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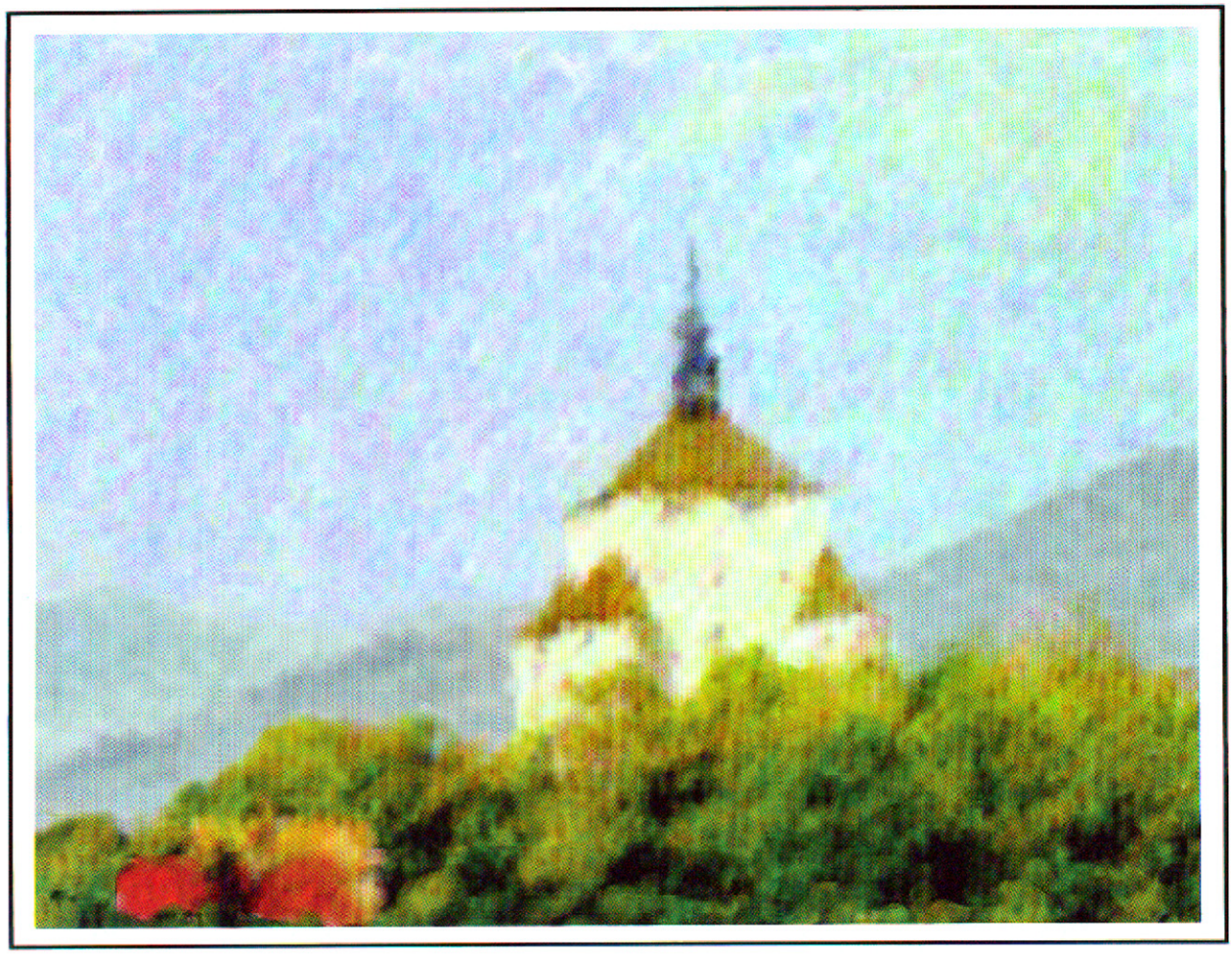
Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects

Edited by:

M.L. McManus
A.M. Liebhold

Banská Štiavnica, Slovak Republic
August 18-23, 1996



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Proceedings

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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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The editors are indebted to Becky J. Squires who accepted the challenge of collating the submitted manuscripts onto a computer and who is responsible for the outstanding appearance of this report. Vince D'Amico III contributed the excellent artwork on the cover. We also thank David Feicht, Sandra Fosbroke, Barbara Johnson, Kathy McManus, Rose-Marie Muzika, and Regis Young for their assistance in preparing this Proceedings.

Table of Contents

IUFRO and the Entomology Research Group, a Success Story.
H. SCHMUTZENHOFER.....1

Oak Decline in Central Europe: a Synopsis of Hypotheses.
E. FUHRER.....7

Gypsy Moths, Mice and Acorns.
J.S. ELKINTON, W.M. HEALY, J.P. BUONACCORSI, G. BOETTNER, H.R. SMITH AND A.M. LIEBHOLD.....25

Periodic Outbreaks of the Beech Caterpillar, *Quadricalcarifera punctatella*, and its Population Dynamics: the Role of Insect Pathogens.
NAOTO KAMATA.....34

Regarding the Outbreak of *Zeiraphera rufimitrana* H.S. on Silver Fir in Romania.
VASILE MIHALCIUC AND MIHAELA BUJILĂ.....47

Towards the Use of Pine Sawfly Pheromones in Forest Protection: Evaluation of a Behavioral Antagonist for Mating Disruption of *Neodiprion sertifer*.
OLLE ANDERBRANT, HANS-ERIK HÖGBERG, ERIK HENDENSTRÖM AND JAN LÖFQVIST.....53

Pheromone Monitoring of the Larch Bud Moth, *Zeiraphera diniana* Gn., in Poland.
WOJCIECH R. GRODZKI.....64

Monitoring Gypsy Moth (*Lymantria dispar* L.) Populations (Lep., Lymantriidae) in Slovakia using Pheromone Traps.
MAREK TURCANI.....70

Cytological Investigations with Regard to Population Dynamics of the Pine Sawfly, *Diprion pini* L. (Hym.: Diprionidae).
J. ROUSSELET, C. GÉRI, F. GOUSSARD, S. MOUSSET, S. MARETHEU AND F. LEMEUNIER.....83

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, CLAUDE GÉRI, CHRISTINE QUENCEZ AND CATHERINE BASTIEN.....91

Sensitivity of the More Important Forest Defoliating Insects in Poland to Insecticides.
HENRYK MALINOWSKI.....100

The Control of the Nun Moth (*Lymantria monacha* L.) in Poland: A Comparison of Two Strategies.
BARBARA GLOWACKA.....108

The Effect of Pesticides Applied Aerially to Forest Stands on Four Species of Native Hymenopterous Parasitoids.
JACEK HILSZCZAŃSKI.....116

Evaluating the Impact of Insect Communities on Pine Caterpillar Density under Different Stand Conditions.
TIANSHENG LI AND GUOFA ZHOU.....122

Towards an Integrated Management of *Dendrolimus pini* L.
ALICJA SIERPIŃSKA.....129

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, JOHN C. CUNNINGHAM, LORRAINE MACLAUCHLAN, PETER HALL AND NICHOLAS CONDER.....143

Ultra-Low-Volume Aerial Application in Forest Protection.
MILAN ŠVESTKA, JÚLIUS NOVOTNÝ AND PAVEL SOKOL.....155

Atta texana, Texas Leaf-cutting Ant, on Typic Quartzipsamments: Ecological Considerations.
D.L. KULHAVY, W.G. ROSS AND R.R. CAHAL III.....166

Pathomorphology of Lepidopteran Chorion during Transgeneration Pathogen Transmission.
A.Y. BARANOV AND M.A. GOLOSOVA.....174

The Effect of Foliage Damage on Transmission of Gypsy Moth Nuclear Polyhedrosis Virus.
VINCENT D'AMICO, JOSEPH S. ELKINTON, GREG DWYER, RAYMOND B. WILLIS AND MICHAEL E. MONTGOMERY.....180

Microsporidia Affecting Forest Lepidoptera.
J.V. MADDOX, M.L. MCMANUS AND L.F. SOLTER.....187

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.....198

The Theoretical Basis for Using Baculoviruses to Control Forest Pests.
EVGENIYA V. ORLOVSKAYA.....206

Classical Biological Control of the Gypsy Moth, *Lymantria dispar* (L.), in North America: Prospects and New Strategies.
MARC KENIS AND CARLOS LOPEZ VAAMONDE.....213

Integrated Control of Species of Geometridae in Oak Forests of Romania.
CONSTANTIN CIORNEI AND GHEORGHE MIHALACHE.....222

Shoot and Needle Losses in Scots Pine: Experimental Design and Techniques for Estimating Needle Biomass of Undamaged and Damaged Branches.
BO LÅNGSTRÖM, HARALD PIENE, RICHARD FLEMING AND CLAES HELLQVIST.....230

Spruce Budworm Defoliation-Foliage Production: Differences Between White Spruce and Balsam Fir.
HARALD PIENE.....247

The Role of Parasitoids in the Population Dynamics of Forest Lepidoptera.
ALAN A. BERRYMAN.....253

Effects of Silvicultural Management on Gypsy Moth Dynamics and Impact: An Eight-Year Study.
R.M. MUZIKA, A.M. LIEBHOLD AND K.W. GOTTSCHALK.....261

The System of Gypsy Moth Population Regulation in the Slovak Republic.
JÚLIUS NOVOTNÝ, MAREK TURCANI AND MILAN ZÚBRIK.....269

Pheromone Monitoring of the Larch Bud Moth, *Zeiraphera diniana*, in the Swiss Alps.
WERNER BALTENSWEILER.....278

Biomass Production of *Pinus pinaster* after Defoliation by the Pine Processionary Moth *(Thaumetopoea pityocampa* Schiff.).
STEPHANOS MARKALAS.....292

Crown Fauna of Birch Stand Caterpillars in a Pollution Area and Their Population Dynamics.
EMANUEL KULA.....303

The Use of *Bacillus thuringiensis* Against *Thaumetopoea pityocampa* Schiff. (Lepidoptera: Thaumetopoeidae) in Greece.
NIKOLAOS D. AVTZIS.....311

Activity of Several Contact Insecticides Against Selected Forest Insect Pests in Poland.
D. WORETA AND H. MALINOWSKI.....317

Pathogens of the Gypsy Moth in Central Europe: Host Range and Interactions.
JAROSLAV WEISER.....322

Oak Defoliating Insects in Hungary.
GYÖRGY CSÓKA.....334

Effect of the Mimic Prototype, RH 5849, on 20-Hydroxyecdysone Titers in Defoliating Lepidopteran Larvae.
MACIEJ A. PSZCZOLKOWSKI.....336

The Stone Pine Needleminer (*Ocnerostoma copiosella* Heyd.) in the Engadine Valley, Switzerland.
BEAT FORSTER.....338

Wind and Bark Beetles - the Most Serious Harmful Agents in the Norway Spruce Stands of Slovakia.
BOHDAN KONÔPKA.....339

Defoliating Insects: History of Outbreaks in the Coniferous Forests of Russia.
ANDREY V. SELIKHOVKIN, DIMITRY L. MUSOLIN AND TAMARA E. SERGEEVA.....340

Damage Caused by Cockchafers (*Melolontha* spp.) in Hungary during the Last 30 Years.
JÓZSEF TÓTH.....341

Reaction of *Cyzenis albicans*, *Ernestia rudis*, and *Parasetigena silvestris* (Diptera: Tachinidae) to Insecticides Used in the Control of the Nun Moth.
CEZARY BYSTROWSKI.....342

Growth and Survival of *Chrysomela tremulae* (Coleoptera, Chrysomelidae) on Transgenic Poplar Containing a *Bacillus Thuringiensis*-Endotoxin Gene.
S. AUGUSTIN, A. DELPLANQUE, J.C. LEPLE, G. PILATE AND L. JOUANIN.....343

Foliage Palatibility of Pine Species and Clones to the Rare Subspecies *galliegloria* of the Beauty Moth, *Graellsia isabellae* Oberthür (Lepidoptera: Attacidae).
CLAUDE GÉRI, FRANCIS GOUSSARD, MARIE-ANNE AUGER-ROZENBERG, CATHERINE BASTIEN AND FLORENCE PASQUIER.....344

Biotic Factors Affecting *Stereonychus fraxini* Populations in the Longoza Forest, Bulgaria.
GALINA MARKOVA.....345

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.....346

Weevils Affecting Reforestation in Poland.
IWONA SKRZECK.....347

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....348

Predicting Gypsy Moth Defoliation Using Spatially Explicit Information.
RONALD M. WESELOH.....349

Phytobia Population Densities in European White Birch (*Betula Pendula* Roth).
TIINA YLIOJA AND HEIKKI ROININEN.....350

Recent Outbreak of the Nun Moth (*Lymantria Monacha L.*) in the Czech Republic.
JAN LISKA AND PETR SRUTKA.....351

IUFRO and the Entomology Research Group, a Success Story

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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

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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.

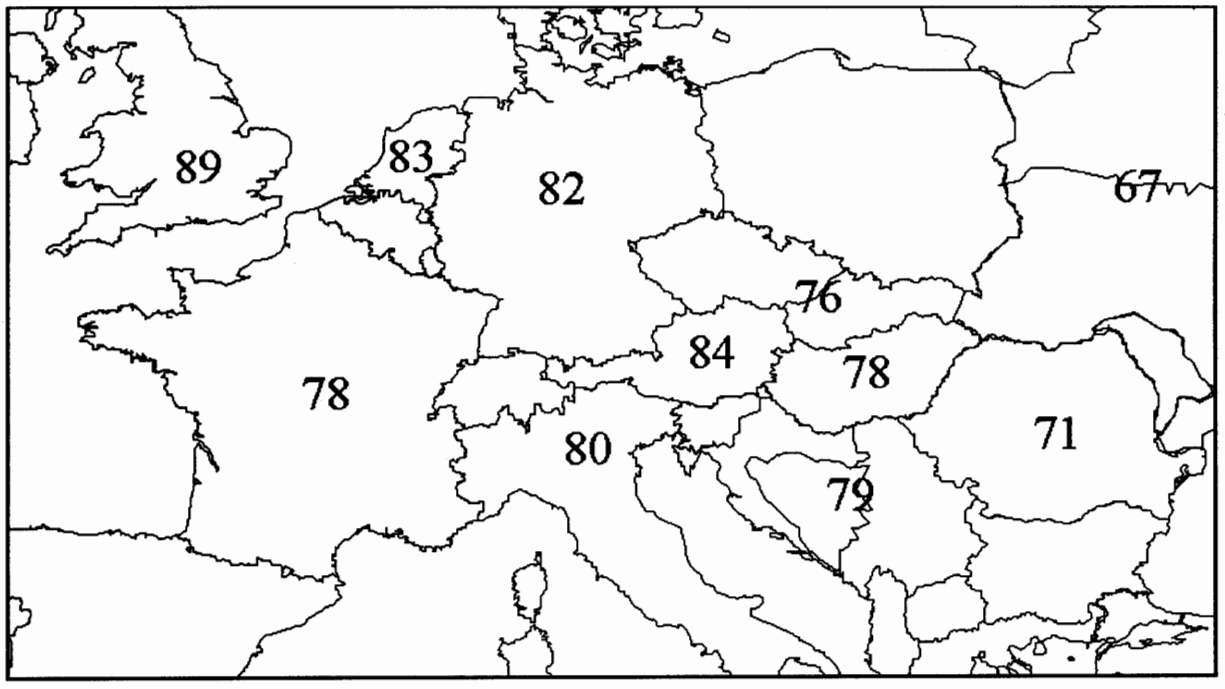

Figure 1. Years when recent oak decline phenomena were first recorded in individual European countries (Hämmerli and Stadler 1989).

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.

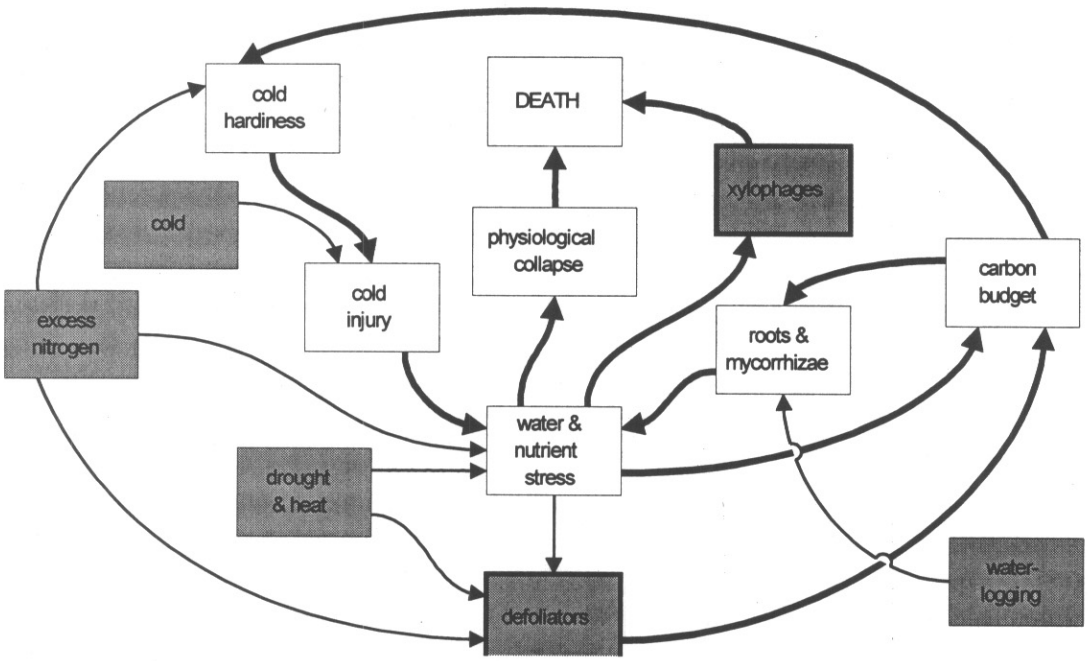

Figure 2. Oak decline: eco-physiological decline cycle, indicating essential effects of environmental factors on the tree, and showing the positions and contributions of defoliating and xylophagous insects, respectively, in the decline process.

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.

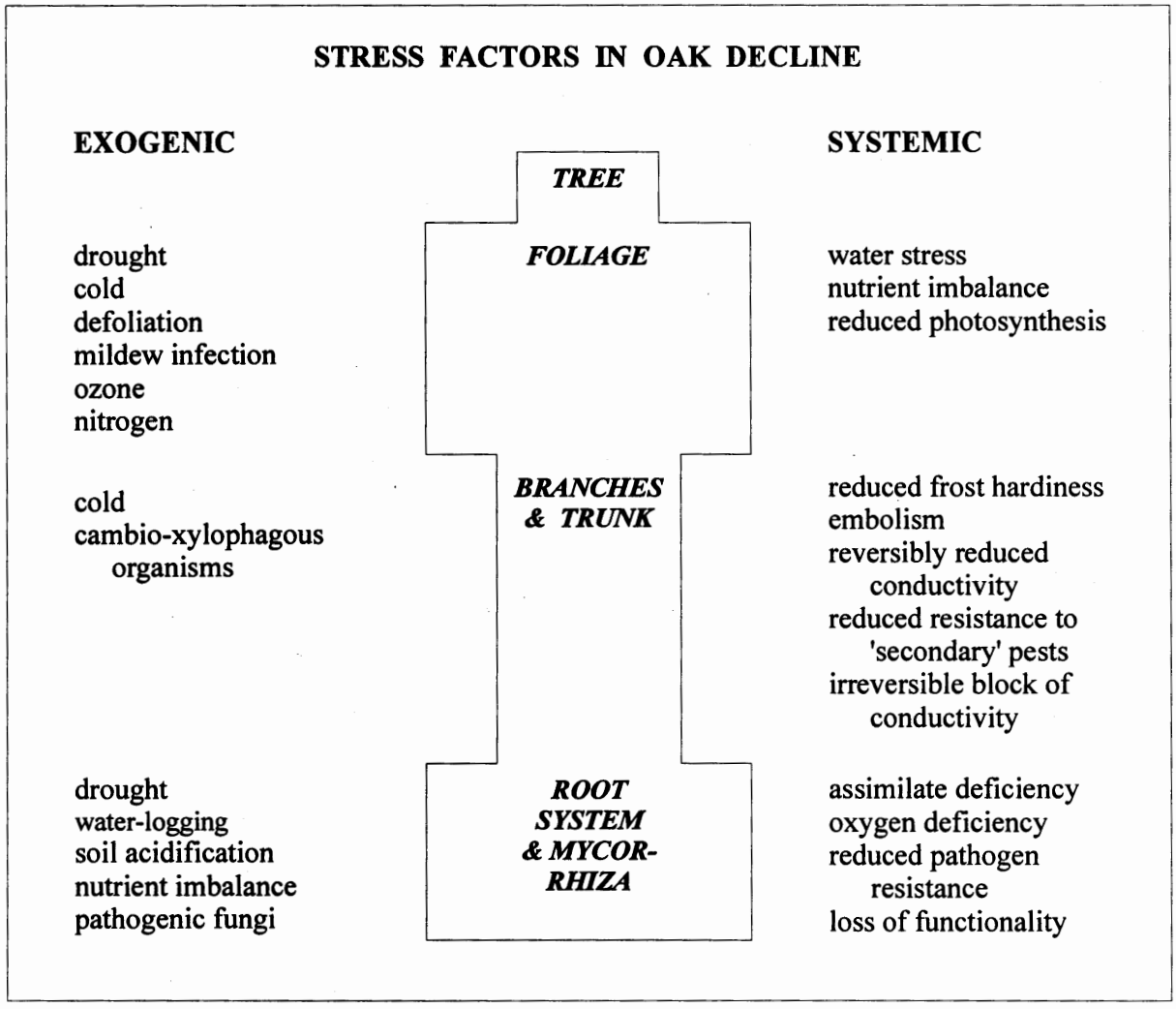

Figure 3. List of exogenic and systemic stress factors relevant for the genesis of oak decline phenomena, arranged by their main points of attack in the tree.

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

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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).

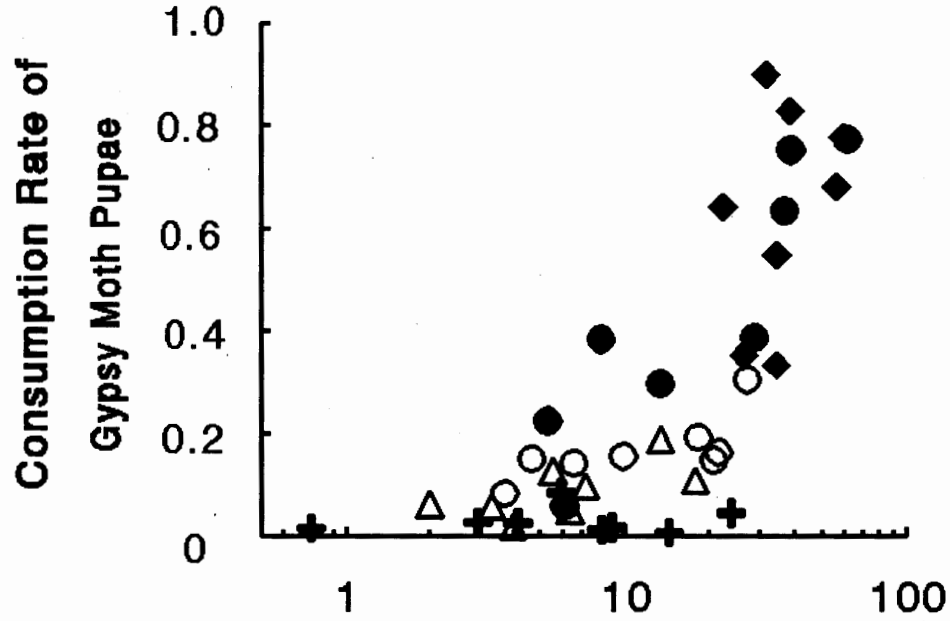

Figure 1. Daily proportion of 300 gypsy moth pupae deployed on each plot that were consumed by all predators versus density of white-footed mice. Symbols indicate different years. Reproduced from Elkinton et al. (1996) with permission from *Ecology*.

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

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

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:

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

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.

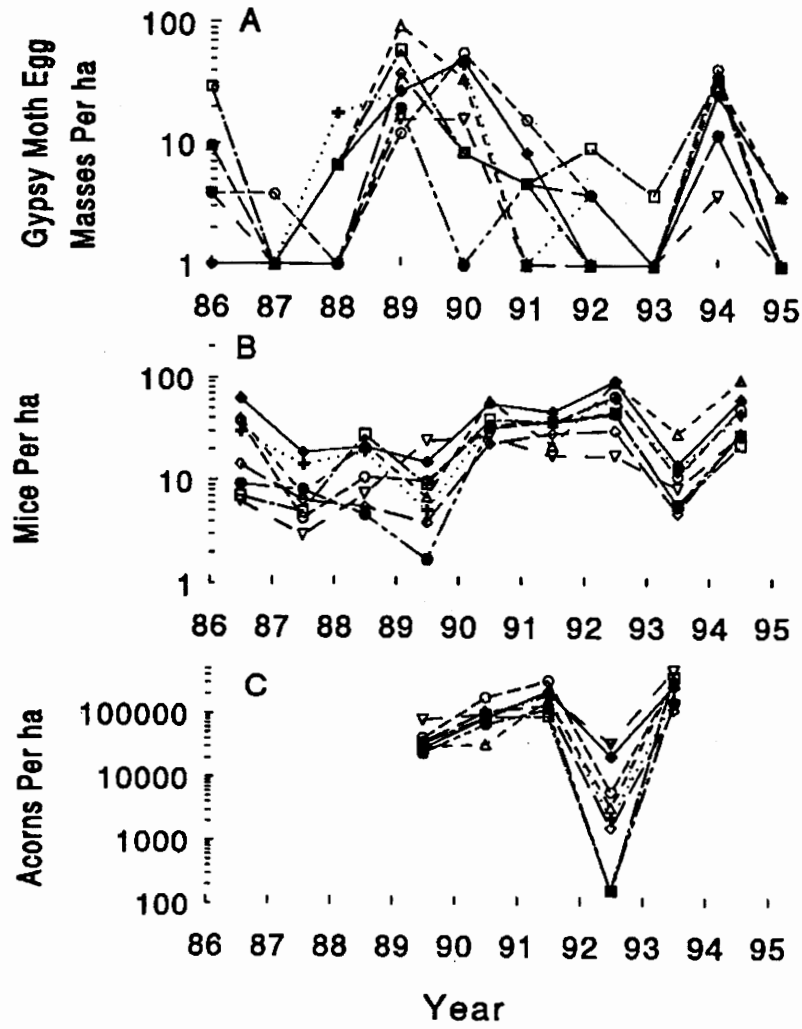

Figure 2. Yearly estimates from each of 8 stands of A) gypsy moth egg masses per ha as determined prior to hatch in each year, B) white-footed mice per ha and C) sound acorns per ha from each stand beginning in 1989. Reproduced from Elkinton et al. (1996) with permission from *Ecology*.

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

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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.

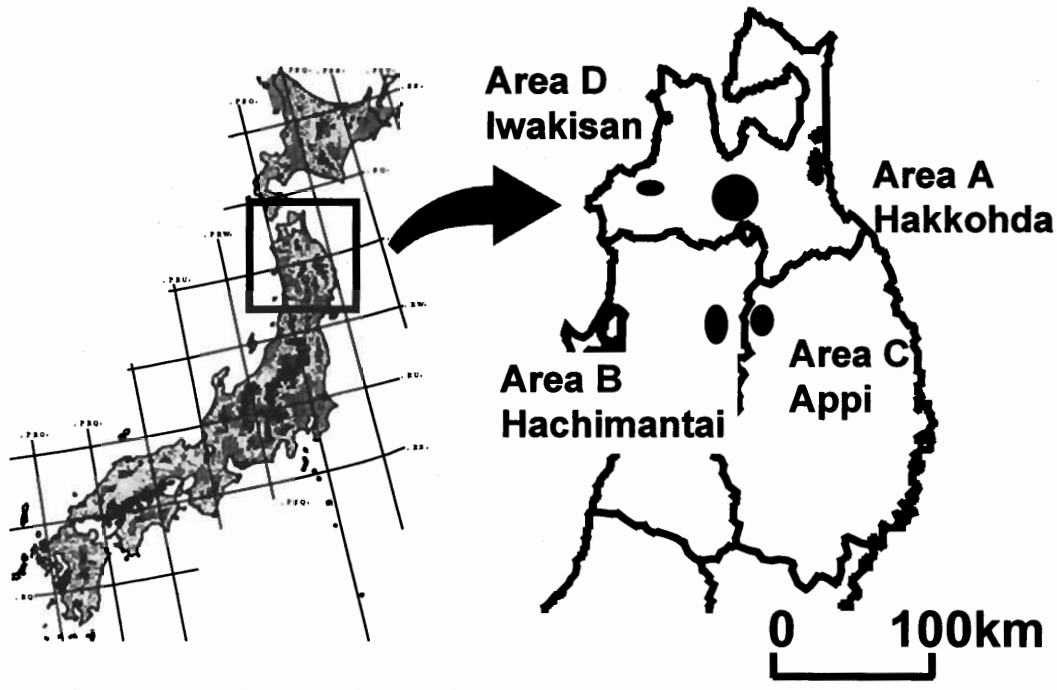

Figure 1. Four study areas in northern Japan, all located in natural deciduous broad-leaved forests mainly occupied by Siebold's beech, *Fagus crenata*.

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.

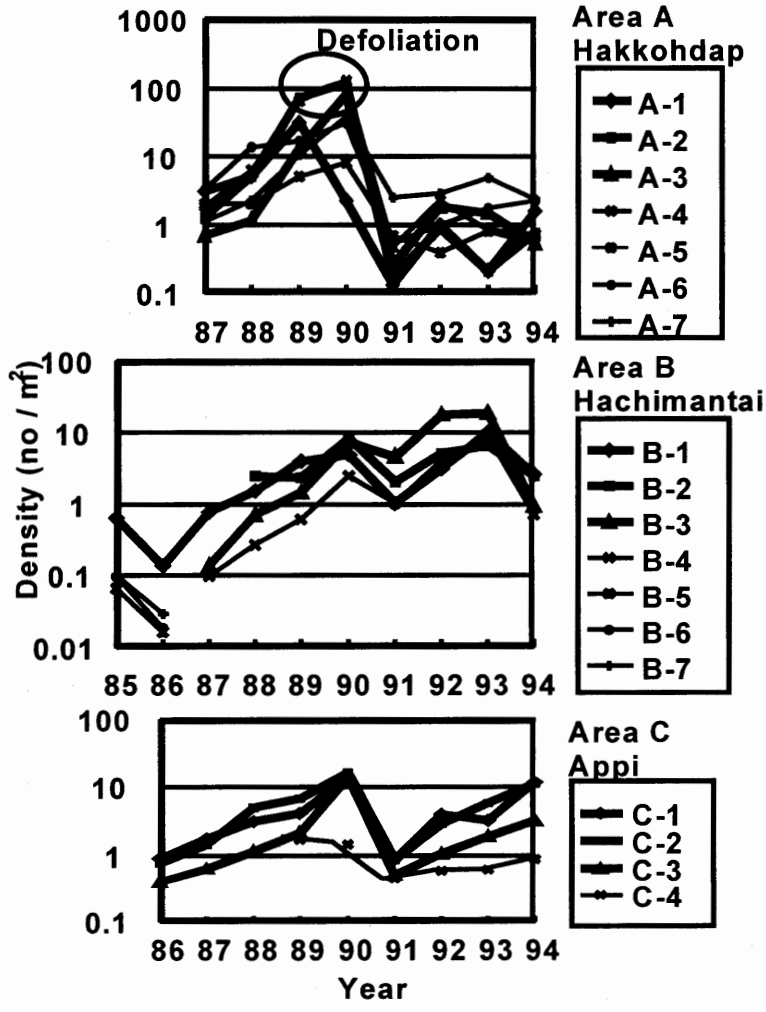

Figure 2. Final instar density of the beech caterpillar, *Quadricalcarifera punctatella* in each study plot of three disjunct beech forests.

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

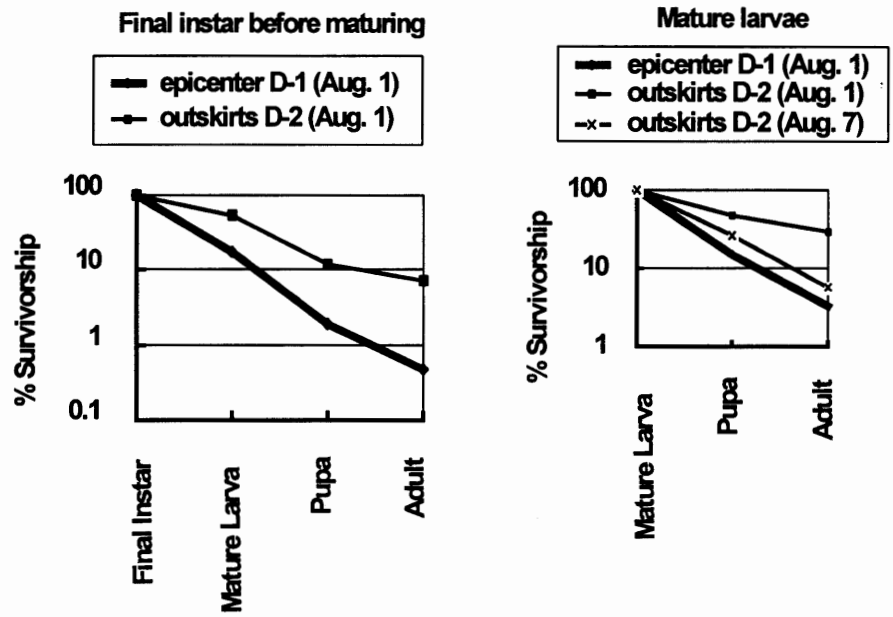

Figure 3. Survivorship curves of *Quadricalcarifera punctatella* collected during population outbreaks in Area D (Iwakisan) in 1994.

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.

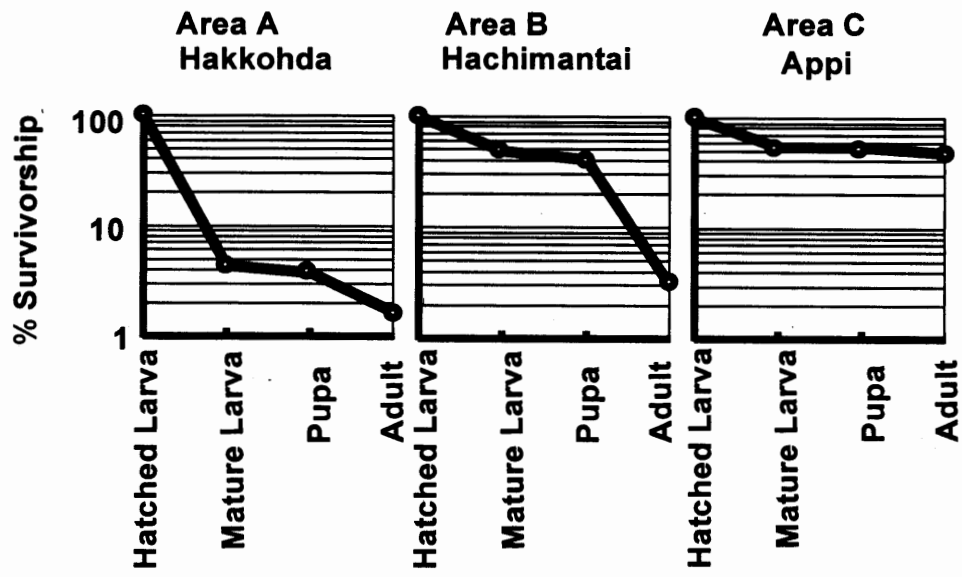

Figure 4. Survivorship curves of *Quadricalcarifera punctatella* reared in netted enclosures in three disjunct beech forests. Survivorship curves are shown for a year of decreasing population in site A, for a peak generation year in site B, and for a year of increasing population in site C.

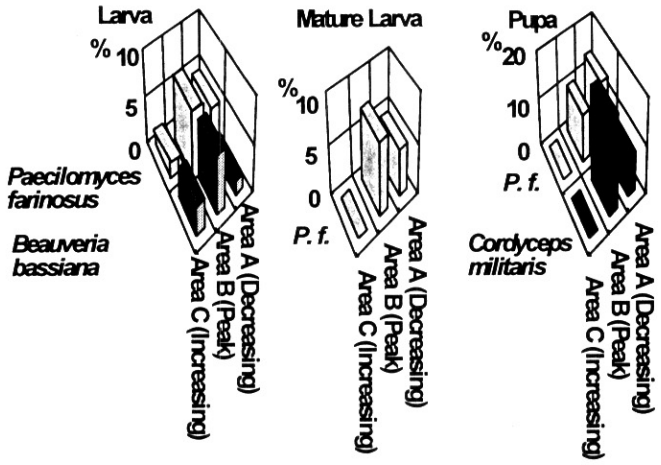

Figure 5. Aerial infection by fungal diseases of *Quadricalcarifera punctatella* larvae reared inside netted enclosures in three disjunct beech forests. Percentage mortality in each developmental stage is shown for each entomopathogenic fungus.

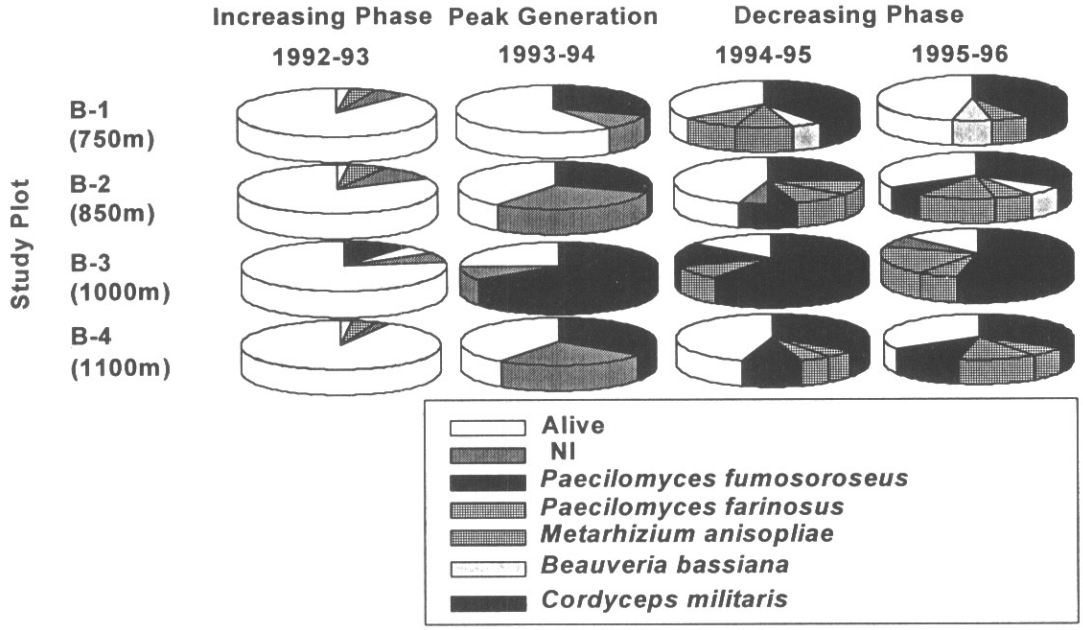

Figure 6. Annual changes in mortality caused by infectious disease when *Quadricalcarifera punctatella* pupae were buried in soil samples placed in plastic cups. Numbers in parentheses are elevations above sea level.

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

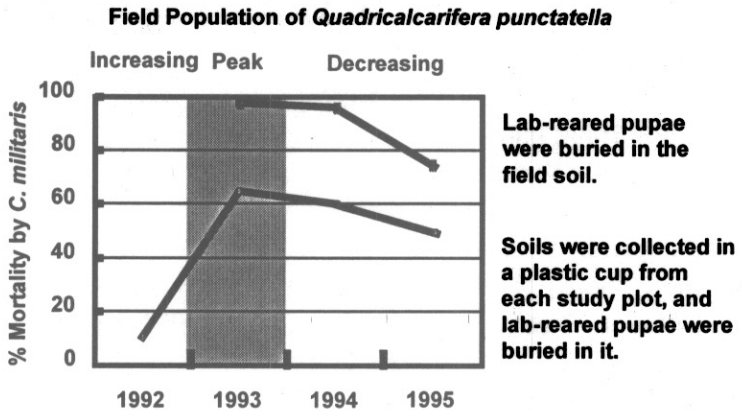

Figure 7. Annual changes in mortality caused by *Cordyceps militaris* when *Quadricalcarifera punctatella* pupae were buried in the soil of plot B-3.

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

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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 Sãnmartin, 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.

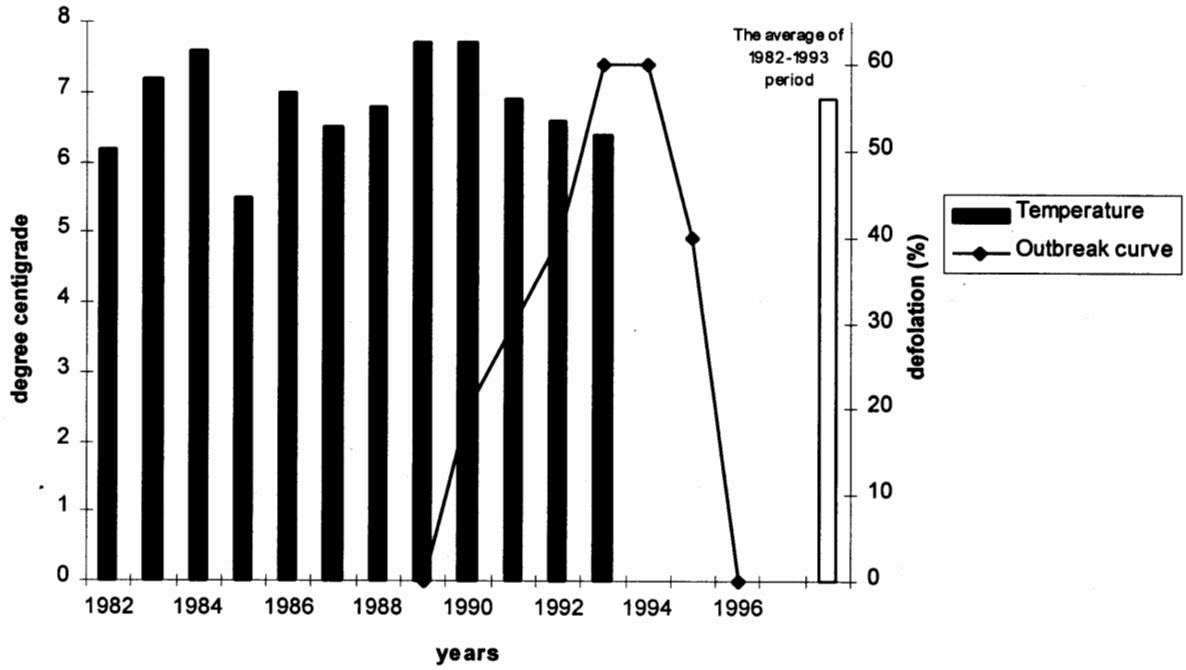

Figure 1. Average yearly temperature (degrees Centigrade).

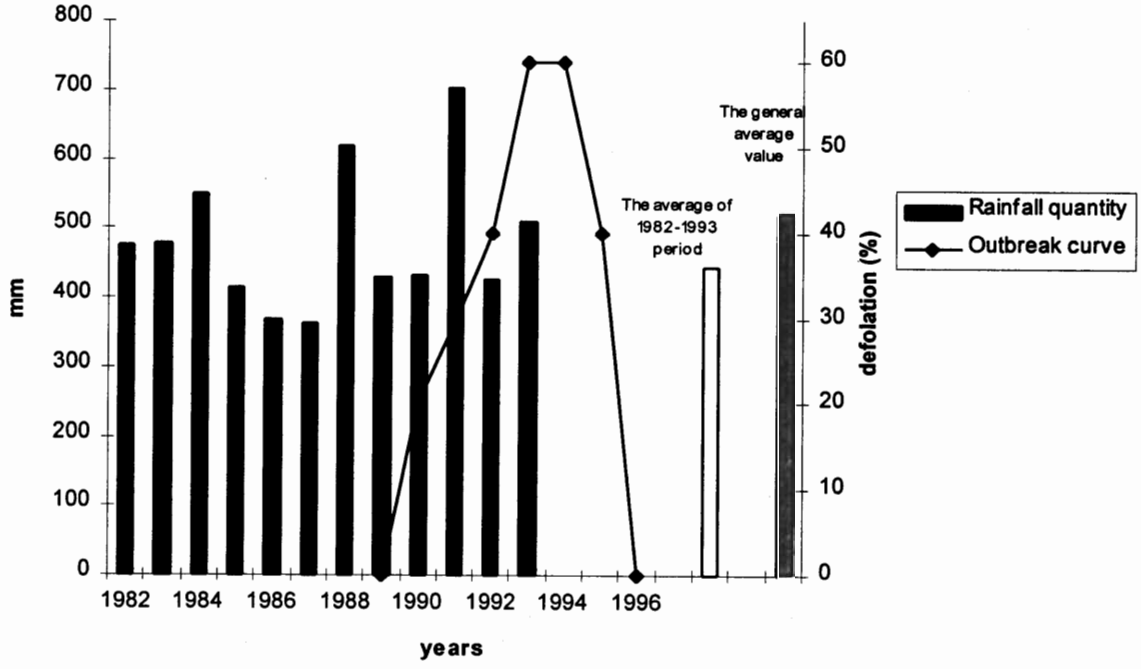

Figure 2. Annual rainfall (mm).

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).

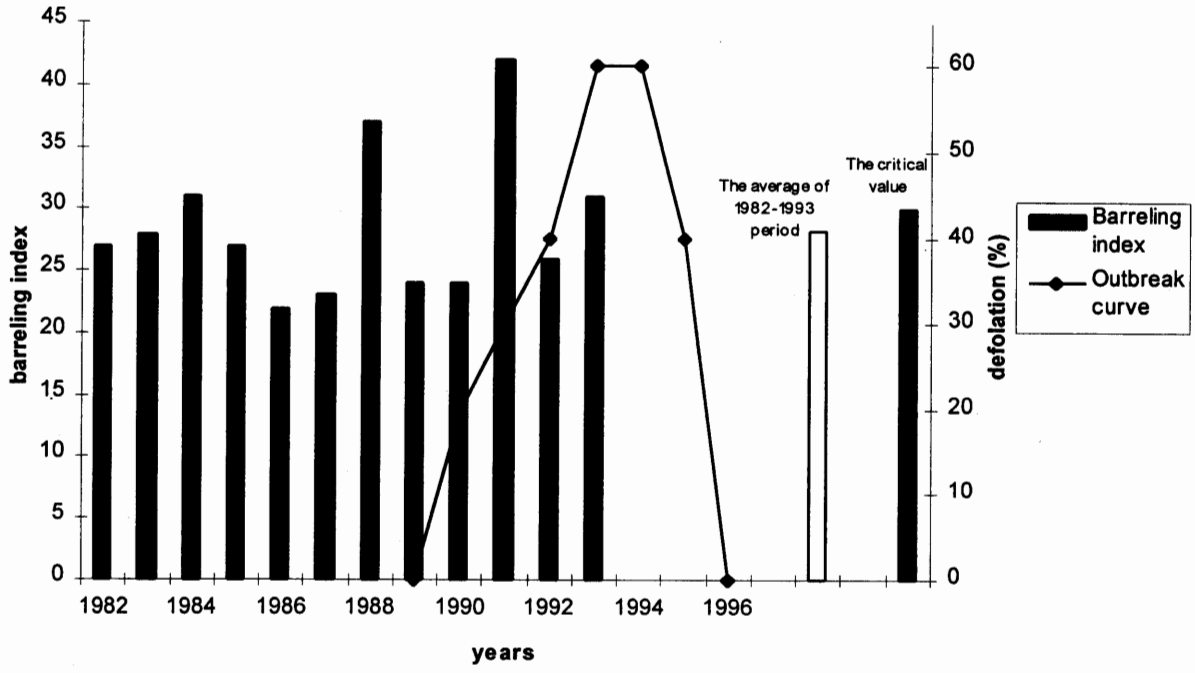

Figure 3. Barreling index.

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

	June 3-4, 1992	June 9-10, 1992
Date No. larvae reared Main instar	6,923 L4	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*

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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}.

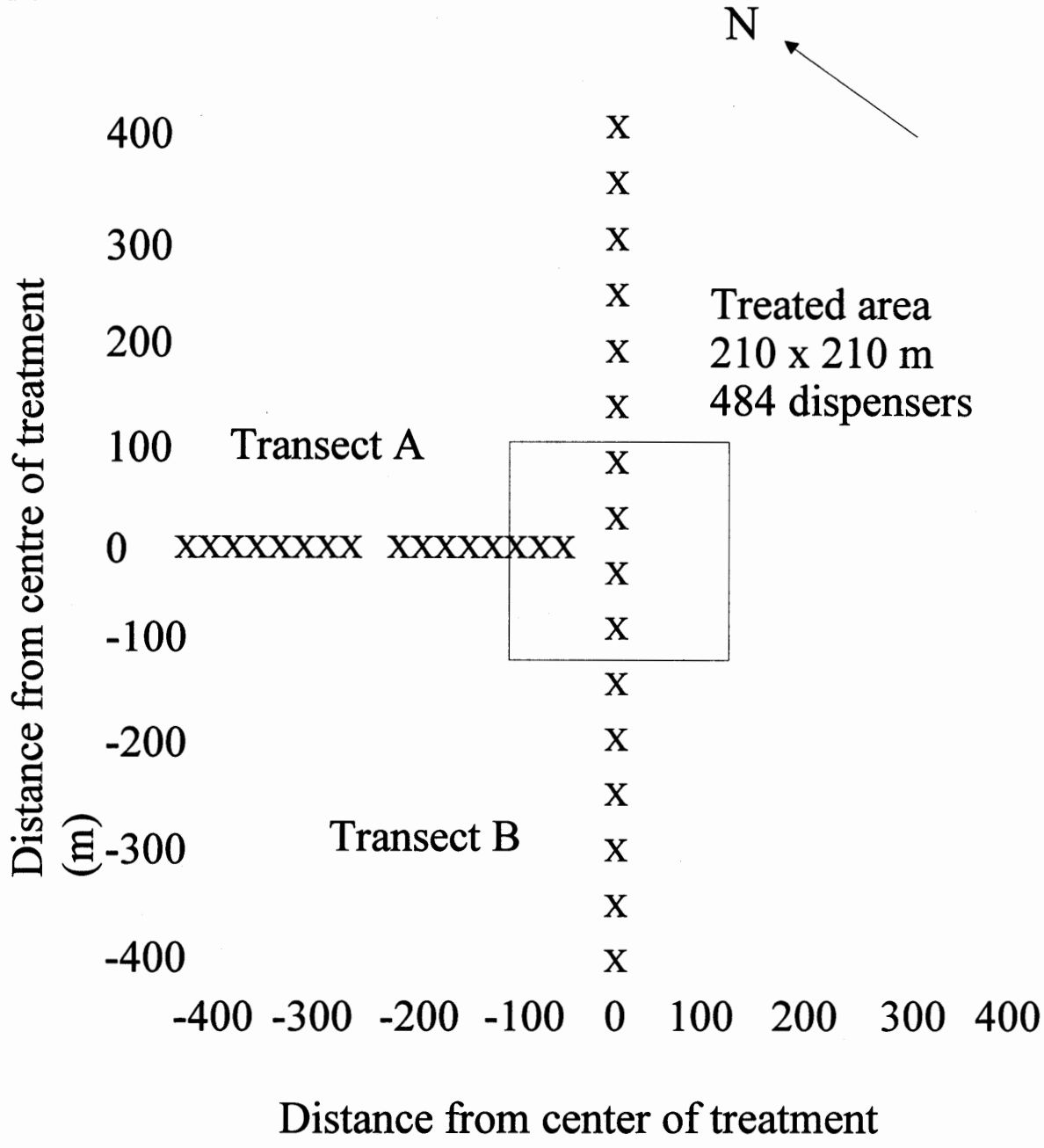

Figure 1. Outline of *N. sertifer* mating disruption Experiment 2 in 1990, showing the area treated with the behavioral antagonist (2*S*, 3*R*, 7*R*)-diprionyl acetate and the two lines with pheromone monitoring traps.

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).

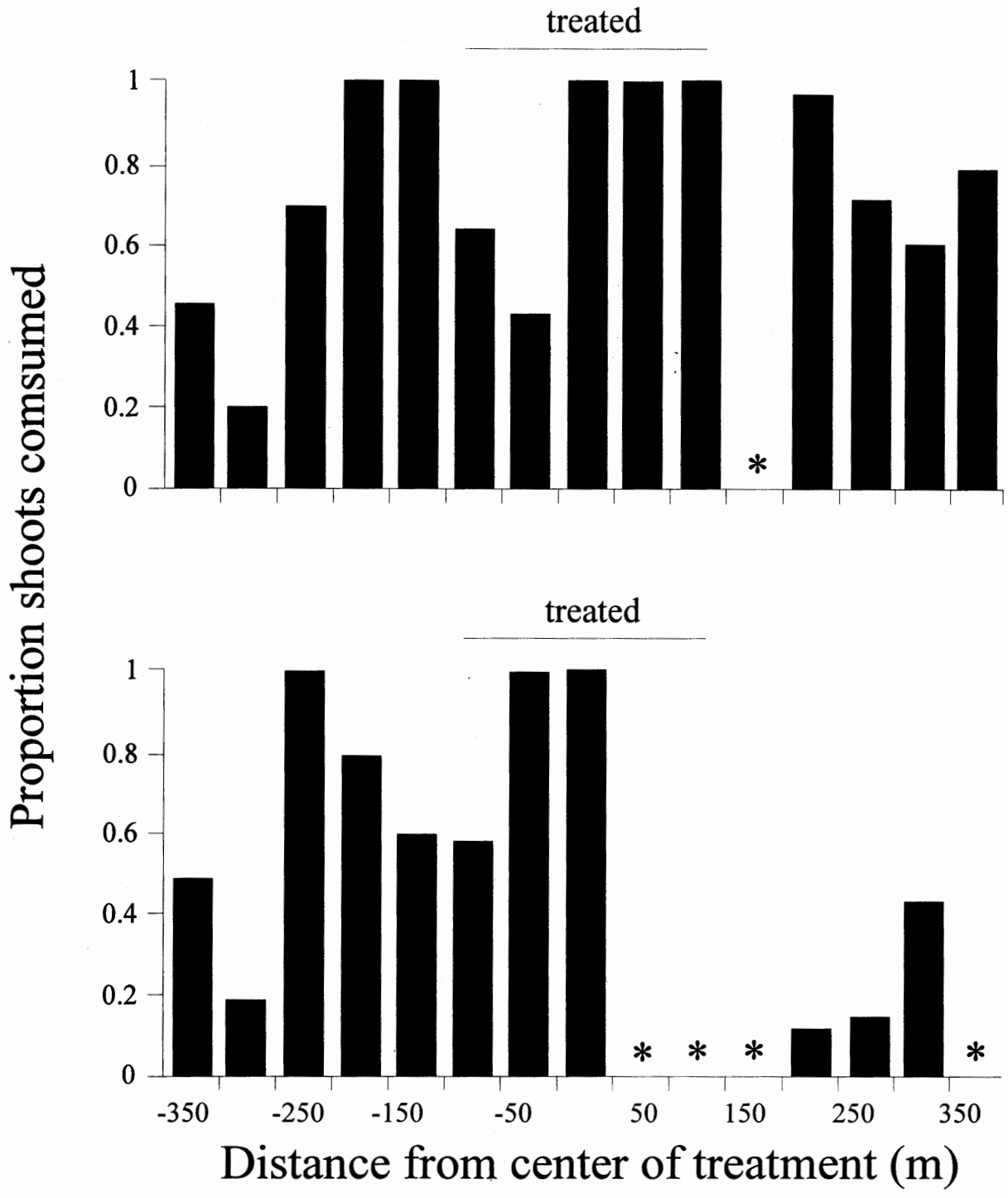

Figure 2. Damage caused by feeding *N. sertifer* larvae during 1990 along transects A (above) and B. An * indicates that no suitable tree for census of the damage was available.

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).

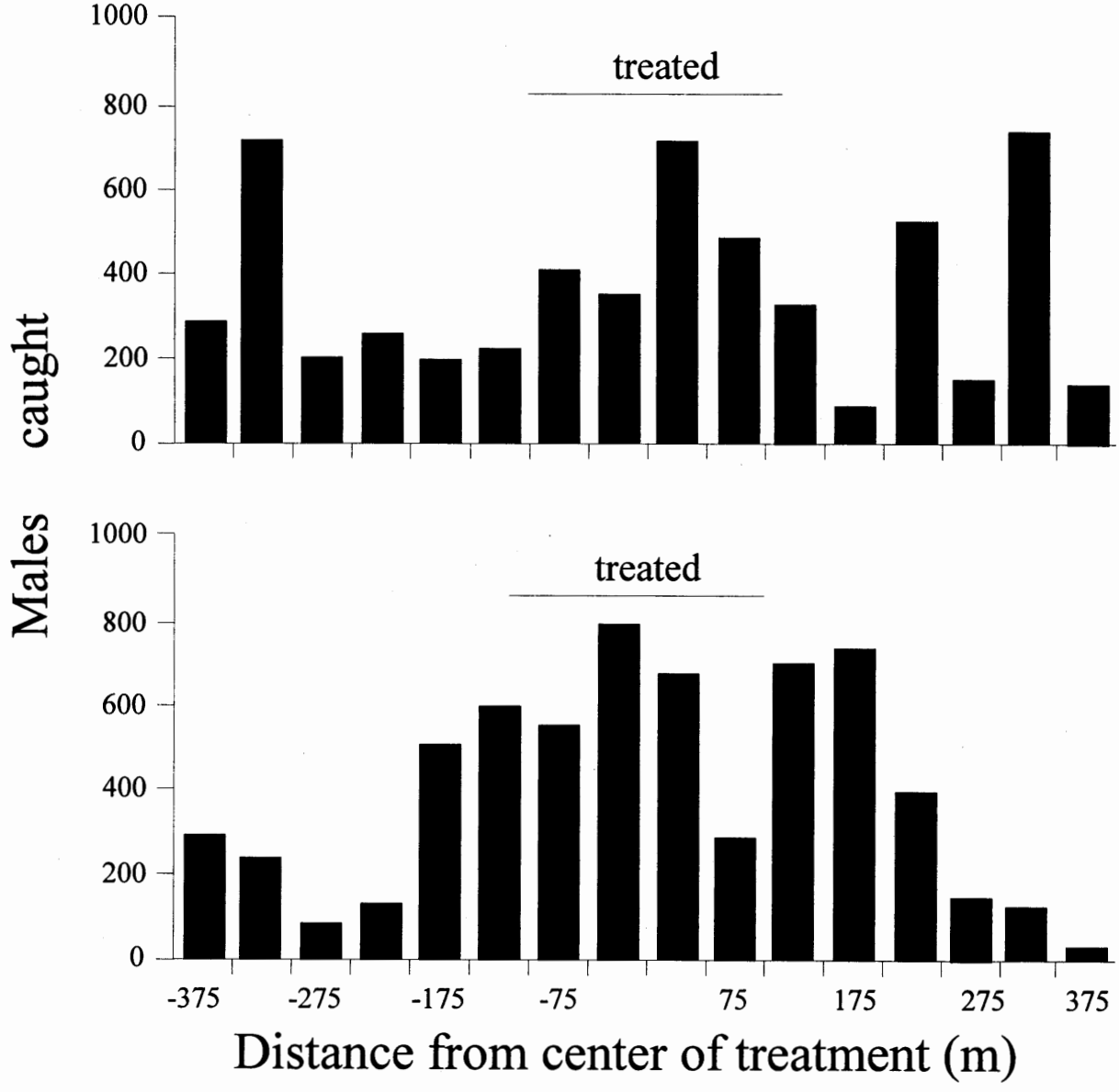

Figure 3. Catch of male *N. sertifer* in pheromone traps along transects A (above) and B.

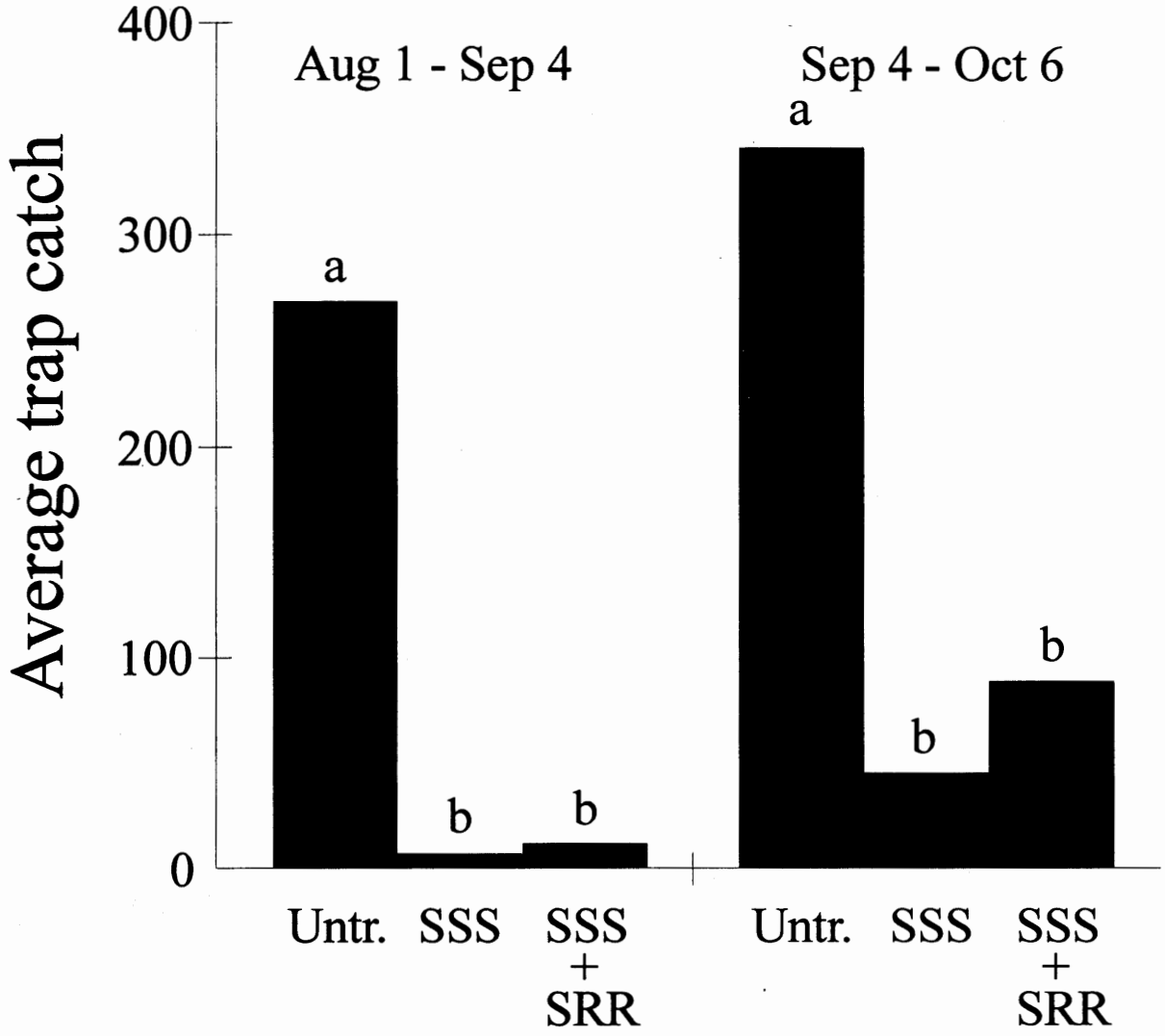

Figure 4. Average catch of male *N. sertifer* in pheromone traps placed in untreated plots (n=12), in plots treated with the attractive *SSS*-isomer (n=4), and in plots where 10% of the antagonistic *SRR*-isomer was added to the *SSS*-isomer (n=4). Within trapping periods, the same letter above bars 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

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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 (≥ 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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