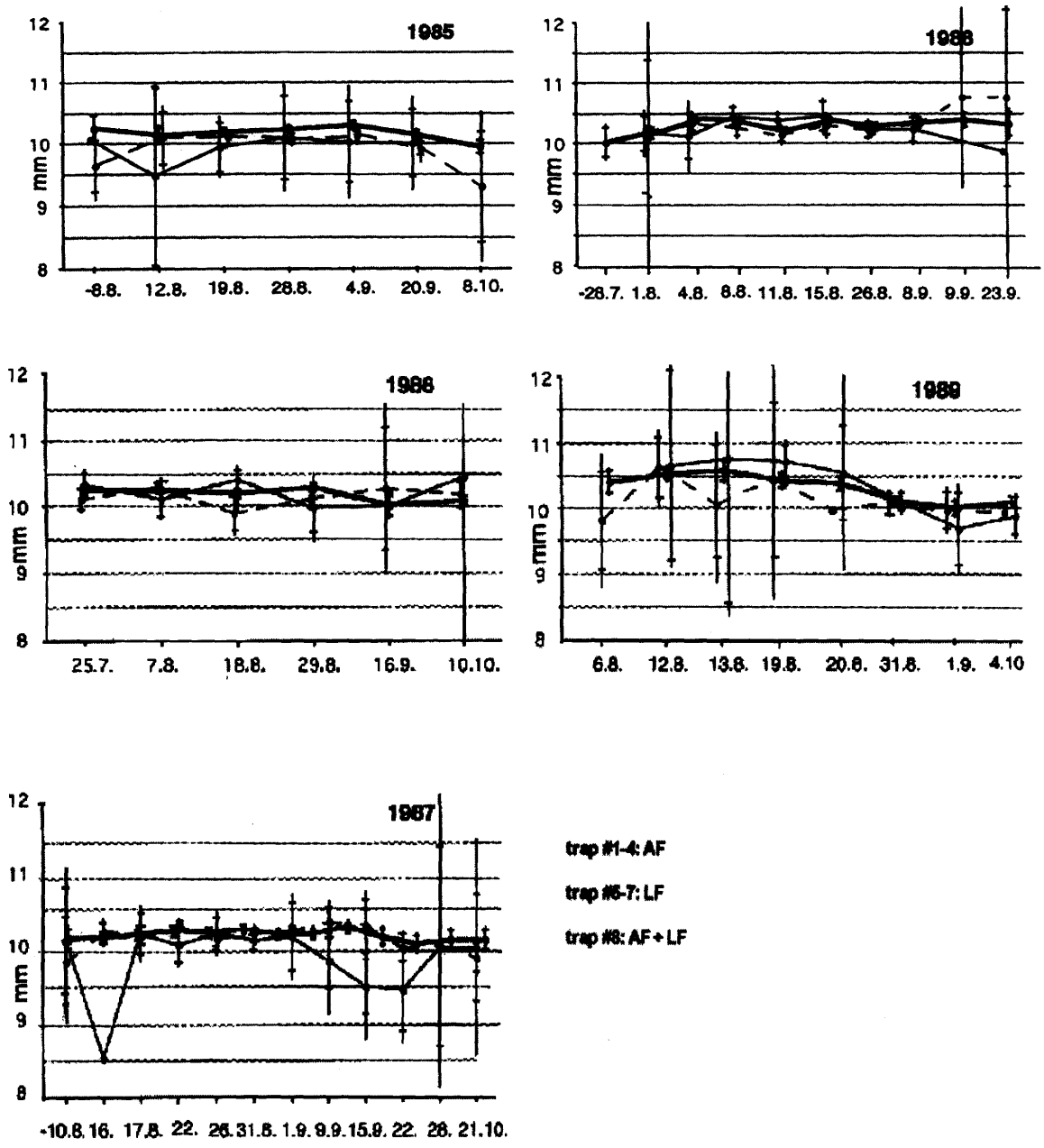


Figure 7. Moth size in the course of the flight season 1985-88 in Sils.

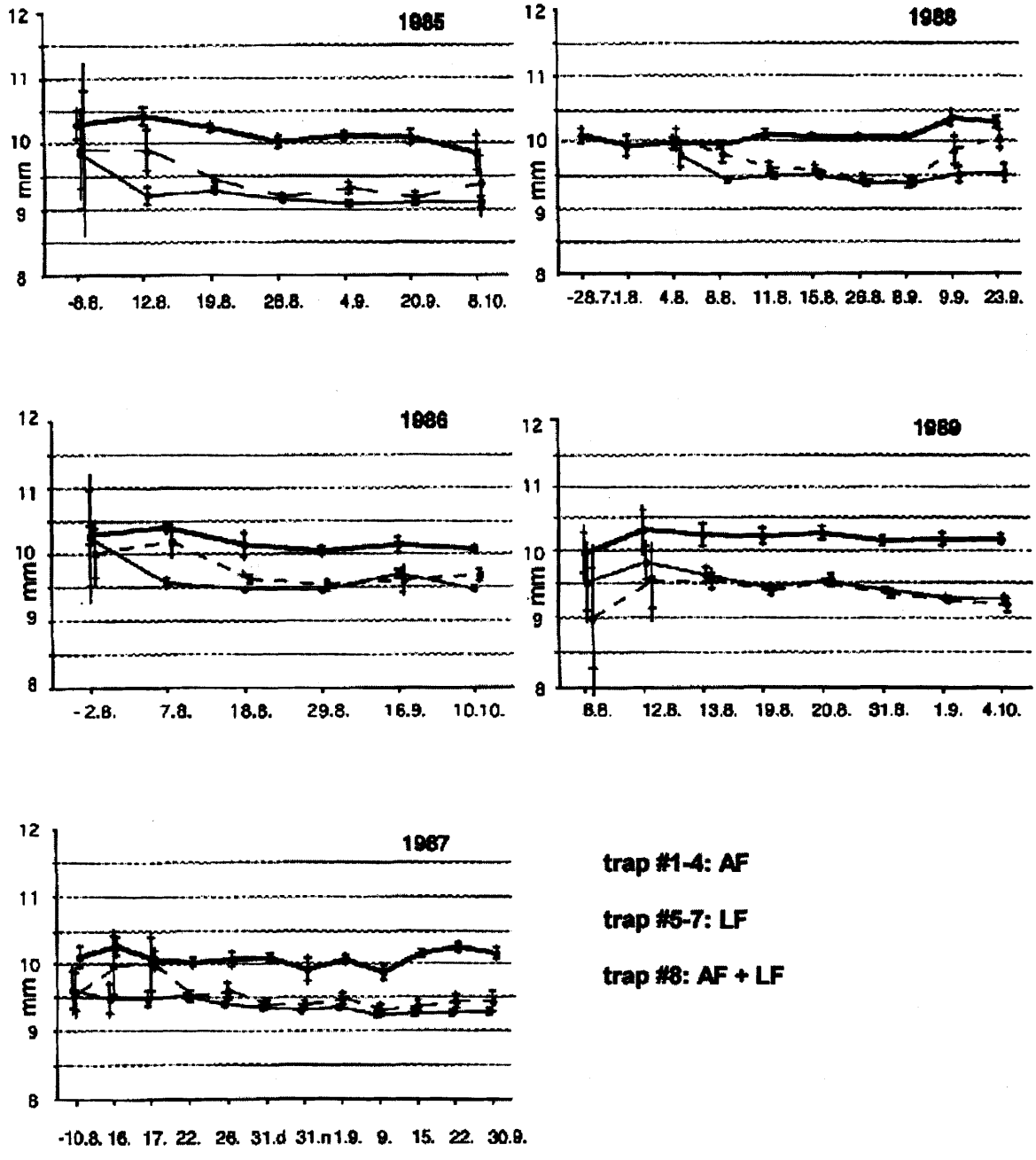


Figure 8. Moth size in the course of the flight season in Pontresina 1985.

Thus pheromone monitoring of the two host races provided much new information, but it could not contribute to the question of the driving force of the cycle at its minimum density. Whether allozyme and/or DNA analysis might help to elucidate this problem will need more research.

Acknowledgements

This work describes some of the results which stem from a long and fruitful research period which I had the privilege to spend together with Ernst Priesner, Max-Planck-Institut, Seewiesen, Germany. This paper is dedicated in memory of Dr. Priesner. Dr. H. Arn, Wädenswil, is thanked for his cooperation, his permanent advice in pheromone work and his providing the chemicals and the traps. The late Mrs. Elizabeth Frei cared from 1985-1989 for the EAG analysis.

This paper represents contribution no. 130 of the Working Group for the Study of the Population Dynamics of the Larch Bud Moth.

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Biomass Production of *Pinus pinaster* after Defoliation by the Pine Processionary Moth (*Thaumetopoea pityocampa* Schiff.)

STEPHANOS MARKALAS

University of Thessaloniki, School of Forestry and Natural Environment, Laboratory of Forest Protection, P.O. Box 228, 540 06 Thessaloniki, Greece

ABSTRACT Biomass production rate was studied in young (5-year-old) *Pinus pinaster* trees at regular time intervals during the growing season following defoliation caused by the pine processionary moth. The change in shoot length, needle length and needle dry weight was measured for four different types of shoots in moderately defoliated, completely defoliated and undefoliated control trees. In defoliated trees, the shoots were significantly shorter and the needles were shorter and lighter than in the control trees. The percentage losses were also calculated during the total growing season. One year after defoliation, losses in total shoot biomass were 41-50% in moderately defoliated trees and 54-64% in completely defoliated trees.

THE PINE PROCESSIONARY moth (*Thaumetopoea pityocampa* Schiff.) is one of the most harmful insects that attack pine trees in many mediterranean countries (Androic 1957, Serafimovski 1959, Zankov 1960, Kailidis 1962, Rive 1966, Demolin 1969, Bellis and Cavalcaselle 1969, Souleres 1969, Buxton 1983, Geri 1983, Markalas 1985, 1986 and 1989a). Complete defoliation, even during consecutive years, seldom causes the death of attacked trees (Ruperez 1956, Kailidis 1962). More common is the dieback of the crown of young trees, especially in situations where the defoliation of artificially planted trees, growing on unsuitable sites, is followed by unfavorable growth conditions, such as severe drought during the spring months (Markalas 1985). In spite of the capability of defoliated trees to refoliate and survive in the following growing season, the effects of defoliation, especially on the so-called "commercial plantations", are very significant (Fratian 1973).

Most efforts to investigate the effects of defoliation caused by the pine processionary caterpillar measured the losses in growth of attacked pine trees (Joly 1969, Cadahia and Insua 1970, Bouchen and Toth 1971, Lemoine 1977, Markalas 1985, 1987 and 1989b, Avtzis and Chatziphilippidis 1993). Decreased biomass production also results in less vigorous and more stressed trees, which are susceptible to other biotic and abiotic factors. In the present study, we investigated the effects of defoliation on the development of biomass production of young *Pinus pinaster* trees attacked by the pine processionary moth.

Methods and Materials

The study was conducted in an area forested with *Pinus pinaster* located near the village of Peristerona, about 50 km east of Thessaloniki. At the end of a severe infestation and defoliation (early April) of the 5-year-old trees caused by the pine processionary caterpillar, three groups of trees with different degrees of defoliation were distinguished:

Pages 292-302 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Techncial Report NE-247.

undefoliated (Control), moderately defoliated (45-55%) and completely defoliated (95-100%) trees. Each group consisted of 25 trees of approximately the same height, diameter and height increment during the last growing season.

The new foliage produced by defoliated and undefoliated trees was measured in four different types of shoots: terminal shoots of the top spondyl, side shoots of the top spondyl, terminal shoots of the second spondyl, and terminal shoots of the third spondyl. Data measurements were initiated in the middle of April and lasted until the end of September. At the beginning, measurements were repeated every 8-10 days, later every 10-11 days and after the middle of July every 13-15 days. In total, 15 measurements were made. Thirteen shoots in every tree was measured on: the terminal shoot and four shoots from each one of the other three shoot types. From the lower part of each shoot, a 2-needle cluster was cut off in order to measure the change in length and dry weight of the needles in the laboratory.

At the end of February of the next year (i.e., one year after the end of defoliation), one side shoot of the top spondyl and one terminal shoot of the second spondyl were cut off from each tree. Every shoot was divided into four equal parts, and from the middle of each part, 10 clusters of needles were cut off. In order to calculate needle biomass production, the average dry weight of the 40 needle clusters of each shoot was used. T-test was for all statistical analysis.

Results and Discussion

The degree of defoliation of pines caused by *T. pityocampa* is a decisive factor in the development and final length of all four types of shoots measured in this study (Fig.1). The lack of photosynthetic biomass in defoliated trees during the beginning of the growing season did not result in the prolongation of the growing period. On the contrary, it was found that the shoot length increment in defoliated trees was completed earlier than in undefoliated control trees.

The development and final length of new needles were affected not only by the degree of defoliation, but also by the type of shoot as well. The differences in needle length between defoliated and undefoliated trees were always highly significant ($P<001$). However, the differences between moderately and completely defoliated trees were not significant in all shoot types. Specifically, the growth rate of needles of the terminal shoots of the top spondyl was almost the same in both moderately and heavily defoliated trees during the whole growing season (Fig. 2).

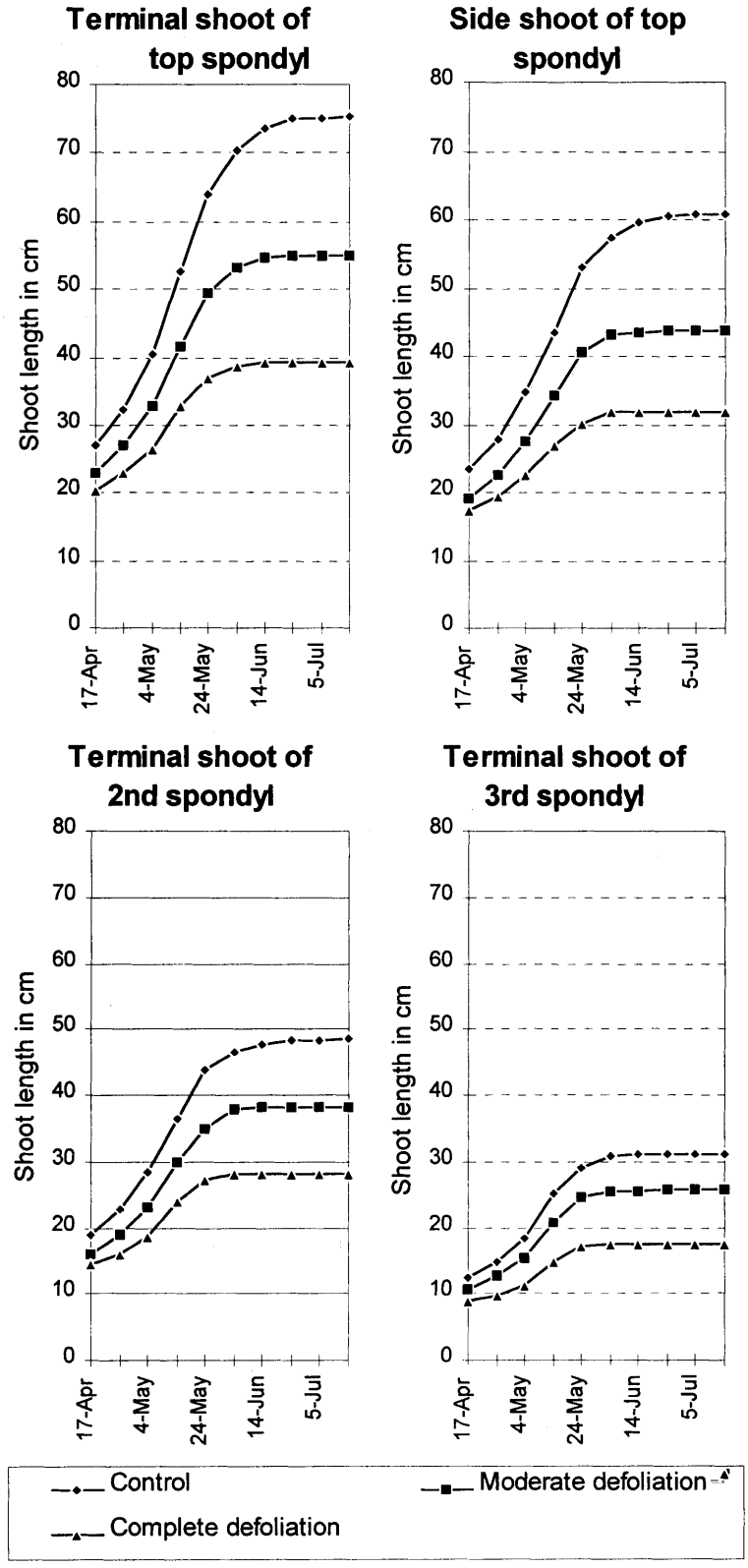


Figure 1. Change in shoot length of *P. pinaster* trees during the first growing season after defoliation by *T. pityocampa*.

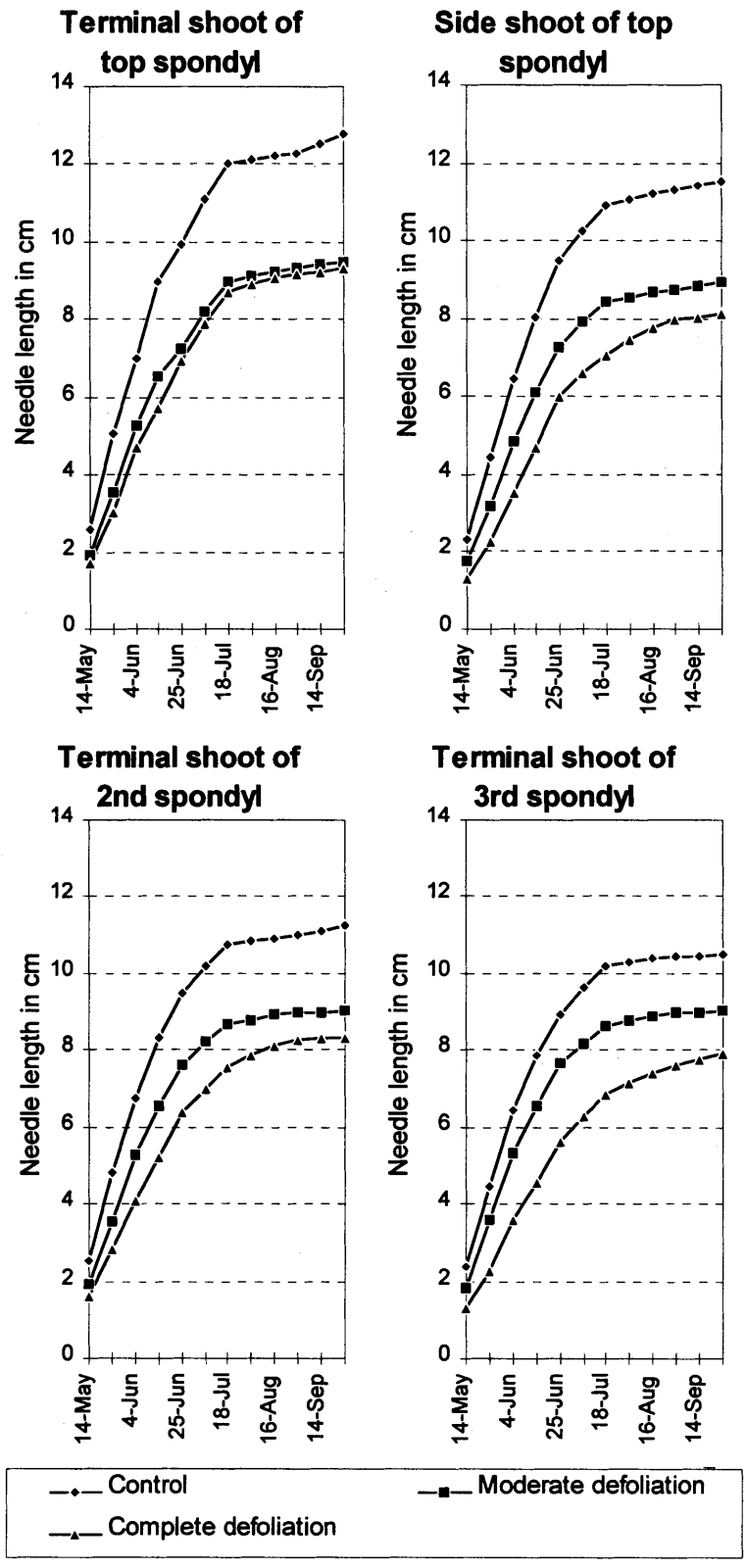


Figure 2. Change in needle length of *P. pinaster* trees during the first growing season after defoliation by *T. pityocampa*.

The increase in dry weight of new needles produced by undefoliated and defoliated trees demonstrated a similar pattern as that previously reported in needle length in almost all cases (Fig. 3). The only remarkable difference was that the increase in the dry weight of needles continued for about 1.5 months after the completion of the length increment.

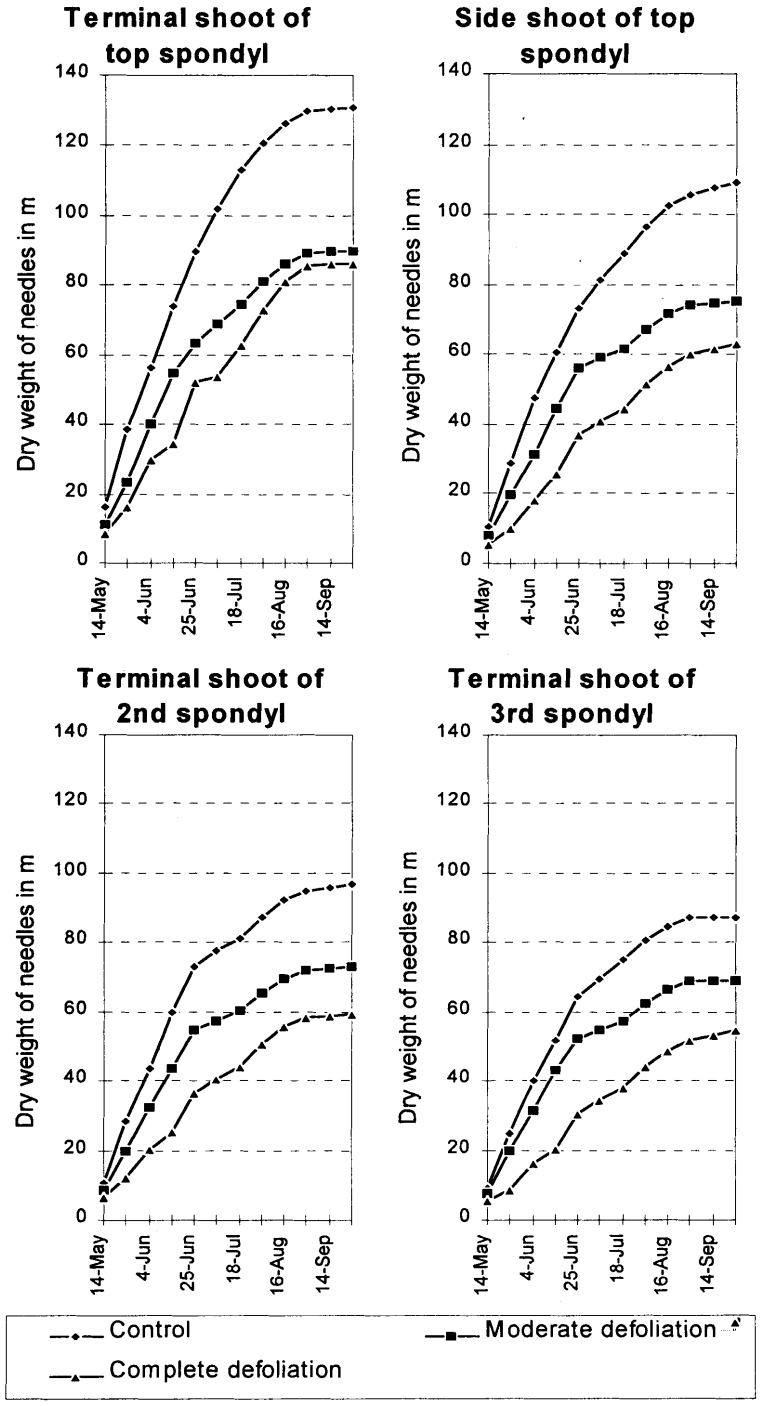


Figure 3. Change in dry weight of a 2-needle cluster in *P. pinaster* trees during the first growing season after defoliation by *T. pityocampa*.

In general, the increment in shoot length was completed in the first half of June, while the increment in needle length (originated always from the lower part of shoots) was completed within the first half of July. The increase in dry weight of needles was prolonged over a longer period of time, even after the end of August. Differences were also found among the three defoliation groups: in moderately defoliated trees, the growth in shoot length, needle length and needle weight was completed a few days earlier than in undefoliated control trees, and the growth of completely defoliated trees was completed earlier than that of moderately defoliated trees.

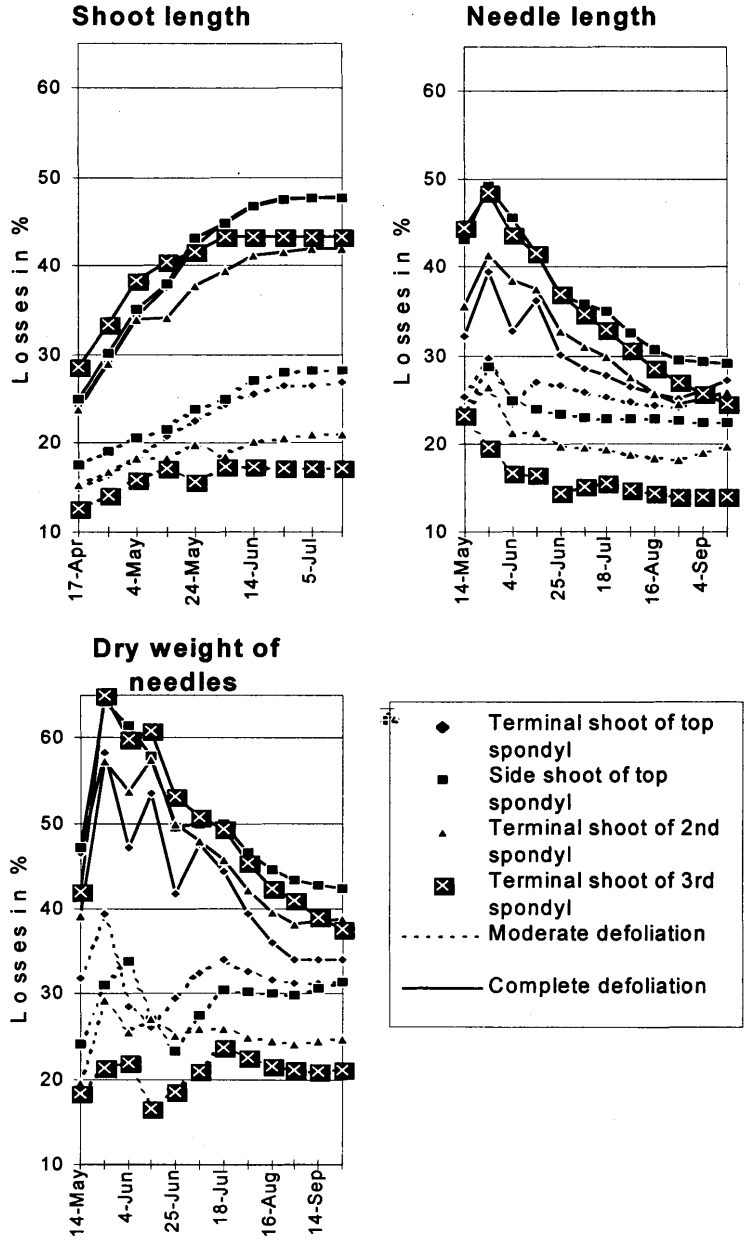


Figure 4. Change in losses in shoot length, needle length and needle weight of *P. pinaster* trees during the first growing season after defoliation by *T. pityocampa*.

The percentage losses in shoot length, needle length and needle weight during the growing season are given in Figure 4. Shoot length losses increased with time for both degrees of defoliation. The losses in needle length and needle weight in the group of moderately defoliated trees were almost invariable, showing only small differences during the growing season, while in the group of completely defoliated trees they were decreasing. The greatest losses were found on the terminal and side shoots of the top spondyl, becoming progressively less as the spondyl's position was near to the ground.

Final losses, measured by the increment of shoot growth, increased to 17.3-26.8% in moderately defoliated trees and to 42.0-47.8% in completely defoliated trees (Fig.5). The 47.8% loss observed after defoliation in the terminal shoot of the top spondyl at the end of the growing season is relatively low compared to the 67.5% and 67.2% losses measured in *P. nigra* and *P. radiata*, respectively (Markalas 1989b). This is because at the end of the defoliation (first days of April), the shoots of *P. pinaster* were already too long. More specifically, when the shoots of the severely defoliated trees were measured for the first time (17 April), they were longer than 50% of their final length.

Final losses in needle length were less than those in shoot length, increasing to 14.0-25.7% in moderately defoliated trees and 24.6-29.2% in heavily defoliated trees (Fig. 5). The losses in dry weight of needles reached 21.1-31.4% in the group of moderately defoliated trees and 34.0-42.3% in the group of completely defoliated trees. Analyzing the final losses in needle length and needle weight, we see that the differences between the two degrees of defoliation were relatively low in the terminal shoot of the top spondyl and greater in the other shoot types.

The results of the last measurement are presented in Table 1, which took place at the end of February of the next year. As expected, the number of needle clusters per shoot was significantly greater in undefoliated control trees than in defoliated trees, since this depends mainly on the shoot length. Interestingly enough, the number of needle clusters per unit length of shoot (10 cm) demonstrated an opposite trend, increasing with the degree of defoliation. Thus, the side shoot of the top spondyl contained 55.1 clusters in the control trees and 97.4 in the completely defoliated trees, while in the terminal shoot of the second spondyl the corresponding numbers were 58.3 and 103, respectively (Table 1).

Taking into account the data in Table 1, we see that in the group of moderately defoliated trees, the needles were 24.7-26.1% shorter and 31.8-33.2% lighter, while in the group of completely defoliated trees, they were 27.4-27.8% shorter and 43.5-45.8% lighter.

The biomass of new shoots produced by pine trees during a growing season is comprised of needle biomass and the biomass of the woody stem of the shoots. The differences found between defoliated and control trees were greater in biomass of the woody stem of the shoot (shoot without needles) than in the biomass of needles (Table 1). Thus, the percentage losses in needle biomass were 39.7-48.6% in moderately defoliated trees and 50.6-60.1% in heavily defoliated trees, but for the woody stem of the shoot the losses were 46.6-52.7% and 68.3-75.6%, respectively (Fig. 6). The losses in total shoot biomass were found to be 41.1-49.6% in moderately defoliated trees and 54.3-63.7% in the completely defoliated trees. In all cases, losses were greater in the terminal shoots of the second spondyl than in the side shoots of the top spondyl.

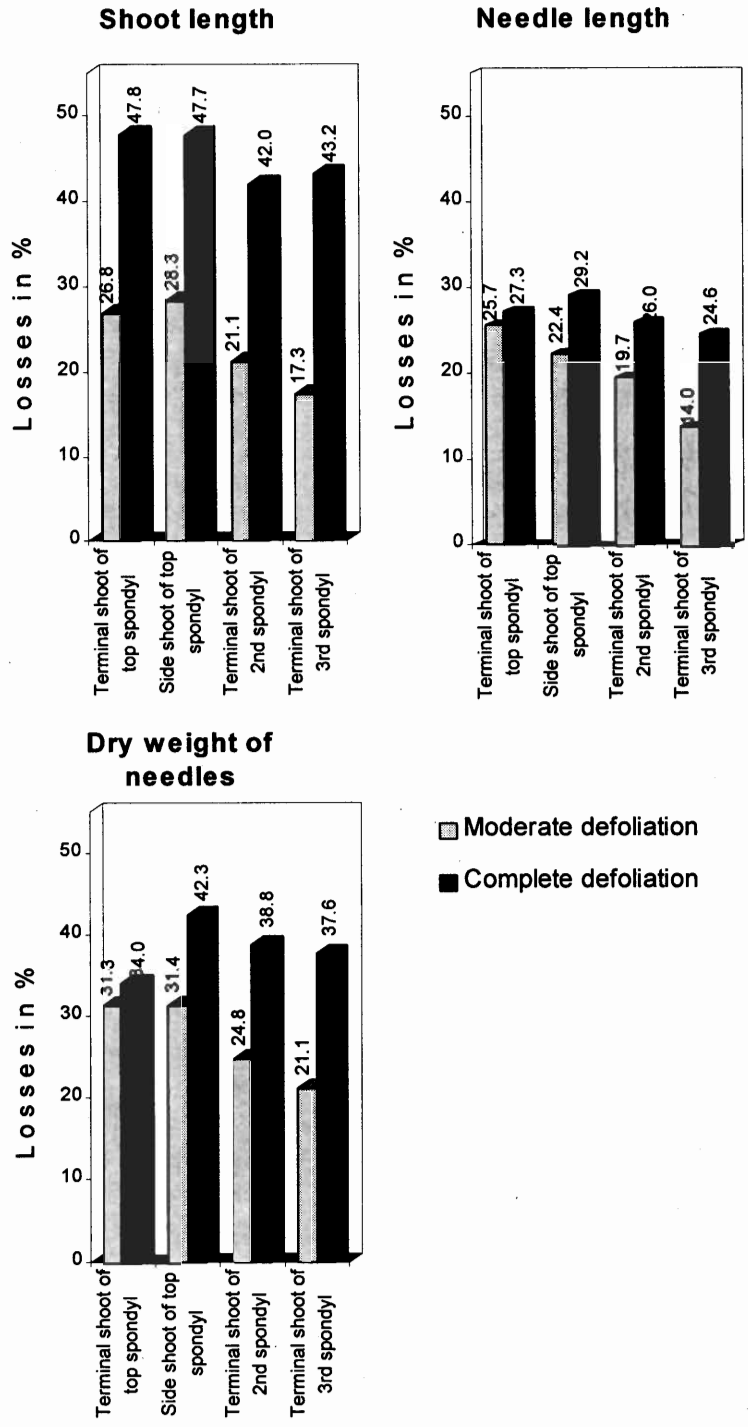


Figure 5. Final losses in shoot length, needle length and needle weight of *P. pinaster* trees at the end of the first growing season after defoliation by *T. pityocampa*.

Table 1. Refoliation and biomass production of *P. pinaster* trees measured one year after defoliation by *T. pityocampa*

Parameter	Side shoot of top spondyl			Terminal shoot of 2nd spondyl		
	Control	Moderate defoliation	Complete defoliation	Control	Moderate defoliation	Complete defoliation
Total shoot length (cm)	64.2	45.5	31.4	51.9	37.4	27.4
Shoot length carrying needles (cm)	60.6	39.4	26.5	50.2	35.3	25.8
Average needle length (cm)	11.7	8.8	8.5	11.5	8.5	8.3
Number of needle clusters per shoot	334.5	269.0	246.3	291.6	256.7	255.7
Needle clusters per 10 cm shoot length	55.1	67.9	97.4	58.3	73.0	103.0
Average needle cluster weight (mg)	147.1	98.3	79.8	134.0	91.4	75.7
Needle biomass per shoot (gr)	50.26	25.84	20.07	39.64	23.92	19.60
Shoot biomass without needles (gr)	15.42	7.29	3.76	10.69	5.71	3.39
Total biomass per shoot (gr)	65.68	33.13	23.83	50.33	29.63	22.99

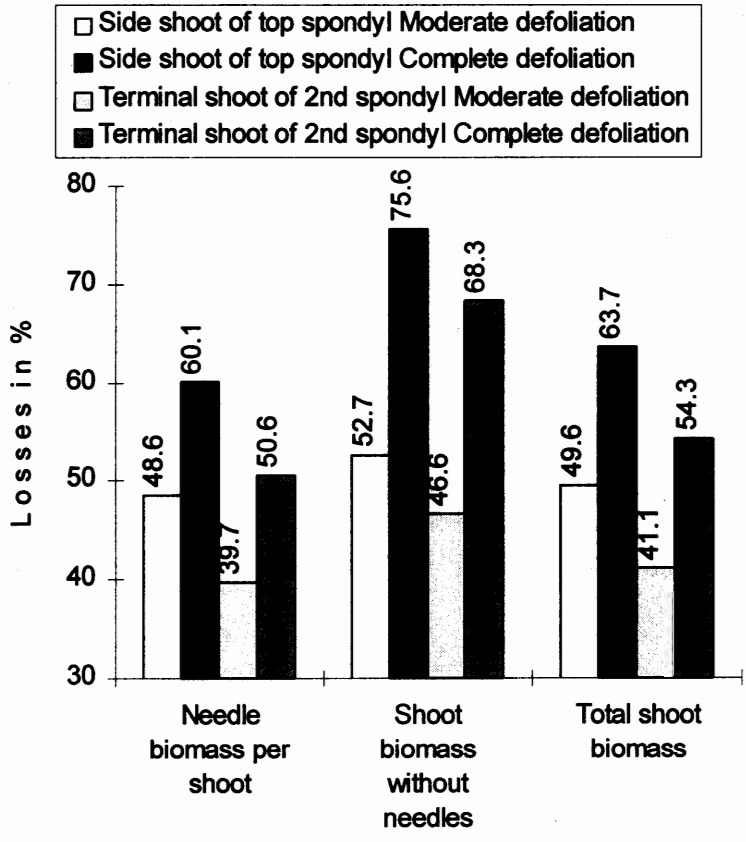


Figure 6. Percentage losses in biomass production of *P. pinaster* trees measured one year after their defoliation by *T. pityocampa*.

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Crown Fauna of Birch Stand Caterpillars in a Pollution Area and their Population Dynamics

EMANUEL KULA

Faculty of Forestry and Wood Technology, Zemedelská 3, CZ 613 00 Brno, The Czech Republic

ABSTRACT In a forested area affected by air pollution in FD Snezník (north Bohemia), the fauna of butterfly caterpillars in birch crowns was sampled by shaking foliage. Among 6,068 individuals collected, 119 Lepidoptera species were identified; the most dominant species were those with high outbreak potential: *Cabera pusaria, Operophtera fagata* and *Coleophora serratella.* Changes in population dynamics significantly influenced which species was dominant. An apparent 3-to 4-year population density cycle was observed for *C. pusaria.* Two periods of increased caterpillar occurrence in birch crowns were observed each growing season: a spring peak with culmination at the end of May and June, and a summer peak with culmination in mid August.

FROM THE EXISTING spectrum of more than 300 phytophagous insect species developing on birch, the majority of representatives are in the order *Lepidoptera.* Free living or mining caterpillars first damage leaves, then buds and catkins. Caterpillar damage is minimized due to a high birch regeneration capacity, weather conditions and a natural enemy complex.

The crown fauna of birch was studied by Gninenko (1974), Kozlov (1984), Kolomiec and Artamonov (1985) and Kutenkova (1986). *Epirrita autumnata* (Eidmann 1964), *Erannis defoliaria* (Badalík 1988), *Eriocrania* sp. (Koricheva 1994) and *Coleophora serratella* (Kula and Vaca 1995) are considered serious birch pests.

Kula (1995a) used light traps to sample in the same area as we report upon here and collected a total of 861 butterfly species of which 123 feed upon birch. The goal of this paper is to evaluate the caterpillar fauna of birch crown: their species and numerical representation, phenology, and seasonal and population dynamics.

Materials and Methods

From 1986 to 1995, we collected 6,068 birch caterpillars by shaking crowns. Butterfly fauna in the caterpillar stage were studied in six birch stands of Forest District (FD) Snezník by shaking caterpillars onto 2 x 2 m linen squares. Caterpillar control in birch crowns was carried out in every locality on 5 trees at 14-day intervals throughout the entire vegetative season (mid-April until the end of October). Different sample trees were treated between successive control applications so that the stand, not only sample trees, could be monitored. Collected caterpillars were preserved in 75% ethyl alcohol.

Pages 303-310 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Techncial Report NE-247.

Description of the Study Area

The experiment was carried out in Forest District (FD) Snezník (north Bohemia) between 450 and 600 m in altitude. The area is characterized by rough topography, mountainous climate with an average annual temperature of 6° C, a total annual precipitation of 800 mm, a vegetative season of 110 to 120 days and a long-term influence of enhanced SO_2 concentrations. Forest stands are situated in the area of maximum (A) and heavy (B) air-pollution endangerment, in complex of forest types (6K) acidic spruce beechwood and is characteristic of substantial weed infestation with dominant representation of *Calamagrostis villosa* (Chaix.) Gmel., *Avenella flexuosa* (L.) Pirl. (Table 1).

Table 1. Characteristics of stands under study

Locality	Birch representation (%)	Year of Forestation	Aspect	Altitude (m)	Degree of pollutant load	Forest types composition	Weed infestation (%)
Vlcák	100	1980	NW	450	B	6K4	100
K. Hrádek	100	1980	N	500	A	6K4	100
Snezník	60	1979	S	560	B	6K1	90
Tisá	100	1980	plain	600	A	6K4	100
Ostrov	100	1979	N	550	A	6K8	50
Letadlo	70	1983	SE	450	B	6K4	75

Results and Discussion

We collected 6,068 caterpillars belonging to 119 species of *Lepidoptera*. The majority of individuals were collected in birch stands within the K. Hrádek and Vlák localities over 10 years using the shake down method.

Dominant species included *Cabera pusaria* (34.7%), *Coleophora serratella* (7.8%) and *Operophtera fagata* (16.4%); subdominant species included *Cyclophora albipunctata* (4.9%) and *Teleoides proximellus* (2.6%). *Biston betularius* (1.5%), *Operophtera brumata* (1.3%) and *Orthotaenia undulana* (1.3%) were classified as receding, and the 111 remaining species were classified as subreceding (< 1%) (Fig. 1).

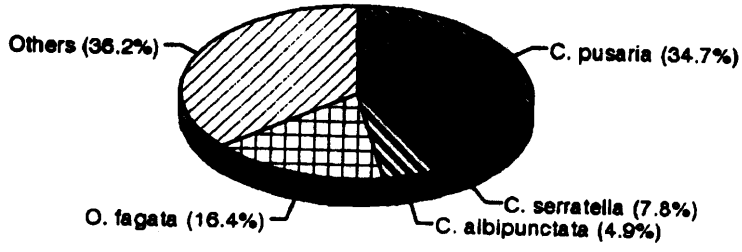


Figure 1. Dominant crown caterpillar species of birch stands (FD Snezník, 1986-1995).

Over the 10 years of the study, three peaks of caterpillar abundance were recorded (1988, 1992, 1995), followed by a significant decrease. It is not yet known if there is a 3- or 4- year gradation phase between peaks of population density (Fig. 2).

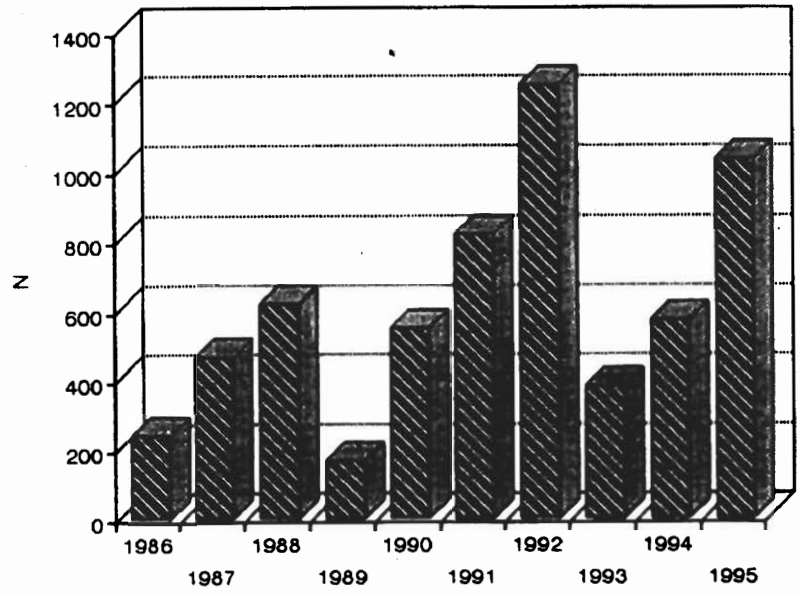


Figure 2. Dominance of caterpillars in the crown fauna of birch stands (FD Snezník, 1986-1995).

The seasonal and population dynamics of the crown fauna varied substantially among eudominant and dominant caterpillar species. The decline of *C. pusaria* in 1990 was substituted by local outbreaks of *C. serratella,* and its decreased dominance in 1991-1994 was offset by increases in *O. fagata* and partially by *C. albipunctata.* Subdominant species usually had one population peak in the course of 10 years (5-8%): *O. brumata* (1988), *Paradiarsia similaria* (1989), *Semiothisa notata* (1992) and *O. undulana* (1993).

Eudominant species *C. pusaria* changed dominance in the following pattern: a peak occurred in 1987 (57.9%); after three successive years of decline to 14.6% in 1990, a second peak occurred (60.6%) in 1991, followed by a significant and rapid decrease of dominance (34.4% and 8.9%) in 1992 and 1993, respectively. In 1995, this species had a partial increase of dominance (28.2%). When comparing absolute values of caterpillars shaken down from the same number of trees, a significant population trend appeared, characterized by 2-year peaks in an almost regular, 3-year cycle in 1987-1988, 1991-1992 and 1995 (268 x 329, 494 x 428 pieces, 292 caterpillars).

C. pusaria was the most significant species of the study area and reached a eudominant position in all localities. Looper *O. fagata* was a eudominant species from 1986 to 1995 with relatively low dominance from 1986 to 1991 (0 - 7.8%). In 1992, we recorded a peak in this species (31.2%) with a mild decrease the following year. The next peak during the 10-year period occurred in 1994 (39.1%). Evaluation of population dynamics from the absolute number of caterpillars caught showed that since 1989, abundance of this caterpillar species in birch crowns was gradually increasing with a peak in 1992 (389 caterpillars)

followed by a decrease. The density of this species remained 2-4 times higher than the density recorded one year before residual (Fig. 3).

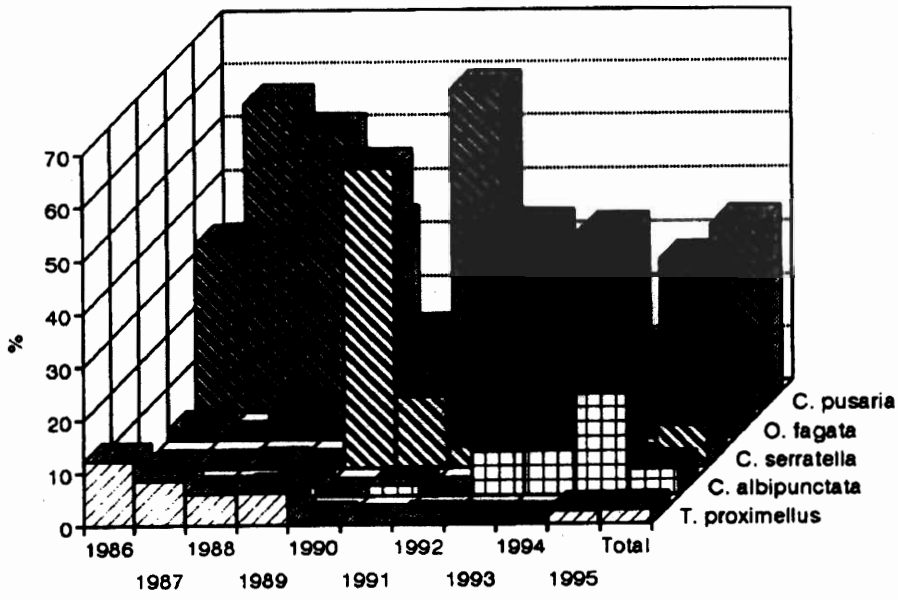


Figure 3. Population dynamics of caterpillars in the crown fauna of birch stands (FD Snezník, 1986-1995).

C. serratella, a dominant species, showed a sudden peak in 1990. It was not collected in birch crowns from 1986 to 1989. This peak was followed by a sudden decrease of dominance in 1991 (13.4%). The absolute values of shaken caterpillars show that this peak can be characterized in the same way as *C. pusaria* (Fig. 3). A higher occurrence of this species occurred in only three localities.

C. albipunctata was a subdominant species, but from 1986 to 1992, we did not collect specimens of this species in birch crowns. In 1993, it appeared as a dominant species. Its representation continually grew to 19.1% (1995); peak absolute values were recorded as well (Fig. 3). *B. betularius*, a receding species, showed long-term, well-balanced dominance within the crown fauna with a slight increase recorded in 1986, 1989 and 1995. *O. undulana* was not found in birch crowns until after 1990; its dominance gradually increased to 7.5% (1994). *T. proximellus* was a dominant species, its dominance gradually decreasing from 1986 (12.2%) to 1991 (0.1%) and then slightly increasing until 1995 (2.4%) (Fig. 3).

During the 10-year period, the dynamics and phenology of the complex butterfly fauna in the caterpillar stage formed two significantly separated stages in FD Snezník. The spring period, which culminated with a peak at the end of May and June, occurred from the beginning of May until mid June. The second caterpillar wave started in mid June and culminated in mid August. The period between the spring and late summer waves of caterpillars was characterized by low, well-balanced caterpillar representation. From phenological point of view, caterpillars were on birch trees from the beginning of leaf flush (last half of April) until the end of the vegetative period at the end of October (Fig. 4).

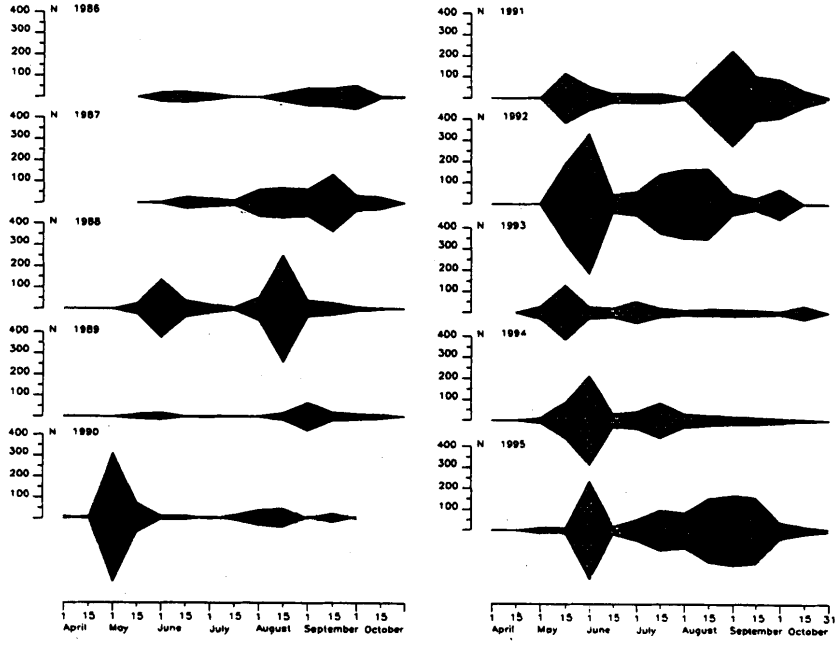


Figure 4. Phenology and seasonal dynamics of crown caterpillars of birch stands (FD Snezník, 1986-1995).

O. fagata which occurred in birch crowns from the beginning of May, was among the important spring species. Its occurrence peaked at the beginning of June and its development was finished by the end of June. The looper, *O. brumata*, occurred at the same time, but it did not reach as high a level of population density.

O. undulana caterpillars were active in mid April with a peak in mid May and sporadic presence in samples at the beginning of June. *Pandemis cerasana*, another spring species, started feeding on birch at the beginning of May; its peak population density occurred at the beginning of June, and a month later it disappeared from birch crowns.

One summer representative is *P. similaria*, which occured from mid June to mid October with estimated peak abundance at the beginning of August and probable second generation in September. *T. proximellus* was collected from mid July until the end of October, with peak abundance occurring in mid August. Two quite evident generations characterized *C. albipunctata,* which was collected in tree crowns from mid June until the end of October with peaks in mid July and mid September. The occurrence of the second caterpillar generation was recorded in mid August. Two generations with a relatively low caterpillar abundance on birch was characteristic of *S. notata,* which appeared in crowns at the beginning of June and remained until the end of September. The first generation peaked in mid July; the second generation appeared in the second half of August and peaked in mid September.

C. pusaria was a late summer species with only one generation. The caterpillars hatched at the beginning of July, a peak lasted from mid August until the beginning of September, and caterpillars were found in birch crowns even at the end of October (Fig. 5).

Phenology and seasonal population density of *C. pusaria* in the 10-year study period showed significant variation in population dynamics, with peaks always occurring after two-year decreasing population density. The timing of caterpillar occurrence from July to October varied among years. In 1992, caterpillars were already developing on birch trees in June. In 1987, 1991, 1993, 1994 and 1995, caterpillars were in the crown at the beginning of July. From mid August in 1990 and from the beginning of August in 1987 and 1989, we found caterpillars of this species in birch crowns.

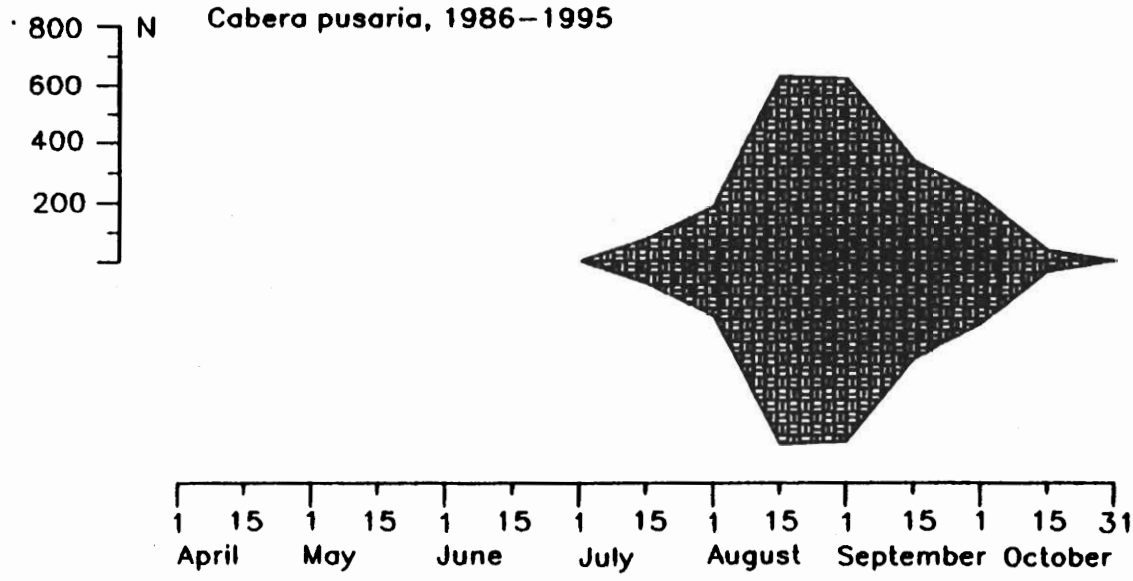


Figure 5. Phenology and seasonal dynamics of *Cabera pusaria* caterpillars (FD Snezník, 1986-1995).

Despite the collection of 119 caterpillar species from birch crowns only a few of these are significant due to their severity of damage (*O. fagata, C. pusaria* and others). A substantial number of species developing in birch crowns do not endanger this tree species; these species often occurred only in limited numbers during the 10-year period. The results discussed above are in agreement with the data of Kutenkova (1986).

Wiackowski et al. (1976) collected 401 species of birch crown fauna, 73.5% of which were made up of phytophagous species and 67 species of butterflies. The highest density of caterpillars, *Macrolepidoptera*, appeared in the study area less affected by air pollution. Under these conditions, *O. fagata* outbreaks appeared.

The 119 species of caterpillars which we collected ranged from butterflies to the most significant forest pests of birch. An outbreak of *Erannis defoliaria* occurred in birch stands in the first half of the 1980s (Badalik 1988) and a casebearer (*C. serratella*) outbreak center appeared in FD Snezník (Kula and Vaca 1995). While *E. defoliaria* showed slight

representation, *O. fagata* had a high population density accompanied by severe damage of birch crowns. Because this species is widely polyphagous, other broadleaved trees in forest stands in polluted areas are endangered. *O. undulana*, which also attacked broadleaved woody plants, also occurred at high population densities. Information about its outbreak potential is lacking. The casebearer *C. serratella*, which prefers birch, is also a monophagous species. Its local outbreak occurred from 1990 to 1991 (Kula and Vaca 1995). Outbreaks of this species are common in Canada (Raske 1976). This species appeared in the entire Krušné hory mountain area (Kula 1995b).

The occurrence of eudominant and dominant species and their joint seasonal dynamics may be significantly influenced by weather. With the looper *O. fagata*, a 10-year cycle of enhanced population density may occur. If an outbreak appeared at the beginning of the 1980s, it may last until the beginning of the 1990s.

According to Wiackowski et al. (1976), crown fauna and their abundance and species composition can be influenced by the degree of air-pollution. For instance, moths of the species *Acleris ferrugana, T. proximellus, Hedya atropunctata* and *Spilonota ocellana* occurred more often in moderately polluted localities. The dominant position of *O. fagata, Achlya flavicornis* and *Coleophora fuscedinella* was closely associated with the severely polluted area and their occurrence decreased with a decreasing degree of pollution. On the contrary, miners of *Eriocrania* sp., *Heliozela betulae* and *Lyonetia clerkella* preferred a clean environment. Caterpillars of *Lithocolletis* sp. and *Incurvaria* sp. seemed unaffected by pollution levels.

Study areas in FD Snezník are part of a larger area which has been affected by air pollution over a long time. Individual localities do not have very different air pollution histories so they could not be evaluated within an air pollution gradient. Our *C. serratella* outbreak data may support the results of Wiackowski et al. (1976), but on the other hand, *O. brumata* reacted population density in the same conditions.

Conclusions

In the crown fauna of birch stands, we identified 119 caterpillar species (6,068 individuals). Species classified as eudominant included *C. pusaria, C. serratella* and *O. fagata*; dominant species included *C. albipunctata* and *T. proximellus*; and subdominant species included *B. betularius, O. brumata* and *O. undulana.* One hundred and eleven species were classified as subreceding.

Evaluation of caterpillar abundance over 10 years suggested that a 3- to 4-year outbreak pattern of crown dwelling butterfly caterpillars exists (1988, 1992 and 1995 were outbreak years) which was decidedly influenced by eudominant and dominant species. These species changed their dominance within the outbreak cycle. *C. pusaria* exhibited a population cycle characterized by a 2-year outbreak every 3 years. *O. fagata* populations appeared to peak every 10 years. Outbreaks of *C. serratella* appeared to be as short-lived.

The birch crown fauna caterpillar complex exhibited two distinct periods within each growing season. The spring peak culminated at the end of May and June, and the summer population reached its peak in mid August. The emergence of spring and summer caterpillar populations, as well as their culmination and duration, were heavily influenced by weather conditions in individual years. *C. pusaria, C. serratella* and *O. fagata* were among the most

significant butterfly species with outbreak potential in birch stands. Species identified as pests that occur in the caterpillar complex, but have not yet had outbreaks, include *Agriopis aurantiaria, Alcis repandata, Archiearis parthemias, Biston betularius, Campaea margaritata, Colotois pennaria, Cyclophora albipunctata, Ochropacha duplaris, Orthotaenia undulana, Pandemis cerasana, Semiothisa notata* and *T. proximellus.*

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The Use of *Bacillus thuringiensis* Against *Thaumetopoea pityocampa* Schiff. (Lepidoptera:Thaumetopoeidae) in Greece

NIKOLAOS D. AVTZIS

Technological Education Institute (TEI) of Kavala, Dep. of Forestry in Drama, Lab. of Forest Entomology, 66 100 Drama-GREECE

ABSTRACT In the pine forests of Greece one of the most common needle-eating insects is *Thaumetopoea pityocampa* Schiff. It attacks all pine species at different levels of intensity and occurs almost everywhere, from sea level to an altitude of 1800 meters.

In the past, *T. Pityocampa* was controlled efficiently by using chemicals such as DDT, BHC, Malathion, Systox and Metasystox. In 1965, *Bacillus thuringiensis* was used against *T. pityocampa* in Greece for the first time by Kailidis. The formulations that were used during that period for aerial application were Thuricide, H.P. (15.8 billion I.U./Kg), Dipel (16.000 I.U./mg) and Bactospeine (16.000 I.U./mg) at a dose of 700-750 g in 50 1 of water/ha. In the 1980's pesticides such as Dimilin, which are chitin inhibitors, were preferred over Bt for control of *T. pityocampa.*

More recently, however, improvements in *B. thuringiensis* formulations, such as their improved stability at a range of temperatures, improved deposit characteristics and environmental safety, have led to the renewed widespread use of Bt products against *T. pityocampa.*

In an effort to confirm the improvements of the new Bt product, Foray 48B, an experiment was conducted using three pesticides: Foray 48B, Dimilin 25wp, and Bactospeine wp (16.000 IUAK/mg) in 10 to 14-year-old plantations of *Pinus bruita.* All three products that were used, under the particular climatic conditions, provided good foliage protection and a high level of mortality (96.1-100%).

IN GREECE, CONIFEROUS forests occupy over 3,359,186 ha, and 25.4% of this land is categorized as commercial forest. The annual increment is estimated to be 1 m^3/ha. In the pine forests, the most significant species are *Pinus halepensis, Pinus brutia, Pinus nigra* and *Pinus silvestris*, which cover about 870,378 ha (60.9%) of the coniferous forests (Eleftheriadsis 1996).

In Greek pine forests, one of the most common insects is the needle-eating *T. pityocampa*, the processionary pine caterpillar. It appears in all pine species at different population intensities (Avtzis 1983c, 1986, Schopf and Avtzis 1987) and occurs almost everywhere in Greece from sea level to 1800 meters altitude on Mt. Olympus. It is absent in only a few areas of Central Greece (e.g. in Karpenisi) because of the unsuitable weather conditions as well as on some islands of the Aegean Sea, possibly because of their geographical isolation (Avtzis 1983b). The problems caused by this insect can be placed into three categories:

a. Health problems to humans (e.g. allergenicity).
b. Aesthetic problems (nests on the trees, defoliation etc.).
c. Economic problems due to the loss of growth caused by the defoliation.

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Because of these effects, individually or collectively, there is a need to control this harmful insect and to minimize its damage. The control of *T. pityocampa* in Greece has passed through many stages, following progress in development of chemical pesticides and then concerns about ecology and the benefits of more environmentally safe approaches in recent years.

Initially, *T. pityocampa* was controlled efficiently by using chemicals such as DDT, BHC, Malathion, Systox and Metasystox (Kailidis 1962b, 1965). Then in 1965, Kailidis used *Bacillus thuringiensis* (Bt) against *T. pityocampa* (Kailidis 1967, from Kailidis 1986). The Bt-based products which were used during that period for aerial applications included Thuricide-HP. (15.8 billion I.U./kg), Dipel (16.000 I.U./mg) and Bactospeine (16.000 I.U./mg) at a dose of 700-750 gr in 50.1 of water/ha (Kiailidis et al. 1977). In subsequent years, *B. thuringiensis* was used in Greece by other researchers for control of *T. pityocampa* with very good results (Vankova and Svestka 1976, Kailidis et al. 1977, Georgevits 1979, Avtzis 1983a, 1984).

Frequently, the Greek Forest Service was unable to provide airplanes at the proper time, and therefore applications of Bt were delayed, especially under difficult weather conditions in Northern Greece.

We obtained experimental confirmation about the effectiveness of Diflubenzuron for the control of *T. pityocampa* in Greece (Georgevits 1979, Avtzis 1981). However, because of the environmental safety of Bt and substantial improvements of new Bt products, including their improved efficacy at low temperatures, we were interested in evaluating their use againt *T. pityocampa* in a Greek forest. In this paper, we report on the experimental application of Foray 48B against *T. pityocampa* in Northern Greece.

We obtained information suggesting that low temperatures have a negative effect on the effectiveness of *B. thuringiensis* (Vankova and Svestka 1976, Kailidis et al. 1977). Spectacular results were obtained with Diflubenzuron for the control of harmful insects (Skatulla 1975a, 1975b, Salama et al. 1976).

Materials and Methods

Foray 48B was applied along with Dimilin 25wp. and Bactospeine wp. (16.000 IUAK/mg) in young plantations of *Pinus brutia* (10-14 years old) in the general area of Kedrinos Lofos near Thessaloniki. To check the effectiveness of the three substances mentioned above as compared to the control, materials were applied twice: first on October 17th, 1993, and then on November 27th, 1993 (Tables 1 and 2). It is significant to point out that on the day of the first spraying (Oct. 17th, 1993), 90% of the larvae had hatched. The effectiveness of the treatment, based on larval mortality, was estimated on the 7th, 14th, 21st, 28th and 35th day after the first spraying. After the second application, larval mortality was estimated on the 7th, 14th and 21st day.

The persistence of the three substances was investigated 7, 14 and 21 days after the first spraying. At each treatment area, three larvae were placed on five trees (3X5=15 in each area). The larval mortality on the control plots at the times the trees were artificially infested was 12.5%, 32.1% and 36.9%, respectively. On December 4, 1993, we estimated the final mortality of larvae and thus the persistence of the products.

Table 1. Technical data of the first application[1] (October 17, 1993)

Characters	Dimilin	Bactospeine	Foray 48B
Dose	250 gr/ 25 L water/ha	700 gr/ 25 L water/ha	1,5 L formulation/ha
Nozzles (number and type)	28 nozzles D-12-45 (pressure 50 PSI)	28 nozzles D-12-45 (pressure 50 PSI)	14 nozzles D- 2-45 (pressure 30 PSI)
Drop Size (μ)	300	300	100
Application Time	12:30	13:00	14:30
Drop number per cm^2	20	20	30
Nozzle positions relative to the airstream	90°	90°	45°

[1] Data of flying:
- Aircraft: CESSNA AG WAGON
- Flight Speed: 100 miles/hr
- Spraying height: 5-10 m above the top of the trees
- Speed of the wind: 5-6 miles/hr

Table 2. Technical data of the second application[2] (November 27, 1993)

Characters	Dimilin	Bactospeine	Foray 48B
Dose	250 gr/ 25 L water/ha	700 gr/ 25 L water/ha	3,0 L formulation/ha
Nozzles (number and type)	28 nozzles D-12-45 (pressure 50 PSI)	28 nozzles D-12-45 (pressure 50 PSI)	14 nozzles D-4-45 (pressure 40 PSI)
Drop Size (μ)	300	300	150
Application Time	9:30	10:00	10:45
Drop number per cm^2	20	20	20
Nozzle positions relative to the airstream	90°	90°	45°

[2] Data of flying:
- Aircraft: CESSNA AG WAGON
- Flight Speed: 100 miles/hr
- Spraying height: 5-10 m above the top of the trees
- Speed of the wind: 6-7 miles/hr

In addition to determining the effectiveness and the length of protection offered by the three substances, we also estimated the possible effect on egg hatching and parasitism.

Results and Conclusion

As shown in Table 3, there was no apparent effect of any of the three insecticides during the first or second application on hatching, parasitism and infertile egg percentages when compared to the control. Larval mortality after the first, as well as after the second spraying, is provided in Table 4. From that table, it appears that the final mortality in both applications was very high, not only in the case of Dimilin, but of the Bt-based products as well. It varied from 96.1% (Bactospeine in the second spraying) to 100% (Dimilin, Bactospeine and Foray 48B in the first spraying). We estimated that the mortality in the control area reached 47.5% after the first application and 52.4% after the second (Table 4).

Table 3. Hatching, parasitism and non-fertile egg percentages (%) after measurements of eggs of the 686 cylinder (batches) used in the experiment

Application	Treatment	Hatching	Parasitism	Non-fertile
1st	Control	65.1	10.4	24.5
1st	Dimilin	58.8	11.2	30.0
1st	Bactospeine	62.5	11.2	26.3
1st	Foray 48B	58.5	13.3	28.2
2nd	Control	65.7	11.0	23.3
2nd	Dimilin	65.4	9.5	25.1
2nd	Bactospeine	73.8	8.7	17.5
2nd	Foray 48B	68.6	10.1	21.3

Table 4. Larval mortality (%) during the two applications

Application	Day	Control	Dimilin	Bactospeine	Foray 48B
1st	7	12.5	80.0	91.2	88.8
1st	14	32.1	100.0	98.6	98.6
1st	21	36.9	100.0	99.9	98.8
1st	28	40.5	100.0	100.0	100.0
1st	35	47.5	100.0	100.0	100.0
2nd	7	48.2	64.5	81.8	85.4
2nd	14	52.3	82.7	90.5	98.5
2nd	21	52.4	98.4	96.1	99.5

Regarding the persistence of products after the plots were re-infested with larvae, larval mortality in the Dimilin plots fluctuated between 95.8% and 100% even three weeks after treatment (Table 5). In contrast, mortality of larvae caused by the Bt products was somewhat reduced but still remained at high levels.

Table 5. Total larval mortality (%) after the three new infestations, which took place 1, 2 and 3 weeks after the first application. (Time of the measurements: one month after the 3rd new infestation)

Day of the new infestation	Dimilin	Bactospeine	Foray 48B	Control
1st week (Oct. 23th)	95.80%	99.00%	96.60%	
2nd week (Oct. 30th)	99.40%	99.55%	91.65%	48.20%
3th week (Nov. 6th)	100.00%	89.70%	90.00%	

Our conclusions are as follows:

1. None of the insecticides had an effect on egg mortality, percent egg hatching or egg parasitism. Regarding the species of egg parasites that we identified in the experimental areas, we found *Tetrastichus servandei* Dom L. and *Ooencyrtus pityocampae* Mercet. These

species coincide with those described by other authors (Kailidis 1962a, 1986, Schmidt 1988). Our results of measuring egg parasitism on our experimental areas are similar to those found by others (Table 3). For example, Biliotti (1958) found that *T. pityocampa* egg parasitism in N. France in 1956 fluctuated between 3 and 28%. Kailidis (1986) determined that egg parasitism near Thessaloniki during 1960-61 was approximately 11.2%.

2. All three pesticides used gave acceptable results, as far as larval mortality was concerned, even 20 days after spraying. This result, which is considered to be very significant for the Bt-based products, is comparable to the results of other authors (Baranova 1972, Avtzis 1983b).

3. Of the Bt-based products used under the particular climatic conditions of both experiments, Bactospeine and Foray 48B provided very high larval mortality. This fact is significant and suggests that we should reconsider the use of Bt products in October and November for the control of *T. pityocampa,* especially in N. Greece. Because we obtained larval mortality ranging from 96.1-99.5% under conditions in which the air temperature was 3.6° C at the time of the second application, and never exceeded 8.3° C during the first 10 days after spraying, concerns about the use of Bt at low temperatures should be reviewed. It was the opinion of many authors, based solely on experimental data, that the effectiveness of Bt-based products was adversely affected by climatic conditions that occurred during and after spraying; this led to the limited use of those products for the control of *T. Pityocampa*, especially in N. Greece (Burdajewa and Schtscheblanov 1975, Korchagin 1980, Molloy et al. 1981). With the development of improved strains and superior formulations, it is now possible that Bt products can be used even during the third and fourth larval instar and will provide very good results.

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Activity of Several Contact Insecticides Against Selected Forest Insect Pests in Poland

D. WORETA AND H. MALINOWSKI

Forest Research Institute, Department of Forest Protection, Bitwy Warszawskiej 1920 r. nr 3, 00-973 Warsaw, Poland

ABSTRACT Four pyrethroids (alphamethrin, deltamethrin, lambdacyhalothrin, and zetacypermethrin) and etofenprox were tested against several insects that are severe pests in Polish forests. Results of the evaluations indicate that adults of the common cockchafer are equally susceptible to the four pyrethroids but 10 times less susceptible to etofenprox. Larvae of the pine moth, nun moth, and Diprionid sawflies were slightly less susceptible than cockchafer adults to the pyrethroids; however, in all cases the LD_{50} was less than 0.3 µg/g. Adults of the large pine weevil were not very susceptible to the pyrethroids used in these evaluations.

IN RECENT YEARS, populations of the common cockchafer (*Melolontha melolontha* L.) and other soil insect pests have increased significantly, especially in agricultural lands that have been abandoned (Woreta 1994). This results in serious problems when attempts are made to reforest these lands by planting trees because of the damage caused to the roots by larvae of *M. melolontha*. The adults of this species also cause significant defoliation of deciduous stands that are adjacent to the plantations.

Application of chemical insecticides is necessary to protect the roots of trees and shrubs that are planted in these areas. These products are applied to the surface of the seedlings prior to planting or injected into the soil after planting (Malinowski et al. 1996). Sometimes, insecticides are applied aerially to deciduous stands to prevent defoliation and to reduce the number of adult beetles that are available to produce progeny for the next generation. In Poland, four pyrethroid insecticides (alphamethrin, deltamethrin, lambdacyhalothrin, and zetacypermethrin) and etofenprox are recommended for control of the common cockchafer, the large pine weevil (*Hylobius abietus* L.), and larvae of other leaf-feeding insects (Glowacka 1995). The objective of this study was to evaluate the activity of these five insecticides against adults of the common cockchafer and large pine weevil as well as against larvae of three defoliating species.

Materials and Methods

The following insect species were tested:

(a) common cockchafer (*M. melolontha*) adults (ca. 7 days old)
(b) nun moth (*Lymantria monacha* L.) second and third instar larvae
(c) pine moth (*Dendrolimus pini* L.) third and fourth instar larvae
(d) conifer sawflies (Diprionidae) second instar larvae (mixed species)
(e) large pine weevil (*H. abietis* L.) adults of undetermined age

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The insecticides studied were:

Pyrethroids

(a) alphamethrin as 100 g/l EC (Fastac 100 EC, Shell)

(b) deltamethrin as 25 g/l EC (Decis 2,5 EC, Roussel-Uclaf)

(c) lambdacyhalothrin as 25 g/l EC (Karate 025 EC, Zeneca)

(d) zetacypermethrin as 100 g/l EC (Zorro 100 EC, FMC)

Arylpropylether

(a) etofenprox as 100 g/l EC (Trebon 10 SC, Mitsui Toatsu)

The activity of the insecticides was determined by topically applying a 1 µl drop of the product dissolved in acetone with a micro-applicator. The droplet was applied to the ventrum of the abdomen of adult beetles and to the dorsum of the larvae. All insecticides were diluted in acetone to produce six to eight different concentrations. Two or three replications of 15 individuals were treated at each dosage and percent mortalities were calculated at 48 or 76 hours after treatment. Controls were treated with acetone alone. Mortality data were subjected to probit analysis (Finney 1952) and LD_{50} values were calculated using four to six doses that caused mortality between 10% and 90%.

Results and Discussion

Adults of the cockchafer were equally susceptible to the four pyrethroids tested (LD_{50} = 0.008-0.012 µg/g) and in most cases were more susceptible to the pyrethroids than were larvae of the nun moth, pine moth, and sawflies (Figs. 1-4). Conversely, the cockchafer was less susceptible than the other species to etofenprox, the LD_{50} being 10 times higher than that calculated for pyrethroids. The $LD_{50's}$ for all species tested against etofenprox were higher than those calculated for pyrethroids (Fig. 5). Adults of the large pine weevil were 500-fold less sensitive to the pyrethroids than were adults of the cockchafer. Etofenprox was not tested against *H. abietis*.

With the exception of alphamethrin (Fig. 1), larvae of the nun moth were slightly less susceptible to the pyrethroids than were larvae of the pine moth and sawflies, though these differences probably are not significant.

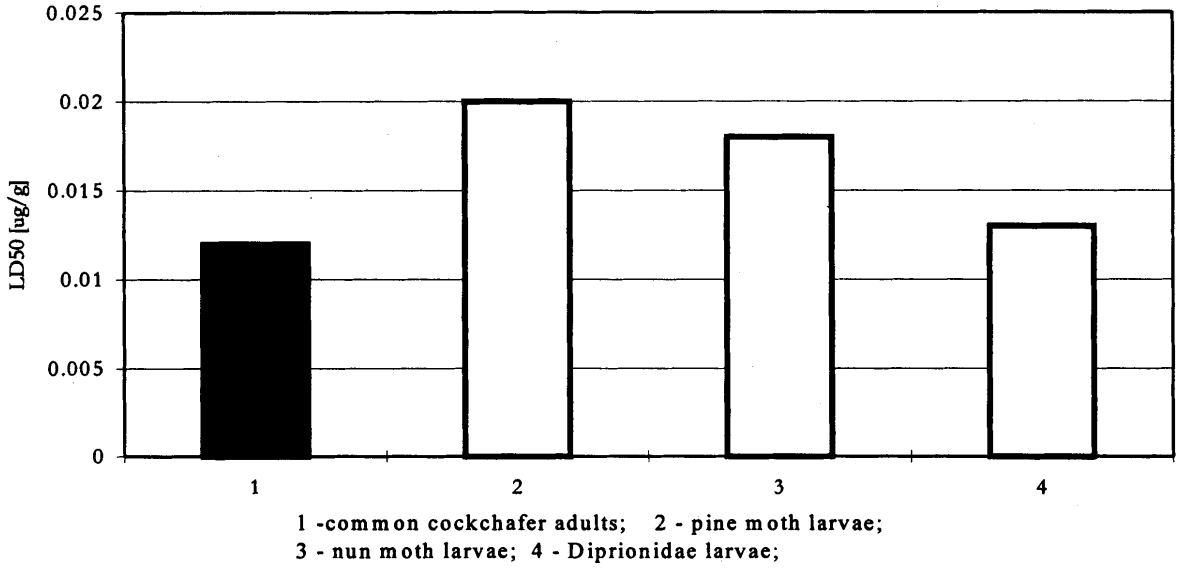


Figure 1. Comparative activity of alphamethrin against the common cockchafer and some important leaf-feeding larvae.

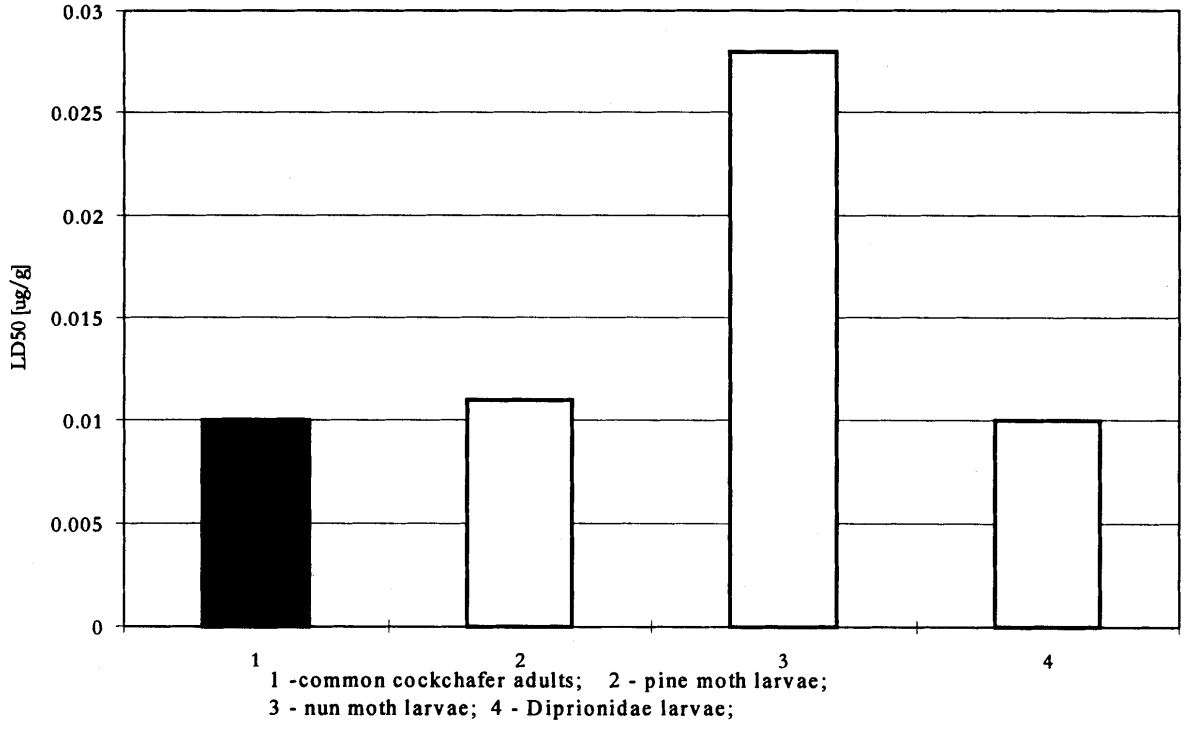


Figure 2. Comparative activity of deltamethrin against common cockchafer adults and some important leaf-feeding larvae.

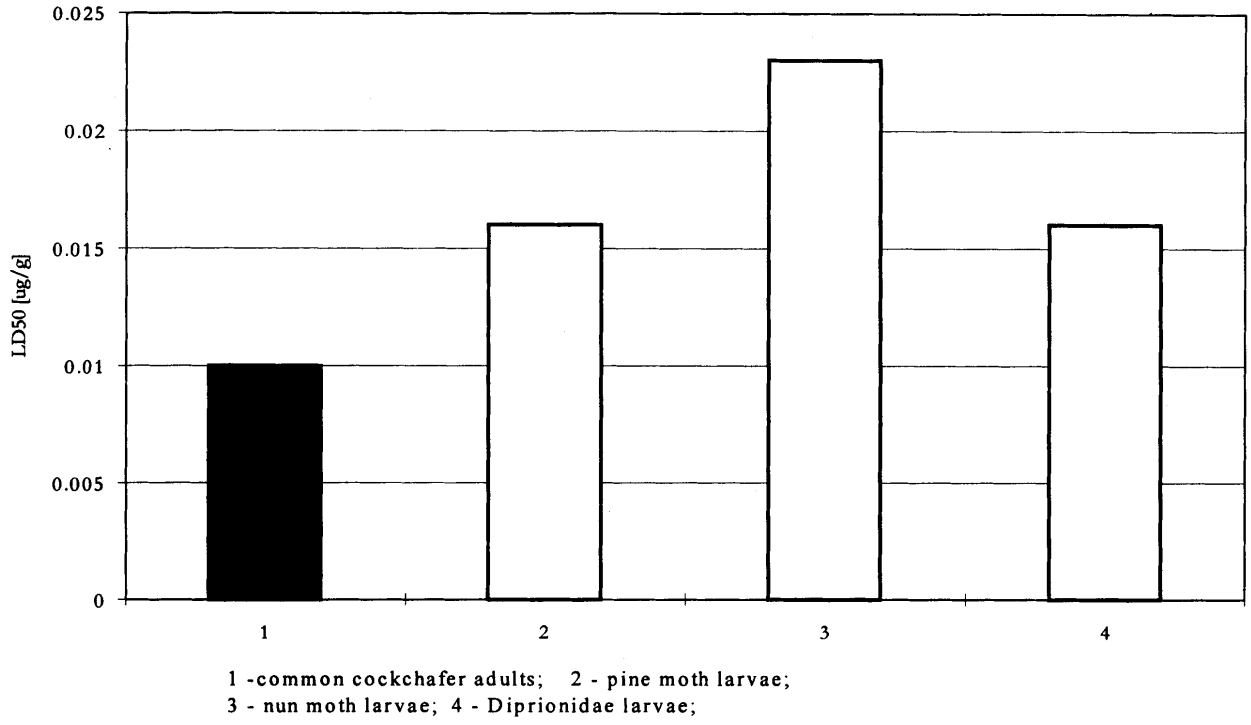


Figure 3. Comparative activity of lambdacyhalothrin against common cockchafer adults and some important leaf-feeding larvae.

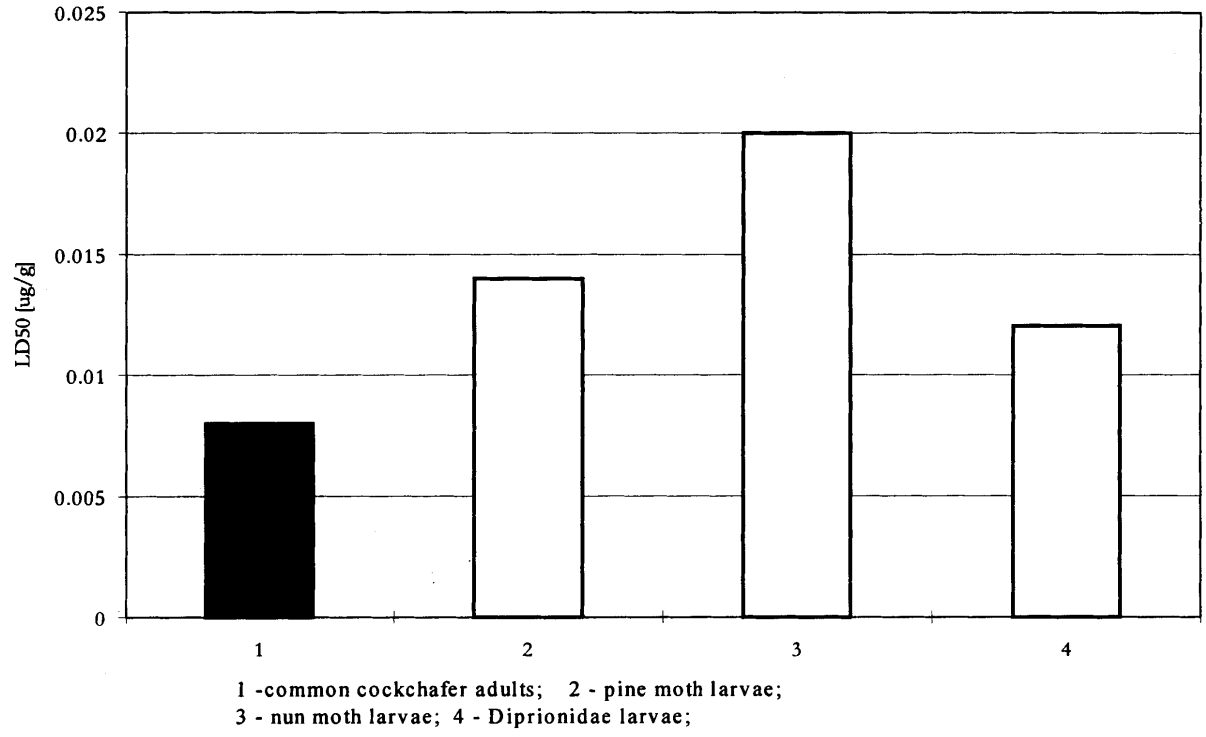


Figure 4. Comparative activity of zetacypermethrin against common cockchafer adults and some important leaf-feeding larvae.

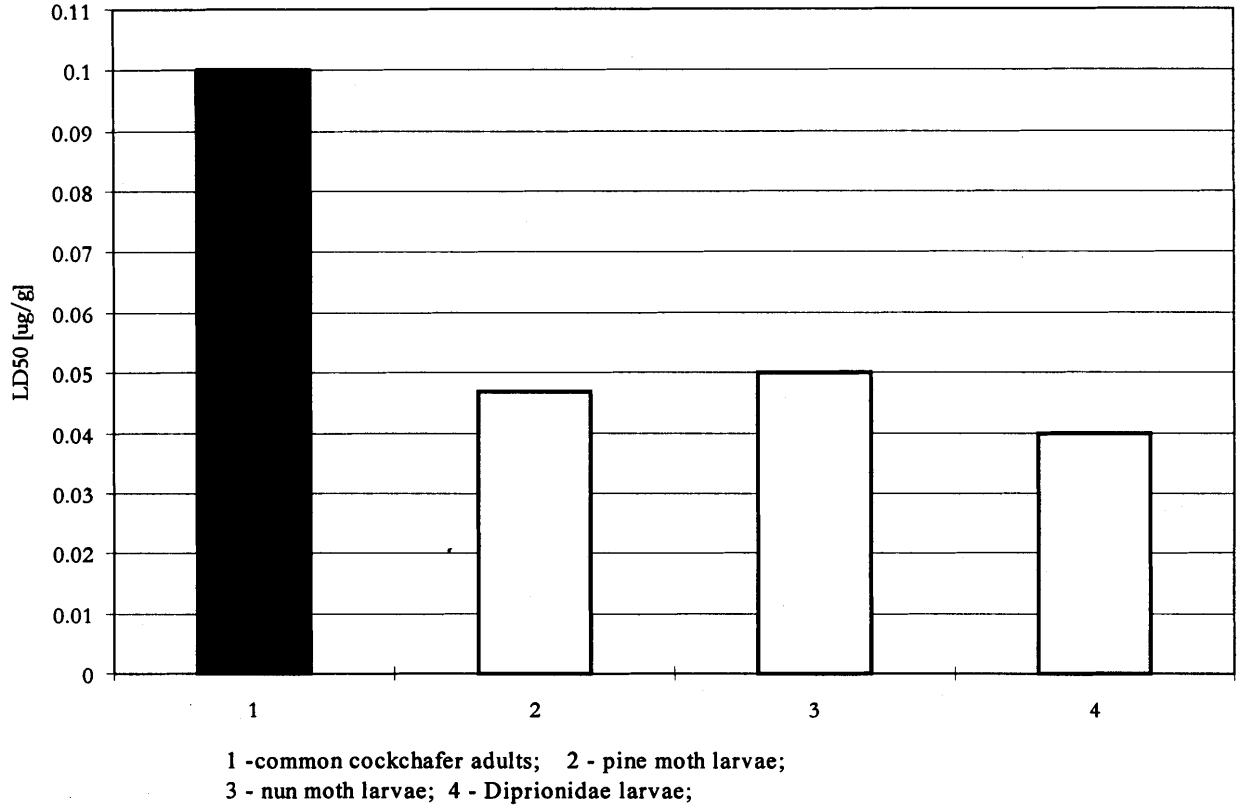


Figure 5. Activity of etofenprox against common cockchafer adults and some important leaf-feeding larvae.

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Pathogens of the Gypsy Moth in Central Europe: Host Range and Interactions

JAROSLAV WEISER

Insect Pathology, Institute of Entomology, Czech Academy of Sciences, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic

ABSTRACT In Europe outbreaks of the gypsy moth are limited by pathogens which cause high mortality and subsequent collapse of peak gypsy moth populations. The most efficient of these pathogens is the very pathogenic nuclear polyhedrosis virus, but the more chronic cytoplasmic virus acts as a complicating factor. Pathogens such as the entomophilic fungi, bacteria and nematodes are of only marginal importance. Several species of microsporidia also influence gypsy moth outbreaks. At specific locations several different microsporidian species, often occurring simultaneously in gypsy moth populations, are involved. The following review summarizes the microsporidian species described from the gypsy moth and provides some new details on the ultrastructure of some of these microsporidia.

PATHOGENS OF THE gypsy moth were first investigated in Central Europe. In the 1920s, Escherich and Breindel first demonstrated that the causative agent of the nuclear polyhedrosis was a filterable virus and in 1947 Bergold produced electron micrographs demonstrating the virus rods inside the polyhedra. In 1927, Zwölfer isolated *Plistophora schubergi*, from the brown tailed moth. This microsporidian was also infectious to *Lymantria dispar* and *Malacosoma neustrium* and was the first report of a microsporidian infection in *L. dispar* (Table 1). Zwölfer also made field applications of *P. schubergi* in an attempt to control these three forest pests. Weiser (1957a) described additional microsporidia obtained from gypsy moths collected during 1956 outbreaks in Slovakia. These species included *Nosema muscularis* and *Nosema lymantriae* together with *Thelohania similis*, recovered originally from the browntail moth. In addition, Weiser (1961a) described *Nosema serbica* from the gypsy moth. Timofeeva (1956) isolated *Thelohania disparis* from gypsy moths collected during an outbreak in the Ukraine. One inter-outbreak period later, *Plistophora schubergi* reappeared in gypsy moth populations but since that time has rarely been found.

Most of the microsporidia listed above were described before ultrastructural information was routinely included as a part of their description. Therefore, spore ultrastructure was not available for use in identifying these microsporidian species. Because ultrastructural information was not available, it has been difficult to identify microsporidian species isolated from gypsy moth outbreaks in different parts of Europe. A study organized by McManus et al. (1989) brought new isolates of microsporidia from gypsy moths collected from several additional European locations. Living isolates of these microsporidia are maintained in liquid nitrogen (Solter et al., 1996). Studies on these isolates will contribute to a better understanding of microsporidia as naturally occurring control agents of the gypsy moth.

Pages 322-333 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Materials and Methods

Type material relative to Weiser's 1957 and 1961 descriptions are available in the Type collection of microsporidia maintained in the author's laboratory. They consist of dry Giemsa-stained smears and histological sections of infected caterpillars and include the following species isolated from *L. dispar*: *Nosema muscularis* Weiser (1957a), *N. lymantriae* Weiser (1957a), *Thelohania similis* (Weiser 1957a), *N. serbica* Weiser (1961a), and *Plistophora schubergi* Zwölfer (1927). These microsporidia, imbedded in paraffin blocks, also are included in this collection. Material in paraffin blocks, which was fixed in Bouin's, were transferred to xylol to remove the paraffin. After a final washing in water the material was fixed again in gluteraldehyde and osmic acid according to the procedure of Weiser et al. (1995). After embedding in Vestopal W the material was sectioned with an ultramicrotome and examined with an electron microscope. Some of the material extracted from paraffin was not suitable for observation but additional material from 1957 experimental infections will also be examined ultrastructurally.

Results

Individual species were characterized using the 1957 protocols and materials. The paraffin-imbedded material, which was processed for the electron microscope as described above, produced ultrathin sections in which spore ultrastructure of some of the microsporidian species could be observed.

***Nosema muscularis* Weiser (1957a)** This microsporidian was isolated from L3 caterpillars of *Lymantria dispar* near Ziar n.H. The infection was localized in the circular and longitudinal muscles of the midgut where the pathogen occurred in longitudinal "galleries" in the muscle strands. The schizonts were short, binucleate stages, some with hypertrophic nuclei of the meiotic series. Oval spores with blunt ends, 6 x 3 μm, contained a visible vacuole at the posterior end. Mature spores of the same shape were 4.8-6 x 3 μm. The midgut muscles were progressively destroyed as the infection entered the tracheal matrix (Fig. 1), especially the terminal asteroid cells adhering to the midgut wall. Later the infection appeared in the secretory cells of the Malpighian tubules. Infection in the gut epithelium did not extend from the primary centers of entry that occurred immediately after ingestion of spores (peroral infection), but when infected Malpighian tubule cells ruptured, they released spores into the feces. Spores appeared in the muscles of the gut on the 5th day after spores were ingested and continuous mortality occurred over the next 20-25 days. Infected larvae appeared emaciated and became desiccated as they died. Apparently the midgut infection inhibited midgut peristalsis and thus inhibited feeding by infected larvae. Bodies of infected larvae were c- or s-shaped with a liquid diarrhea. Dying larvae had no fat body and the midgut was brown in color. Spores of *N. muscularis* were fed to other Lepidopteran hosts by placing spores on leaves of their host plants. The browntail moth and the fall webworm, *Hyphantria cunea*, were infected by *N. muscularis* while *Malacosoma neustrium*, *Aporia crataegi*, *Eriogaster lanestris* and *Bombyx mori* were refractive. In susceptible hosts the infection was localized in the muscles of the midgut. Material for EM analysis was not available.

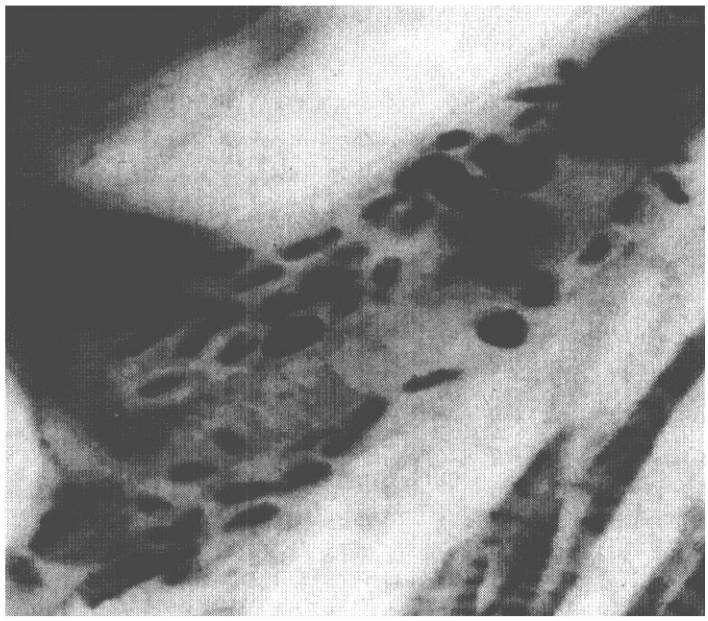


Figure 1. Tracheal matrix infected with *Nosema muscularis*. Magnification 1200x.

***Nosema lymantriae* Weiser (1957a, 1957 b)** *Nosema lymantriae* was isolated from infected gypsy moth caterpillars and maintained in laboratory rearings. Fat body and silk glands were infected (Fig. 2). Long ribbonlike merozoites with a longitudinal row of nuclei 30 x 2.5-3.5 μm were formed during schizogony. Young spores, 6 x 2.5 μm had an apparent vacuole at the posterior end. Fresh mature spores (Fig. 3) measured 5-6 x 2-2.5 μm and were spindle-shaped. Polar filaments, 125 μm long, were occasionally extruded. Eleven days after ingestion of spores (20-30,000 spores per larva on leaves) small pockets of infection were present in the silk glands and fat body. Fifteen days after ingestion of spores, two-thirds of the silk gland was filled with spores and the fat body was infected. Infected larvae lived up to 30 days in controlled laboratory rearings. The original isolate did not contain any octospores. Spores from infected silk glands were used to initiate laboratory infections; feces from infected caterpillars was not infectious. Infected larvae exhibited reduced feeding and less movement than was observed in non-infected caterpillars. Infected larvae had a well developed fat body and demonstrated no symptoms of starvation. Dead infected caterpillars were desiccated. Spores of *N. lymantriae* were fed to other Lepidopteran hosts by placing spores on leaves of their host plants. *Euproctis chrysorrhoea*, *Aporia crataegi*, *Malacosoma neustrium*, *Hyphantria cunea*, *Eriogaster lanestris*, and *Bombyx mori* were all refractive to infection using the same spore suspension that produced infections when fed to *L. dispar*.



Figure 2. Silk gland of *L. dispar* infected with *Nosema lymantriae* (black spots). Magnification, 100x.

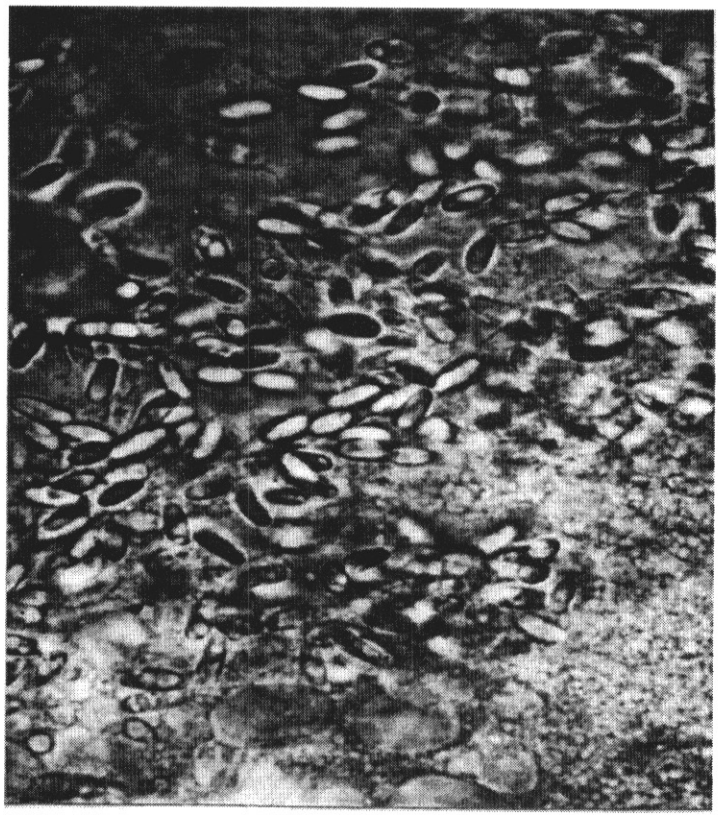


Figure 3. *Nosema lymantriae,* fresh spores. Magnification 1000x.

In ultrathin sections of material restored from paraffin, (Fig. 4) spores of *N. lymantriae* have a thick, rigid electron-negative endospore and a thin granular electron-positive exospore. The spore contains a pair of nuclei and a polar filament coiled in a single row directly under the spore wall in 10/11 or 12/13 isofilar coils.

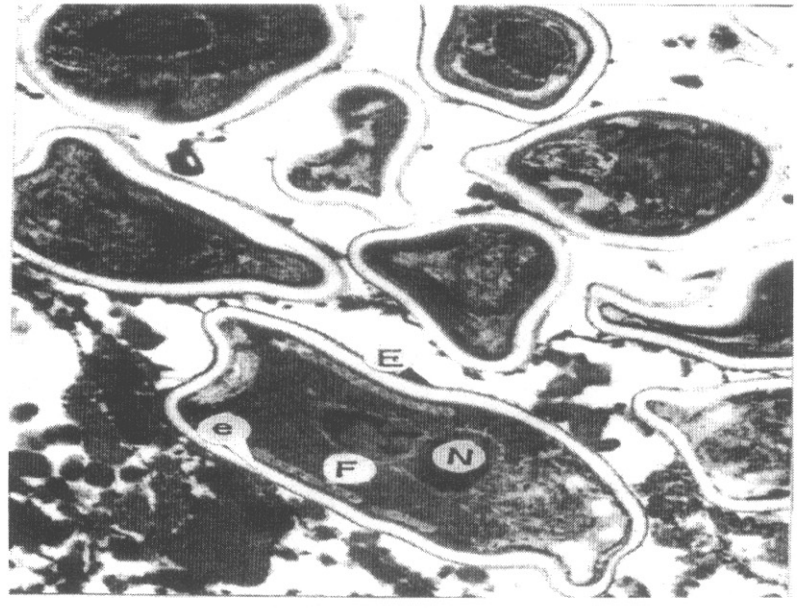


Figure 4. *Nosema lymantriae*, type of 1957. Spores with thick endospore (e), thin exospore (E), and the polar filament in single row with 12/13 coils (F). Diplokaryon (N) in the center of the spore. Magnification, 12,000x.

***Nosema serbica* Weiser (1961a)** *Nosema serbica* was collected in Serbia by L. Vasiljevic. The same microsporidian also infected eggs of the gypsy moth from Varna, Bulgaria and from Cherson, Crimea, USSR. Larvae hatching from infected eggs were infected and contained broad oval spores, 5-6 x 4 and 6-8 x 3-4 mμ, in all tissues of the body. The muscles of the midgut, the silk glands, and the fat body were first infected and later the infection moved to the Malpighian tubules and segmental muscles. In adults, the microsporidian enters the nutritive cells of the gonads and infects the developing egg follicles. The earliest eggs laid by the infected female have a lower percent infection than eggs laid later. The eggs oviposited latest die and desiccated. Eggs that do hatch produce larvae that are infected. Octospores were not mentioned in the original description of *N. serbica*. Spores of *N. serbica* were fed to other Lepidopteran hosts by placing spores on leaves of their host plants. *Malacosoma neustrium*, *Hyphantria cunea*, and *Euproctis chrysorrhoea* were successfully infected by *N. serbica*. No difference in the feeding behavior and larval activity was noticed in infected larvae. The original type material in paraffin blocks is not available.

***Thelohania similis* Weiser (1957a, 1957b)** *Thelohania similis* was not originally a pathogen of the gypsy moth but invaded gypsy moth populations when an outbreak of the browntail moth occurred contiguous to an outbreak of the gypsy moth in Slovakia. *T. similis* spores infected gypsy moth larvae and the infection occurred in the fat body as was the case

in the browntail moth. Schizogony was with stages with only a few nuclei with some stages of the meiotic sequence. During sporogony, spherical plasmodia with 2, 4 and 8 nuclei were formed. These developed eight sporoblasts and eight spores. Fresh spores were broadly oval, 5-6 x 2-2.5 μm, but in dry smears, spores measured 5 x 3 μm. In the original material only fat body was infected. Silk glands, Malpighian tubules, and muscles of the midgut were not infected. Development of the infection in the gypsy moth was slow and with no apparent symptoms. *Euproctis chryorrhoea*, *Lymantria dispar*, and *Stilpnotia salicis* were all susceptible to infection by T. similis. When the three microsporidia, *N. lymantriae*, *N. muscularis*, and *T. similis* occurred as mixed infections, each microsporidian species infected only the host tissues typically infected by that species. *Nosema muscularis* infected muscles of the midgut, *N. lymantriae* the fat body and silk glands, and *T. similis* the fat body. Although *N. lymantriae* did not infect the browntail moth, mixtures of spores developed in the browntail moth. The mixture of *N. lymantriae* with *N. muscularis* did not infect *Euproctis*, however, the mixture of *T. similis* with *N. lymantriae* did infect that species.

In ultrathin sections, spores of *T. similis* (Fig. 5) have a thick, electron-positive exospore and a rather thin electron negative endospore. The spore content is less distinct. The polar filament is coiled in an irregular double row in 24/25 coils. The pansporoblast membrane is formed of a granular layer and inside is a dense mass of secretion granules, sometimes organized in long tubules, without evident fixation on the surface of the spores or the pansporoblastic membrane.

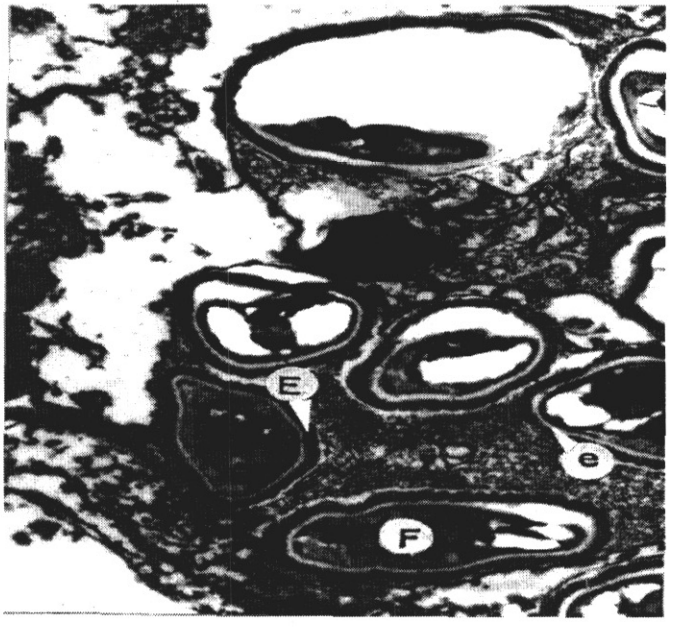


Figure 5. *Thelohania similis*, type 1957. Thick foamy exospore (E) and thin endospore (e) of mature spores. Polar filament (F) in double row of 24/25 coils. Pansporoblast membrane amorphous, granular (p), inside the pansporoblast are secretion granules and tubules (T). Magnification, 12,000x.

***Nosema lymantriae* (David and Weiser 1989)** The material on which this study is based was collected in 1988. Both binucleate single spores and octospores were present in ultrathin sections. In fresh material, binucleate single spores were 5-6 x 2.5-3μm and octospores were 4.2-4.5 x 2.5-3 μm. The pansporoblastic membrane surrounding the octospores was a unit membrane with a fine granular deposit on its outer surface (Fig. 6).

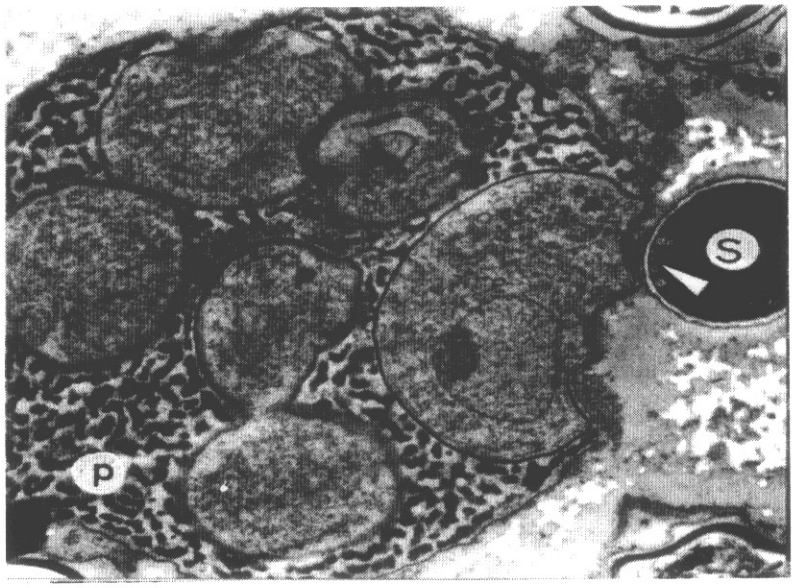


Figure 6. "*Nosema*" –*Vairimorpha lymantriae* of David and Weiser 1989. Octosporous pansporoblast with sporoblasts and secretion granules. Thin pansporoblastic membrane (p). On the right, a mature spore (S) with 5 cross-sections of coils of the polar filament (F). Magnification, 2000x.



Figure 7. Final spore and sporont of the binucleate sereas of *N.-V. lymantriae.* Polar filament in 5 coils (F), polaroplast activated (P) with anchoring disc. Magnification 10,000x.

Secretion granules and tubules typical for *Vairimorpha* species fill the space between the spores. Binucleate spores have a rigid endospore and a very thin, smooth exospore. The polar filament is isofilar with a minimum of 5/6 coils and is attached to a knoblike anchoring disc (Fig. 7). The structure of the polaroplast, which is not visible, is activated during fixation. Octospores, produced in an octosporous sporoblast, have a rather thick exospore and a thin endospore. The polar filament (Fig. 8) has five coils, but in young spores only three coils.



Figure 8. Part of octosporous pansporoblasts with young spores of *N.-V. lymantriae* with cross-section of 5 coils (arrow). Magnification 2000x.

***Plistophora schubergi* Zwölfer (1927) (Weiser 1961a)** *Plistophora schubergi* infections occur when infected *Euproctis* come in contact with *Lymantria*. The infection is confined to the midgut. Only the epithelial cells of the midgut are infected and, when heavily infected, these cells are filled with spores (Fig. 9). Infected cells, filled with spores, separate from the midgut and are eliminated in the feces. Regeneration nodules produce replacement midgut epithelial cells. Spores develop in compact pansporoblasts with multinucleate plasmodia. These divide within spherical sporoblasts and mature into small oval spores 2.5 x 1.5µm. Later, in disorganized tissues, the pansporoblasts are dissolved and sporoblasts mature free into spores. *Plistophora schubergi* is included in the genus *Endoreticulatus*, but the type species, *Endoreticulatus fidelis* differs in some parts of its development and this transfer should be evaluated further. *Plistophora schubergi* occurs in many different Lepidopteran hosts representing several different families. Although the strains from different hosts are morphologically identical, they are not equally infectious in cross-transmission studies. The strain occurring in the gypsy moth (Weiser 1961a) also infects *Euproctis chrysorrhoea*, *Stilpnotia salicis*, *Hyphantria cunea*, and *Barathra brassicae*. In *B. brassicae* large quantities of spores can be produced in the laboratory. The strain isolated from *Choristoneura fumiferana* in Canada will not infect *L. dispar*. *Plistophora schubergi* is not commonly found even in outbreak populations of *L. dispar*. Spores are less resistant to storage, however, they survive in hibernating L1 larvae of *E. chrysorrhoea*. Spores first appear in the feces of infected L. dispar larvae 6-8 days after oral infection. For the next 15-

20 days, the number of spores in the feces increases constantly. Infection of the progeny occurs when the egg mass is contaminated with feces. The feces are rich in proteins from the infected epithelial cells of the midgut and are attractive as food when larvae hatch from the egg mass.

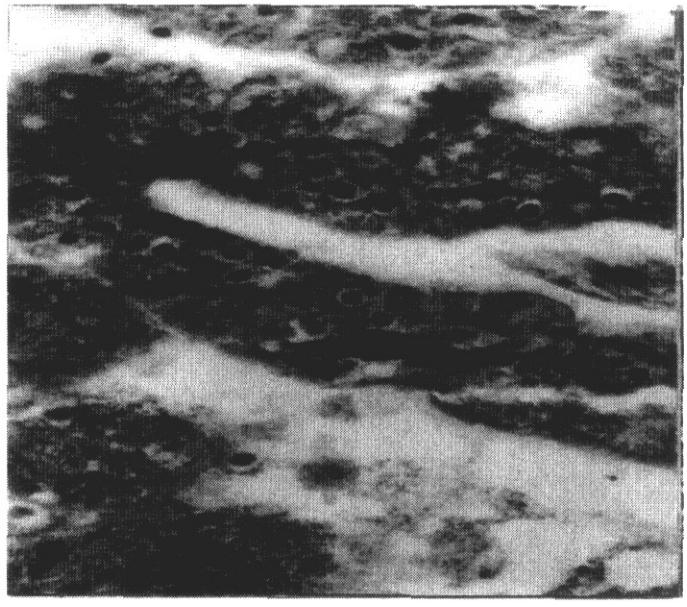


Figure 9. ***Plistophora (Endorectulatus) schubergi*****, masses of spores in the midgut (epithelium of** ***L. dispar.*** **Magnification, 450x.**

Discussion

Outbreaks of the gypsy moth develop from low level populations which cover all of Europe and these are detectable by pheromone traps. The build-up of gypsy moth populations is influenced primarily by climatic conditions, the physiological status of the population including resistance to pathogens, and by the quantity and availability of infectious agents in the forest. The eleven year inter-gradation period indicated in older textbooks is today more variable, usually 6 years or less. The use of biological means such as *Bacillus thuringiensis* (in Bulgaria and Slovakia) breaks the periodicity of outbreaks. There is evidence of a wave-like migration from outbreak frontiers in the Crimea (Tchugunin, 1958) and in Yugoslavia. Gypsy moth populations at the border of the Black Sea or Adriatic are consistently higher, but do not necessarily result in outbreaks. In this region, gypsy moth populations contain a high percentage of the eggs infected with microsporidia and parasitized with egg parasites (these observations may be related).

Among the factors affecting outbreak populations of the gypsy moth, the nuclear polyhedrosis virus is the most important and is usually responsible for the final collapse of populations. After one year with high infestations of late instar caterpillars, the "Wipfeln" syndrome is evident and eggs deposited by infected females hatch into larvae that die in the early larval instars. There is no evidence of more or less virulent strains of NPV in nature, but in artificial introductions of NPV in early phases of the outbreak, there are strains of NPV

that cause immediate infections and other strains that produce only protracted, inapparent, egg-transmitted infections. Active virus strains can be selected by using for recycling virus produced from the first caterpillars that appeared infected. In order to acquire NPV material that is highly active, this process must be repeated 4 to 6 times.

The cytoplasmic polyhedrosis virus only appears in populations of the gypsy moth that are in close contact with the browntail moth or the fall webworm. The CPV has an incubation period of 8 days in the gypsy moth but it is efficient only in combination with other pathogens. No other virus is transmitted to *L. dispar* from other Lepidoptera that attack oak trees. This includes the NPV and granulosis virus of *H. cunea* and the poxvirus of *Operophtera.*

Bacillus thuringiensis does not cause the collapse of gypsy moth outbreaks and does not typically occur in Lepidopteran defoliators of oak. Its use as a microbial insecticide reduces defoliation and, in an artificial way, breaks the periodicity of gypsy moth outbreaks. Bacillus thuringiensis does not protect the oak flowers from destruction by the gypsy moth and thus is not effective in protecting the acorn crop.

Fungus infections develop only in caterpillars or pupae that have been damaged or killed by other factors. *Entomophthora aulicae* is primarily a pathogen of smooth caterpillars (Tortricids, Noctuids, etc.). In Europe, gypsy moths (primarily early instars) are infected with this fungus only from outbreaks of smooth caterpillars. Nematodes and mermithids sometimes occur in gypsy moth caterpillars in young stands, close to the soil.

Several species of microsporidia infect the gypsy moth, more than any other group of insect pathogens. At the time when most of the microsporidia were described from the gypsy moth, species with similar spore sizes and shapes were differentiated mainly on the basis of host range and development in the host. These are no longer the most important criteria used for identifying and classifying microsporidia and it is appropriate to reevaluate these microsporidian species using ultrastructural characteristics and, eventually, molecular characteristics. In recent studies some authors have provided details of the internal structure of the spores.

Nosema sp. studied by Sidor (1976) had a polar filament with 10/11 coils, a thin exospore and a solid endospore.

Nosema sp. from Romania collected by Saftoiu (1976) had a polar filament with 6/7 or 7/8 coils and a thin exospore. Other spores in this material had a polar filament with 10/12 coils.

Nosema from Bulgaria studied by Pilarska and Vavra (1987) had binucleate spores and a polar filament with 5/6 coils.

Since the first microsporidian was described from the gypsy moth over 40 years ago, several complicating factors have developed. These factors must be considered when evaluating and comparing the older microsporidian descriptions with the newer descriptions. One of these factors was the creation of the genus Vairimorpha. This genus has a diplokaryotic single spore sporogony as well as a sporogony with eight sporoblasts and spores. The sporogony with eight sporoblasts and spores copies the development of the genus *Thelohania* in the old concept. Another complicating factor is the formation of two types of spores in the host tissue, early spores for autoinfection and distribution of the microsporidian in host tissues, and the persistent spores for transmission and infection of other hosts. Except for differences in spore size and in the structures of the spore wall, there are, in some cases,

no simple method for identifying these types of spores. These differences are reflected in the old descriptions by indications of the range of spore sizes. The development of infections in different hosts, the ranges of host tissues, and the development from larval to adult stages and eventual transovarian transmission is, according to actual knowledge, variable to some extent and influenced by the method of transmission from host to host.

The project supported by the US Forest Service, and implemented by M. L. McManus and J. V. Maddox, has produced a large collection of microsporidia from gypsy moths collected from different parts of Europe. This collection of microsporidia, viable spores of which are stored in liquid nitrogen, will allow the old observations to be compared with modern evaluations of existing species. This report was prepared in support of this effort.

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Oak Defoliating Insects in Hungary

GYÖRGY CSÓKA

Forest Research Institute, Hegyalja u. 14., 3232 Mátrafüred, Hungary

ABSTRACT Oaks are the most important species in Hungarian forests both from an ecological and economic point of view. Of the total forested area in Hungary (1.7 million hectares), ca. 35% is occupied by oak forests. The indigenous oak species are *Quercus petraea, Q. robur, Q. cerris, Q. pubescens, Q. farnetto* and *Q. virgiliana*. In addition to the native species, the North American *Q. rubra* is planted widely.

The insect folivore guild of oaks is extremely rich in species. Four hundred and forty-five species of herbivorous insects have been found to feed on the foliage of oaks in Hungary. Folivores represent 72% of the 629 species of all known oak herbivorous insects. Sixty-two percent (280 species) of all folivore species (455) are Lepidoptera. The proportion of species that are found only on oaks is very high; therefore, the oaks play an extremely important role in maintaining the diversity of herbivorous insects.

Of the 455 folivore species, 74% are leaf-feeders, 10% are leafminers, 10% are gall-makers, and 6% are sap suckers. The monthly abundance of folivore species shows a characteristic seasonal pattern, whereby they peak in early June, then decline continuously. The spring/early summer fauna is dominated mainly by polyphagous larvae of the Geometrid/Noctuid group in hilly and mountainous regions, and by Lymantriids in lowland oak forests. The late season fauna is dominated mainly by more specialized groups such as leafminers, leafgallers, Notodontid larvae, etc.

The Forest Research Institute has maintained a forest damage monitoring system since 1961. All forest owners and forest companies are required to report abiotic and biotic damage that occurs in their forests, including that caused by all of the major pests. This long-term database provides us with an excellent opportunity to investigate the trends of different pests and their characteristic damage. Based on this database, the Geometrid/Noctuid group dominates the spring/early summer folivore fauna, especially in sessile oak (*Q. petraea*) stands in the hilly and mountainous regions. This group has caused defoliation on an average of 9,138 ha/year during the past 35 years. The most common and abundant species of Geometrids are *Operophtera brumata, Erannis defoliaria, Colotois pennaria, Alsophila aescularia, Agriopis aurantiaria, and A. marginaria*. In addition, several Noctuids, such as *Orthosia gothica, O. incerta* and *O. stabilis*, play a significant role in this group. *Lymantria dispar* is by far the most significant defoliator of forests in lowlands and on hills at lower elevations. *L. dispar* prefers *Quercus robur* and *Q. cerris,* but seldom causes severe damage in sessile oak (*Q. petraea*) stands. Outbreak areas can be found all over the country, though the average area defoliated is around 6000 ha/year.

Tortricid leafrollers cause damage on ca. 1200 ha/year, though significant increases in damage have occurred over the last 35 years. The most important species are *Tortrix*

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viridana and *Archips xylosteana*. *Euproctis chrysorrhoea* and *Malacosoma neustria* defoliate mainly lowland pedunculate oak forests, especially younger stands.

E. chrysorrhoea causes damage on ca. 974 ha/year, although the area defoliated by this pest has increased significantly over the last 35 years. Defoliation by *M. neustria* occurs on 560 ha/year.

The largest areas defoliated were recorded in the early sixties and in the early nineties. The Geometrid species group caused the most damage in 1963 (ca. 71,000 ha), whereas *L. dispar* damaged more than 34,000 ha in 1994. The weather during both periods was extremely dry and warm. It has been demonstrated statistically that drought played a key role in provoking more serious outbreaks of several forest insects (i.e. oak defoliators), leading to a significant expansion of territory damaged. In addition to the increasing damage caused by oak defoliators, several other species that are favored by warm and dry conditions appeared as new pests in the last two decades in Hungarian oak forests. These include *Tischeria* leafminers, *Caliroa* sawflies, and the oak leaf beetle, *Haltica quercetorum*.

Effect of the Mimic Prototype, Rh 5849, on 20-Hydroxyecdysone Titers in Defoliating Lepidopteran Larvae

MACIEJ A. PSZCZOLKOWSKI

Department of Forest Protection, Forest Research Institute, Bitwy Warszawskiej 1920r. nr. 3, 00-973 Warsaw, Poland

ABSTRACT The first nonsteroidal ecdysteroid agonist, RH 5849 (1,2-dibenzoyl-1-tert-butylhydrazine), is a prototype of MIMIC, a novel insect growth regulator that can induce a lethal premature moult in larval Lepidoptera. The effects of RH 5849 applied to Lepidopteran larvae on changes in levels of endogenous ecdysteroids titers are reported here. Larvae of *Spodoptera littoralis* (Noctuidae), a defoliating pest of cotton, were used as the model insect in this study.

LARVAE WERE TREATED with RH 5849 at varying times before the onset of pupation. Non-lethal doses of RH 5849 (5 μg), dissolved in acetone, were applied topically. 20-hydroxyecdysone (20E) levels were determined by means of an enzyme immunoassay using acetylocholinesterase as label.

During the day of pupation, the concentration of ecdysteroids in the haemolymph of untreated larvae increases, reaches its peak (so called transient peak), and then decreases. As in many other insect species, a rapid increase in the rate of pupation is observed in *S. littoralis* during the decrease of 20E level. Application of RH 5849 before the transient peak resulted in a remarkable increase in endogenous ecdysteroid titre. The decrease in ecdysteroid levels occurred about 12 hours later in insects treated with RH 5849 than in larvae which received solvent alone. When the concentration of endogenous ecdysteroids reached the transient peak, application of RH 5849 had an opposite effect. The level of endogenous ecdysteroids increased and then rapidly dropped, attaining its minimum about 12 hours earlier than in solvent-treated controls. As a consequence of treatment with RH 5849, larvae delayed or precipitated the time of pupation depending on the time of treatment.

It is noteworthy that the doses of RH 5849 (5 μg) used in this study were non-lethal. Even a dose of 50 μg of RH 5849 did not cause any lethal effect in *S. littoralis*, when applied during the day of pupation. However, low doses of RH 5849 caused shifting of pupation time and treated insects pupated in daylight whereas untreated controls pupated during the night. This means that although insects treated with non-lethal doses of RH 5849 do not die, they can change their circadian rhythms of pupation (i.e. they can change their ecological niche). Consequently, insects treated with non-lethal doses of RH 5849 may be eliminated by day active predators (e.g. by birds).

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The data presented on RH 5849 effect indicate that non-steroidal ecdysteroid agonists can interfere differently with ecdysteroid-dependent physiological processes, depending upon the time of treatment. Thus, potential users of ecdysteroid agonists probably should consider not only the proper dose of these insecticides, but also the proper time of application, particularly with respect to those species that develop synchronously in the field.

The Stone Pine Needleminer (*Ocnerostoma copiosella* Heyd.) in the Engadine Valley, Switzerland

BEAT FORSTER

Forest Insect and Disease Survey, Swiss Federal Institute for Forest, Snow and Landscape Research WSL/FNP, CH-8903 Birmensdorf, Switzerland

ABSTRACT During the last two decades, outbreaks of the stone pine needleminer *Ocnerostoma copiosella* have occurred more frequently than before. The affected Swiss stone pines (*Pinus cembra* L.) show needle loss and are more susceptible to secondary pests.

Ocnerostoma copiosella is a small, silver-greyish moth with a wing span of approximately 5 mm that completes two generations per year. The young larvae feed inside last year's and older needles which turn yellow and later brown. Then the larvae leave the needles through oval holes and spin their cocoons inside the five-needled fascicles. Adults emerge in June and July. The second generation overwinters as larvae within the needles.

The stone pine needleminer is common in the Central Alps within the natural distribution of Swiss stone pine. In the Upper Engadine Valley, between 1700 and 2000 m in elevation, the insect has optimum conditions. Trees that are attacked lose a high proportion of their older needles. Typically, stone pines that are attacked experience only a small growth reduction and recover in subsequent years. Since the needleminer has been attacking the pines more frequently, the crowns have become thinner and the trees more susceptible to secondary pests. Sometimes weakened trees die due to subsequent attacks by bark beetles, such as *Ips amitinus, Pityogenes conjunctus* or *Polygraphus grandiclava.*

There is concern that, in the near future, an outbreak of the stone pine needleminer will occur simultaneously with an outbreak of the larch bud moth (*Zeiraphera diniana* Gn.). Larch bud moth larvae also affect stone pines; however, they attack the youngest needles, which are normally spared by the needleminer. Until now, the outbreaks of the two species have never occurred at the same time.

Occasional outbreaks of this needle-mining moth have been recorded in the last century; however, over the past two decades, outbreaks have occurred more frequently. Since 1989, outbreaks have occurred every two years in the odd numbered years. To date, we have not been able to demonstrate a correlation between the mass attacks and yearly weather conditions. But since 1983, the average temperature in July has been 0.8°C higher than before, and there have been deficits of precipitation. The causes of the 2-year cycles are still unknown and require further investigation.

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Wind and Bark Beetles - the Most Serious Harmful Agents in the Norway Spruce Stands of Slovakia

BOHDAN KONÔPKA

Forest Research Institute, Masarykova 22, 960 92 Zvolen, Slovak Republic

ABSTRACT Wind is the most serious harmful abiotic agent in the forests of Slovakia while bark beetles are the most serious biotic agent. The volume of timber removed due to wind damage was recently approximately 800,000 m^3 annually, and timber removal due to bark beetle damage was approximately 200,000 m^3 annually, which together represented almost 20% of total annual fellings. However, the total damage in forest ecosystems caused by wind and consequently by bark beetles is much higher. Heavy damage to ecological conditions in forest stands caused by wind and bark beetle outbreaks create suitable conditions for other pests. Wind storms and subsequently bark beetles, cause great economic losses due to the premature decline of stands, increased costs of tree removal, worsened timber quality and sudden deforestation of land with all its unfavorable consequences (e.g., soil erosion). Late timber processing and replanting of forest plantations on gale-disaster areas results in higher costs of weed control and soil preparation.

In cases of large wind damage, there is a threat of bark beetle outbreak which could last during the following years. One example of a bark beetle outbreak due to wind destruction was a situation in Slovakia in the mid-1960's. In that case, the volume of timber removal caused by bark beetles tripled after extraordinary high wind disaster. Recently, emissions, weather extremes, wind storms and total weakening of forest ecosystems (especially in Norway spruce stands) in Slovakia have created optimum conditions for further outbreaks of bark beetles. For this reason, the significance of forest protection against this group of injurious agents will increase continually.

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Defoliating Insects: History of Outbreaks in the Coniferous Forests of Russia

ANDREY V. SELIKHOVKIN, DIMITRY L. MUSOLIN, AND TAMARA E. SERGEEVA

Dept. of Zoology, St. Petersburg Forest Technical Academy, Institutskiy per., 5, 194021, St. Petersburg, Russia

ABSTRACT Moths (*Dendrolimus superans sibiricus, D. pini, Lymantria monacha, Bupalus piniarius, Panolis flammea)* and sawflies (*Diprion pini, Neodiprion sertifer, Acantholyda spp.*) are usually considered as the most important defoliating pests in Russian taiga forests.

The history of outbreaks of these species have been analyzed based upon statistical data (calculations and estimates according to reviews of the Federal Forest Service of the Russian Federation, 1977-1994) and publications in forestry periodicals (1870s - present).

We determined that there are no common trends in the distribution of outbreak areas of these insect pest species, and that there are no common environmental factors that either regulate the dynamics of outbreaks of these species or that occur simultaneously in all of the Russian forests. It is very probable that there is a periodicity to outbreaks in nature, but that they occur only in localized populations.

The appearance of outbreaks of *D. superans sibiricus* and some other pests in more northern regions (in comparison with the records examined in several previous decades) may be related to trends in global climate change. However, we suggest that this appearance is possibly caused by the absence of accurate information about historical outbreaks in the sparsely populated regions of Siberia.

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Damage Caused by Cockchafers (*Melolontha* spp.) in Hungary during the Last 30 Years

JÓZSEF TÓTH

Forest Research Institute, Frankel L. 42-44., 1024 Budapest, Hungary

ABSTRACT There are seven tribes of *Melolontha melolontha* that occur in the Carpathian Basin, and three of the seven tribes occur in Hungary. The distributions of the tribes are different, but at some locations two or even three tribes are sympatric. In Hungary, *Melolontha* completes its development in 3 years.

Tribe	Years of swarming
V.	1989-1992-1995-1998
VI.	1990-1993-1996-1999
VII.	1991-1994-1997-2000

The cockchafers react positively to artificial light; therefore, they can be collected easily using light traps. We have been using a network of 25 light traps in Hungary since 1962 to monitor cockchafer populations.

The cockchafer causes serious damage in forests. The adults can totally defoliate trees, and the larvae can kill even older trees by feeding on the roots. In the last 34 years, the average yearly defoliation by adult cockchafers has been 15,095 hectares. In the same period, the larvae caused damage on 1,947 hectares. *Melolontha hippocastani*, which occurs simultaneously with *M. melolontha*, also causes damage. This species also requires 3 years to complete its development; however, distributions of its tribes are not well understood. Other common and abundant cockchafer species include: *Anomala dubia, Anomala vitis, Anoxia orientalis, Melolontha pectoralis, Polyphylla fullo, Rhizotrogus aequinoctalis* and *Rhizotrogus vernus*.

Helicopter spraying of pesticides against the adults and soil treatments against the larvae have been recommended.

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Reaction of *Cyzenis albicans*, *Ernestia rudis*, and *Parasetigena silvestris* (Diptera:Tachinidae) to Insecticides Used in the Control of the Nun Moth

CEZARY BYSTROWSKI

Department of Forest Protection, Forest Research Institute, Bitwy Warszawskiej 1920 r., no 3, 00-973 Warsaw, Poland

ABSTRACT The nun moth is the most destructive defoliator of coniferous trees in Europe. Its outbreaks have been recorded in Scots pine and spruce stands in Poland since the 19th century. During the period 1946-1984, approximately 6 million ha of infested coniferous stands were treated with organochlorine and pyrethroid insecticides to control the nun moth. Beginning in 1991, increases in the density of nun moth populations were observed. In 1994, the project "The Integrated Control of Nun Moth in Polish Forests" was developed and financed by Polish and foreign funds. The use of pyrethroids was reduced because of environmental concerns and consequently Foray 02.2 UL and Dimilin 480 SC were used on 90% of the treated area. A study of the reaction of tachinids to these insecticides was initiated by the Forest Research Institute as a part of research to determine the impact of the control treatments on the forest environment.

In 1994, four nun moth-infested experimental plots were established in the Ostrów Mazowiecka forest district in the eastern part of Poland within even-aged Scots pine stands. The insecticides were applied on the 22nd of May. Two experimental plots were treated with contact insecticides (Decis 2.5 EC and Trebon 10 SC) and two were treated with stomach insecticides (Dimilin 480 SC and Foray 02.2 UL). Six Moericke's traps were placed in the tree crowns in each experimental plot. The traps were checked every two weeks from April to October in 1994 and 1995.

Six thousand individuals representing 42 tachinid species were collected in 1994, and about three thousand individuals representing 25 species were collected in 1995. In 1994, the most numerous species recorded were *Cyzenis albicans, Ernestia rudis* and *Parasetigena silvestris.* In 1995, the numbers of two species, *Parasetigena silvestris* and *Ernestia rudis,* were drastically reduced apparently due to both the control treatment and unfavorable weather conditions during the development period of their hosts. However, the number of *Cyzenis albicans* increased in 1995 apparently due to its early emergence and rapid development of both this fly and its host.

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Growth and Survival of *Chrysomela tremulae* (Coleoptera, Chrysomelidae) on Transgenic Poplar Containing a *Bacillus thuringiensis*-Endotoxin Gene

S. AUGUSTIN[1], A. DELPLANQUE[1], J.C. LEPLE[2], G. PILATE[2] AND L. JOUANIN[3]

[1]INRA, Station de Zoologie Forestiére, 45160 - Ardon, France
[2]INRA, Station d'Am,lioration des Arbres Forestiers, 45160 - Ardon, France
[3]INRA, Laboratoire de Biologie Cellulaire, 78026 Versailles Cedex, France

ABSTRACT In France, the chrysomelid beetle *Chrysomela tremulae* is the main defoliating pest in both young plantations and short rotation stands of poplars. Larvae and adults of *C. tremulae* feed on leaves of young poplars, leaving only the vein, and can be a limiting factor for biomass production. They also attack the bark when foliage is no longer available, frequently killing the seedlings.

In view of the problems concerning the use of insecticides (i.e., prohibitive cost and environmental safety), the introduction into plants of genes confering resistance to this insect is a new promising strategy.

The *Bacillus thuringiensis*-endotoxin gene Cry III A was introduced via cocultivation with *Agrobacterium tumefasciens* in a Leuce hybrid clone (*Populus tremula* x *P. tremuloides*) that is very sensitive to *C. tremulae*. Three transformants were tested for their effects on survival and development of *C. tremulae*.

C. tremulae survival was significantly reduced on transgenic foliage tested compared to non-transformed foliage. Larval development time was also affected by foliage: it was longer on leaves of the three transgenic than on the non-transgenic control leaves. Male and female pupal wet-weights, measured as an estimate of reproductive potential, were lighter on leaves of the three transgenic foliages.

The three transformants assayed on *C. tremulae* survival and development provided protection to poplar, but this protection was not absolute. The results on mortality suggested that the level of expression of the endotoxin was moderate, but sufficient to induce effects on insect development that will enhance the teratological action.

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Foliage Palatibility of Pine Species and Clones to the Rare Subspecies *gallieglоria* of the Beauty Moth, *Graellsia isabellae* Oberthür (Lepidoptera: Attacidae)

CLAUDE GÉRI[1], FRANCIS GOUSSARD[1], MARIE-ANNE AUGER-ROZENBERG[1], CATHERINE BASTIEN[2] AND FLORENCE PASQUIER[1]

[1]INRA, Station de Zoologie Forestière, 45160 Ardon, France
[2]INRA, Station d'Amélioration des Arbres Forestiers, 45160 Ardon, France

ABSTRACT The suitability of foliage from various Scots pine clones to the sawfly *Diprion pini* L has previously been shown. We studied their suitability to the beauty moth *Graellsia isabellae*. Throughout its range in France and Spain, *G. isabellae* Graells feeds principally on Scots pine, *Pinus sylvestris*. It is the only endemic Attacidae in Europe. The French subspecies *gallieglоria* Oberthür only exists in specific alpine valleys, and is protected. The vividly colored caterpillars feed individually on foliage during 5 instars before spinning a cocoon. Pupae overwinter in diapause.

First we established a laboratory strain in order to conduct experiments without collecting insects from the field. The colony was founded from 150 eggs in 1990 with authorization from the French Department of Environment. Batches of 5 to 10 caterpillars were fed cut pine shoots in field and laboratory conditions. In order to avoid inbreeding, females were placed in small open cages in the Alps and mated with wild males. The colony produced several thousand insects per year. Simultaneously, experiments were carried out on the insect's biology and on the range of its host plants in order to identify its potential range and improve rearing methods. The diapause of *G. isabellae* could not be prevented by varying photoperiod, temperature or food. However, diapause was successfully broken at any moment by injection of ß-ecdysone. Adults emerge 20 days following injection and insects can thus be obtained during the entire year. This species can mate, oviposit and feed in field conditions at low elevation. Feeding bioassays described above were conducted using cut shoots of the foliage of different pine species and confirmed that *P. sylvestris* was the most preferred. *Pinus uncinata* and *P. contorta* were nearly as suitable, but Austrian, Salzmann and Jeffrey pines were not fed upon at all. Bioassays with the foliage of 13 clones, previously ranked as favorable (G) or unfavorable (B and B+) for *D. pini*, were also performed in 1992, 1993, 1994 and 1995. They showed significant differences in mortality, development rate and pupal weights. The worst performance was observed on the B+ clones; the G clones were highly suitable. Performances was found to be better on these clones then on naturally occurring trees. The high performance of insects fed on certain clones indicates that the selection of trees for silvical properties alone may be problematic.

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Biotic Factors Affecting *Stereonychus fraxini* Populations in the Longoza Forest, Bulgaria

GALINA MARKOVA

Forest Research Institute, K1. Ochridski 132, 1756-Sofia Bulgaria

ABSTRACT The ash weevil, *Stereonychus fraxini* Deg., is a major insect pest of ash trees in Bulgaria and other European countries. At very high infestation levels, some damaged stands in the Longoza Forest in Bulgaria looked like winter, because the trees did not produce leaves. Because of environmental concerns associated with the use of chemical control, there is interest in alternative control measures, such as biological control, for maintaining this pest at low densities.

A study was conducted to estimate the natural biotic factors that regulated ash weevil populations during the period 1988-1995. Examination of the adult *S. fraxini* population for entomopathogens indicated that the fungus *Beauveria bassiana* was quite abundant. This fungus reduced the population density of adults by 58% in 1988. Laboratory experiments demonstrated that this fungus strain was very virulent against adult weevils. Although the epizootic occurred only during the period of high host density, infected beetles were observed in subsequent years.

After the collapse of *S. fraxini* populations in 1988, three species of parasitoids were consistently recovered in rearings: *Mesopolobus mediterraneous*, *Pteromalus cioni* and *Entedon cionobius*. Combined parasitism by these species varied from 35.7-65.1% each year, though there appeared to be no relationship between richness of the parasitoid complex and host population density. It is concluded that these parasitoids play an important role in maintaining *S. fraxini* populations at low densities.

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Significance of *Glyptapanteles liparidis* (Hym., Braconidae) as a Regulator of Gypsy Moth, *Lymantria dispar* (Lep., Lymantriidae) in Different Host Population Densities

AXEL SCHOPF AND GERNOT HOCH

Institute of Forest Entomology, Forest Pathology and Forest Protection, University of Bodenkultur Vienna, Hasenauerstrasse 38, A-1190 Wien, Austria

ABSTRACT The significance of the endoparasitic braconid *Glyptapanteles liparidis* was studied from 1993 to 1995 at three experimental sites in Austria with high, medium and low density *Lymantria dispar* populations. To ascertain rates of parasitism and acquire data on the bionomics of *G. liparidis*, gypsy moth larvae were collected at specific stages at the sites and reared in the laboratory until parasitoids emerged, larvae died, or they pupated. At low density sites, we had to supplement the native population with *L. dispar* eggs and young larvae in order to perform the studies. Additionally, we tested the feasibility of calculating rates of parasitism retrospectively from densities of parasitoid cocoon clusters and gypsy moth egg masses.

The highest percent parasitism by *G. liparidis* (47.6%) occurred among larvae collected as 3rd and 4th instars from a latent population in 1993. This braconid species was the dominant species at this low density site where we artificially augmented host populations. At sites with high gypsy moth densities, parasitism by *G. liparidis* did not exceed 3% parasitism in 1993. In 1994, after the medium to high gypsy moth populations had collapsed, parasitism by *G. liparidis* increased at these localities. In the third year, the studies were performed only at the former high and low density sites, where it was necessary to artificially augment gypsy moth populations. In both locations, rates of parasitism were estimated to be at about 15%. Apparently, due to its excellent searching capacity, this parasitoid species is believed to be especially effective in low density gypsy moth populations and in focal areas where populations increase.

Rates of parasitism by this braconid species were also favoured by retarded host larval development in 1994 and 1995, due to low temperatures in the spring.

Most of the *G. liparidis* larvae emerged when hosts were in their 4th instar. However, in 1994, a higher percentage of parasitoids emerged from 3rd instars than the previous year; this may have been caused by early hatch of *L. dispar* larvae in 1994, and then their retarded development. This also influenced the pattern of emergence of the parasitoids over time, which was bimodal in 1994. In 1993, there was only a single dominant peak of emergence. Rates of parasitism calculated from estimates of parasitoid cocoon cluster density and gypsy moth egg density, did not accurately reflect actual rates of parasitism. Thus, counts of cocoon clusters of *G. liparidis* should not be used to retrospectively estimate parasitism by this species.

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Weevils Affecting Reforestation in Poland

IWONA SKRZECK

Forest Research Institute, Bitwy Warszawskiej 1920r No. 3, 00-973 Warsaw, Poland

ABSTRACT In Poland, even-aged forest plantations that are established on clearcut areas and in which Scots pine (*Pinus sylvestris* L.) occupies more than 60% of the reforested areas, are infested by pest insects of the family *Curculionidae.* Conifer stumps on the clearcuts favor the development of the large pine weevil (*Hylobius abietis L.*) and the spruce pine weevil (*Hylobius pinastri Gyll.)*, which are the most serious pests of Polish forest plantations. Both species oviposit in roots of fresh conifer stumps and the larvae develop under the bark of roots. Adult weevils feed on the bark of seedlings, which eventually leads to seedling death. Serious economic loss is caused primarily by *H. abietis*, which is much more abundant than *H. pinastri.*

Forest plantations and natural stands, especially those established on poor plagiatus sandy soils and on burned areas, are damaged by such species as *Cneorhimus plagiatus* Shall and *Strophosomus capitatum* Deg. The most serious damage is caused by the adult beetles of those species which feed on pine needles, which leads to their senescence. Premature shedding of young pine tree needles is also caused by the adult beetles of *Brachyderes incanus* L. and *Brachonyx payk.*

At present, there is no successful method to predict the amount of tree damage caused by weevils. Our estimation of the threat to forest plantations by the weevils is based on the number of adults captured in traps baited with pine billets, pieces of fresh pine bark, or IBL-4 artificial traps containing food attractants.

The abundance of weevils in forest stands is determined by estimating the extent of needle damage caused by the pests.

The following control methods are used to protect reforested areas against pest weevils:

1. mechanical methods with the use of traps (pine billets, artificial traps) for capturing adults;
2. chemical methods that consist of dipping seedlings in contact insecticides prior to planting or spraying young trees after planting;
3. biological methods based on using the Julich fungus *Phlebiopsis gigantea* (Fr.: Fr.) to reduce colonization of stumps by *H. abietis.*

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Effect of Litter and Soil-Borne Entomogenous Fungi on Mycoses of Pine Sawfly (*Diprion pini* L.) During Hibernation Period

CEZARY TKACZUK, RYSZARD MIÊTKIEWSKI AND JAROSLAW GRODZICKI

Agricultural and Pedagogical University, Department of Plant Protection, ul. Prusa 14, 08-110 Siedlce, Poland

ABSTRACT At the beginning of June, 1994 and again in 1995, 20 samples of litter were selected in a pine forest (stand age about 35-40 years) situated in Lysow. From each sample (0.25 m^2 in area), all cocoons of the pine sawfly were removed along with samples of litter and soil down to a depth of 10 cm. The same methods of investigation were also used in another forest near Chotylow; however, at this location, cocoons were collected in mid-November 1995 rather than in June. The causes of mortality of pine sawfly larvae in cocoons were determined in the laboratory. Insects infected by fungi were incubated in moist chambers at 22° C until the presence of fungal pathogens was evident, at which point we were able to identify the organism to species. In addition, we used *Galleria mellonella* larvae as "bait insects" in order to determine the spectrum of entomopathogenic fungi that occurred in the samples of pine litter and soil from which the *D. pini* cocoons were removed. The larvae were placed in plastic Petri dishes filled with either litter or soil. The dishes were incubated at 22°C in 1994, and at 18°C and 26°C in 1995.

Entomopathogenic fungi infected from 12.3% to 52.2% of cocoons containing larvae of *D. pini*. *Beauveria bassiana, Paecilomyces farinosus, P. fumosoroseus* and an unidentified species of *Entomophaga* were isolated from hibernating larvae. The fungus *B. bassiana* infected up to 85.2% of the total number of larvae that were infected by fungi in the forest city near Lysow in 1994 and 1995. Unidentified species from the genus *Entomophaga* infected 74% of *D. pini* cocoons in the forest situated near Chotylow. *Paecilomyces farinosus* and *P. fumosoroseus* were occasionally found in dead pine sawfly larvae. *Beauveria bassiana, P. farinosus, P. fumosoroseus* and *Metarhizium anisopliae* were isolated from litter and forest soil using the "insect bait method". The fungi *B. bassiana, P. farinosus* and *P. fumosoroseus,* which infected hibernating larvae of the pine sawfly, were also isolated from forest soil. *Beauveria bassiana* was the dominant species that occurred in localities and at all temperatures. *Beauveria bassiana* infected relatively more *G. mellonella* larvae at 18°C and 22°C than at 26°C, whereas the fungus *M. anisopliae* was recovered only at 26°C from soil taken from the Chotylow locality. *Beauveria bassiana* and *P. fumosoroseus* were also isolated from pine litter using the bait insect method.

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Predicting Gypsy Moth Defoliation Using Spatially Explicit Information

RONALD M. WESELOH

Department of Entomology, Connecticut Agricultural Experiment Station, New Haven, CT 06511 USA

ABSTRACT A procedure has been developed to predict forest defoliation by the gypsy moth, *Lymantria dispar* L., in Connecticut, U.S.A. The procedure uses elevation, percent of soil region with poor soil drainage, average defoliation from 1969 to 1994, past defoliation (obtained from hand-sketched aerial survey maps), and egg mass counts (obtained from a regular grid throughout the state and interpolated by inverse-weighting) to fit logistic regression models that have been used to predict defoliation for 1985 and 1989-1995. When defoliation was substantial, the models predicted locations of defoliation accurately, but when defoliation was low, predicted and actual defoliation did not often correspond. However, the models accurately forecast the amount of defoliation that occurred in most cases. Thus, for years in which defoliation is moderate to heavy, the models can be expected to be useful in predicting both the amount and location of defoliation. In sparse years, the models will at least indicate that expected defoliation will be low, in which case the actual locations are not as important. The procedure should be useful in helping to make control decisions, and will be validated in future years.

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Phytobia Population Densities in European White Birch (*Betula pendula* Roth)

TIINA YLIOJA[1] AND HEIKKI ROININEN[2]

[1]Finnish Forest Research Institute, Punkaharju Research Station, Finlandiantie 18, FIN-58450 Punkaharju, Finland
[2]University of Joensuu, Department of Biology, P.O. Box 111, FIN-80101 Joensuu, Finland

ABSTRACT Larval boring holes of *Phytobia betulae* Kang. (Diptera: Agromyzidae) in birch stems constitute a record of *Phytobia* population densities in the past. A larva, which hatches from an egg laid into a growing shoot in the canopy, mines in the differentiating xylem towards the base of the host tree. The tree fills the larval tunnel with brown parenchyma cells and resin and, therefore, the larval tunnel remains visible during the tree's life span.

We randomly sampled 26 European white birches (*Betula pendula* Roth) from a 30-year-old stand. The number of late instar *Phytobia* larvae was measured from wood disks taken from the stems at a height of 1 meter. We calculated the annual mean population density in the sampled trees, which provided us with a time series of 28 years.

The number of larval tunnels per tree correlated positively with the breast height diameter of the host tree ($r=0.69$, $N=26$, $P<0.0001$). The individual host trees and the age of the host tree explained 19% and 41% of the annual variation in population size, respectively. Some host trees maintained high populations and others sustained low populations. Our results support the plant vigor hypothesis: strong growth in host tree diameter is more suitable for larval development than is weak growth.

A trend in the population trajectory indicated nonstationarity: the population was going through a growth phase. A simple regression curve was fitted to the time series in order to remove the trend. The partial rate correlation function showed a single negative spike at lag 1, indicating a first order density-dependent process. This suggests that the population is resource regulated. Both *Phytobia* population densities and the yearly variation in the size of populations are low. The population growth follows an annually increasing food resource provided by the host tree. The close relationship of *Phytobia* and its host indicates that, most probably, the factors limiting the density of *Phytobia* populations are associated with the characters of host trees.

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Recent Outbreak of the Nun Moth (*Lymantria Monacha L.*) in the Czech Republic

JAN LISKA AND PETR SRUTKA

Department of Forest Protection, Forestry and Game Management Research Institute, Jiloviste - Strnady, Czech Republic

ABSTRACT In this century, several outbreaks of the nun moth (*Lymantria monacha* L.) have been recorded in the territory of the Czech Republic. The largest and best known outbreak was during the period of 1917-1927 when more than one-half million hectares of mostly spruce forest stands were infested. Several less severe outbreaks occurred in 1930-1932, 1938-1943, 1946-1950 and 1964-1967. The total area infested in these periods was approximately 22,000 ha. The first symptoms of the present outbreak occurred in 1993, roughly a quarter of a century since the last outbreak period had faded out. During the years 1994-1996, approximately 34,000 ha of forest stands, almost exclusively monocultures of Norway spruce (*Picea abies*), have been infested by the nun moth in the Czech Republic. It was necessary to protect most of this area by means of aerial spraying.

Population Dynamics

As in the past, the initiation of the current nun moth outbreak followed a period of dry and warm weather, which occurred mainly in 1989, 1990, and 1992. In most cases, single outbreak foci were located in the same sites where at least one outbreak occurred in the past (so-called historical foci). What differed from the past, however, was that most of the infestations were at higher elevations, between 600-700 m. The infestations occurred almost exclusively in spruce monocultures 50-80 years old. Centers of the single foci, however, often comprised mixed stands of Norway spruce (*Picea abies*) and European larch (*Larix decidua*). The area of these centers varied from a few hectares to a few tens of hectares.

Pest Management

Monitoring Methods Prior to the most recent outbreak, nun moth populations were monitored mainly with pheromone traps. However, since 1993, the system for monitoring populations has been modified and emphasis has been placed on more conventional methods. This consists of using pheromone traps to determine the period of peak flight, and then checking the incidence of swarming moths during this period (the walk-and-watch method).

Another method being evaluated is to measure the amount of excrement (frass) produced by larval populations. In endangered localities, efforts are made to estimate the number of female moths at the bases of sample trees (the Wellenstein method). Before a

Pages 351-352 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

decision is made to conduct control measures in the Spring, trees are limed with sticky bands to estimate the abundance of early instar larvae.

Control Methods The most frequently used insecticides were Trebon 30EC and Trebon 10F used with a carrier of light mineral oil or an emulsion of oil with water. These products were applied at a dose of 1 L/ha using micronair AU 4000 rotary atomizers. Trebon was applied in those sites where it was determined that a critical population density occurred. The effect of the treatment was immediate and reliable. Even in those cases where the weather was not favorable before and after application, the effectiveness of treatment varied from 90 to 95%.

In locations where lower-density populations of nun moth occurred, the biopreparation Foray FC 48B (*Bacillus thuringiensis*) and the chitin synthesis inhibitor (Dimilin 45 ODC) were used. Their effectiveness was adequate when the weather was favorable during and after they were applied.

Behavior of other Lymantriid Moths The characteristic phenomenon of the recent nun moth outbreaks was its synchrony with outbreaks of other species of the family Lymantriidae. Immediately preceding the nun moth outbreak, the largest outbreak of the gypsy moth, *Lymantria dispar,* occurred in the Czech Republic. Furthermore, local outbreaks of the following related species were recorded: *Orgyia antigua, Calliteara* (*Dasychira*) *pudibunda*, *Euproctis chrysorrhoea,* and *Leucoma* (*Stilpnotia*) *salicis*.

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

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