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Classical Biological Control of the Gypsy Moth, *Lymantria dispar* (L.), in North America: Prospects and New Strategies

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ABSTRACT On-going programs and future strategies for the biological control of the gypsy moth are reviewed. The most promising directions are: a continuation of the introduction of the two tachinid parasitoids *Blepharipa schineri* and *Ceranthia samarensis*, investigations on egg predators which are important natural enemies of the gypsy moth in eastern Europe and North Africa, studies on parasitoids specialized in low host densities, especially in poorly investigated regions in Asia, and investigations for the existence of more efficient biotypes of *Parasetigena silvestris* and *Cotesia Melanoscelus*, two parasitoid species already established in North America.

THE GYPSY MOTH has been the target of several extensive biological control programs since its introduction into North America in the 19th century. More than 60 species of natural enemies, parasitoids, predators and pathogens were introduced from 1906 to present but most failed to establish, for various reasons (Hoy 1976). Only 11 parasitoids, two predators and two pathogens became established, and among these some became major natural enemies of the gypsy moth in North America (Doane and McManus 1981, Schaefer et al. 1989, Hajek et al. 1993). The impact of these exotic natural enemies on gypsy moth populations in North America is hard to assess because of the difficulty of determining what would be the situation had these natural enemies not been introduced. Several authors claim that exotic natural enemies play an important role in regulating gypsy moth populations both at sparse densities and in outbreak situations (e.g. Clausen 1978, Berryman 1991). Nevertheless, the impact of these exotic natural enemies cannot be considered as totally satisfactory. Indeed, the gypsy moth is still the major pest of broadleaved forests in eastern North America and its distribution is expanding further west and south, despite the expensive eradication programs carried out at the edge of its present distribution.

Considering the enormous efforts made in the past to import exotic natural enemies into North America, one may conclude that everything has already been tried in the biological control of gypsy moth. However, before drawing such a conclusion, it is important to note that the gypsy moth still causes more damage in North America than in its native range and natural enemies play a more important role in the control of gypsy moth populations in Europe and Asia than in North America (see Doan and McManus 1981 for review). Furthermore, most of the introductions were done in the early days when not much was known on biological control techniques (DeBach and Rosen 1991). In view of this, and considering the low costs of biological control programs compared to the enormous losses caused by the gypsy moth in North America, and the costs of present monitoring and control

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methods, it seems reasonable to continue investigations on the importation of exotic natural enemies.

This paper reviews on-going programs and future strategies for the biological control of the gypsy moth in North America. These strategies can be categorized as follows:

(1) re-introduce natural enemies that failed to establish in previous trials but which are major components of Eurasian natural enemy complexes;

(2) introduce new natural enemies that were never considered, or seriously considered, for introduction;

(3) introduce new, better adapted biotypes of natural enemies already established in North America.

Strategies for the BioControl of Gypsy Moth

1. Re-introduction of Natural Enemies that Failed to Establish. In this section, only parasitoids will be discussed, as they represent by far the most important group of agents tested against the gypsy moth. Several European parasitoid species that failed to establish in North America are major components of the parasitoid complex of the gypsy moth in their region of origin, e.g. the two braconids *Glyptapanteles liparidis* (Bouché) and *G. porthetriae* (Muesb.). Hoy (1976) lists several reasons that could explain why these parasitoids did not establish. For the most important European parasitoids, the main reason of non-establishment appears to be the lack of alternate and/or overwintering hosts. Table 1 shows a list of the most important parasitoids established and not established in North America. The majority of the parasitoids that became established do not require an alternate host to complete their cycle. Those parasitoids established in North America that require an alternate host are extremely polyphagous, such as the tachinids *Compsilura concinnata* (Meigen) or *Exorista larvarum* (L.), which are recorded from 137 and 49 host species, respectively (Herting 1980). In contrast, all parasitoids that failed to establish despite large release programs are bi- or multivoltine and require a particular alternate host which probably does not exist in North America. Thus, releases of new individuals of the same species would probably result in the same failure. However, Fuester et al. (1988) suggested that, because all previous releases were made in New England and the gypsy moth is now spreading further north, south and west, new releases should be made in newly invaded regions where alternate hosts might be present.

2. Introduction of New Species. Despite the numerous introduction programs carried out for the last 90 years, there are still potentially important natural enemies which have never been seriously tried for introduction. The tachinid fly *Blepharipa schineri* (Mesnil) is a univoltine, oligophagous parasitoid that is a major natural enemy of the gypsy moth in Asia (Pemberton et al. 1993). In Europe, its importance has probably been largely underestimated because it has often been mistaken for the closely related species *B. pratensis* which is established in North America (Maier 1990). Recent studies in Germany showed that *B. schineri* was sometimes much more important than its congeneric species, reaching up to 96% parasitism (Maier 1990). Some individuals of *B. schineri* were already introduced in the United States at the beginning of the century, but the number of individuals released was too low to consider this a serious attempt (Hoy 1976). *B. schineri* is presently collected in

Europe by the United States Department of Agriculture and seriously considered for introduction into North America (F. Hérard, personal communication).

Table 1. Characteristics of the European and Asian parasitoids of the gypsy moth established and not established in North America

Parasitoids established in North America	Host stage attacked [b]	Host range [c]	Life cycle [d]	Alternate host required [e]
Anastatus japonicus Ashmead (=*disparis* Rushka) (Eupelmidae)	E	O	U	N
Ooencyrtus kuvanae (Howard) (Encyrtidae)	E	O	M	N
Cotesia melanoscelus Ratzeburg (Braconidae)	L	O	M	N
Phobocampe disparis (Viereck) (Ichneumonidae)	L	O	U	N
Blepharipa pratensis (Meigen) (Tachinidae)	L	O	U	N
Compsilura concinnata (Meigen) (Tachinidae)	L	P	M	Y
Exorista larvarum (L.) (Tachinidae)	L	P	M	Y
Parasetigena silvestris (Rob.-Desv.) (Tachinidae)	L	O	U	N
Monodontomerus aereus Walker (Torymidae)	P	P	M	Y
Brachymeria intermedia (Nees) (Chalcididae)	P	P	U-M	N-Y
Pimpla disparis Viereck (Ichneumonidae)	P	P	M	Y
Parasitoids released but not established [a]				
Glyptapanteles porthetriae (Muesebeck.) (Braconidae)	L	O	M	Y
Glyptapanteles liparidis (Bouché) (Braconidae)	L	O	M	Y
Meteorus pulchricornis (Wesmael) (Braconidae)	L	O	M	Y
Blondelia nigripes (Fallén) (Tachinidae)	L	P	M	Y
Carcelia separata (Rondani) (Tachinidae)	L	P	M	Y
Exorista japonica (Towsend) (Tachinidae)	L	P	M	Y
Exorista segregata (Rondani) (Tachinidae)	L	P	M	Y
Palexorista inconspicua (Meigen) (Tachinidae)	L	P	M	Y
Pimpla hypochondriaca (Retzius) (= *instigator* F.) (Ichneumonidae)	P	P	M	Y
Pimpla turionellae (L.) (Ichneumonidae)	P	P	M	Y

[a] Only common parasitoids of the gypsy moth that were released in adequate numbers are listed here (Hoy 1976).

[b] E = egg; L = larva; P = pupa.

[c] O = oligophagous; P = polyphagous (at least 10 hosts recorded in Herting 1980, 1982).

[d] U = univoltine; M = bi- or multivoltine.

[e] N = no; Y = yes.

Other important natural enemies have been neglected for other reasons. Of particular interest are the egg predators, particularly dermestid beetles. Dermestids are sometimes considered as the most important natural enemies of the gypsy moth in eastern Europe (Nonweiler 1959, Mihalache et al. 1995) and Morocco (Hérard 1979, Villemant 1995), where over 50% of the egg masses might be attacked in the declining phase of the outbreaks. In Romania, dermestids have already been used in augmentative releases as part of IPM programs (Ciornei et al. 1995). In addition to the direct effect of predation, dermestids have two other possible beneficial effects. First, they open the egg masses which are then more susceptible to egg parasitoid attack. Indeed, in the absence of egg predation, the two egg parasitoids *Ooencyrtus kuvanae* (Howard) and *Anastatus japonicus* Ashmead (= *disparis* Ruschka) have a limited effect because they can parasitize only the eggs in the top layers of the egg masses (Prota, in Brown and Cameron 1982, Hérard 1979). Second, dermestids are supposed to play an important role in the dispersion of pathogens, particularly nucleopolyhedrosis virus, because they feed on the dead larvae before feeding on the eggs (Pirvescu 1978). In North America, egg predation by invertebrates plays a minor role in the natural control of the gypsy moth (Brown and Cameron 1982). Dermestids, or other egg predators, would therefore fill an empty niche in the natural enemy complex of the pest.

The lack of interest in dermestids as biological control agents is undoubtedly due to their reputation as pests of stored foods and fabrics. Indeed, one of the dermestids feeding on gypsy moth eggs is the famous bacon beetle *Dermestes lardarius* L.. However, the three most important dermestids found on gypsy moth in eastern Europe, *Dermestes erichsoni* Ganglbauer, *Megatoma undata* (L.) and *Megatoma ruficornis* Aub (= *pici* Kalik) (Nunweiler 1959, Mihalache et al. 1995), are not known as pests and apparently have a fairly narrow food range (Freude et al. 1979). It is strange that, until now, such important natural enemies received so little attention, and it would be of high interest to investigate in further detail their exact impact on gypsy moth populations, their role as pathogen vectors, and their food range.

Other potential biological control agents might be found in previously unexplored regions. While Europe and Japan have been extensively surveyed, large regions within the distribution range of the gypsy moth remain largely unexplored. This is particularly the case for China, eastern Russia and the Middle East, where only casual collections were made without much information on the impact of natural enemies on the local gypsy moth populations (e.g. Schaefer et al. 1984; Kolomiets 1987). In these regions, the gypsy moth, although present over large areas, is usually considered as a relatively minor pest, and it remains to be seen why damage is limited compared to North America.

Surveys should not be limited to outbreaks. It is a well known fact that parasitism is sometimes very different at high and low host densities (Mills 1990). All parasitoids introduced into North America were collected during outbreaks and other parasitoids might play an important role in limiting host populations at low density. In the 80's, the International Institute of Biological Control and the Canadian Forest Service initiated a study on low host density parasitoids using the host exposure technique (Mills 1990, Mills and Nealis 1992). Larvae were exposed on isolated trees in Switzerland, Germany and France at sites which never or rarely suffer from gypsy moth outbreaks. The main parasitoid attacking these exposed larvae was the tachinid *Ceranthia samarensis* (Villeneuve). This species was only found three times in natural populations of gypsy moth: in Austria (Fuester et al. 1983), Germany (Maier 1990), and France (M. Kenis, unpublished data). However, it was reared at 10 of the 11 sites where gypsy moth larvae were exposed (Mills and Nealis 1992, M. Kenis, unpublished data). Hence, *C. samarensis* may act as an important factor preventing the gypsy moth from producing outbreaks in regions where the pest usually stays at endemic levels.

Parasitoids attacking hosts at low density are likely to be polyphagous. Indeed, when similar host exposure experiments are made in North America, the main parasitoid reared is the polyphagous tachinid *Compsilura concinnata* (Gould et al. 1990). However, there are good indications that *C. samarensis* is not polyphagous. First, the only one other host record besides the gypsy moth is the lymantriid *Orgyia recens* Hbn. (Mihalyi 1986). Second, extensive collections of macrolepidopteran larvae at sites where *C. samarensis* was reared in high numbers from exposed gypsy moth larvae did not give rise to any *C. samarensis* (M. Kenis and C. Lopez Vaamonde, unpublished data). Finally, to test the ability of *C.*

samarensis to develop in other hosts, artificial inoculations of *C. samarensis* maggots found by dissection of mature females were made on larvae of several macrolepidopteran species. This method was successful on the gypsy moth (Quednau 1993) while on the other hosts, the maggots usually penetrated into the larvae but failed to develop further (M. Kenis, unpublished data).

Ceranthia samarensis is presently reared in Canada to augment the number of females available for release (Quednau 1993) and field cage releases started in 1991 in Ontario (V. Nealis, personal communication).

Such investigations on parasitism in low density populations should not be restricted to western Europe. Similar studies could be done in other regions where the gypsy moth usually remains at endemic levels, particularly in Asia.

3. Introduction of New Biotypes of Natural Enemies already Established in North America. The identification and characterization of biotypes in biocontrol agents is essential in a biological control program. Biotypes of parasitoids or predators are known to differ in various traits (Ruberson et al 1989, Hopper et al. 1993), and variations in traits such as developmental responses, temperature tolerance, encapsulation resistance or host preference are likely to affect the efficiency of these natural enemies as biological control agents. It is thus very important to select the biotype which is better adapted than others to the target host in the target region.

Almost all natural enemies of the gypsy moth established in North America were introduced at the beginning of the century using strains from various parts of Europe and Asia. However, it is not known which strains became established, and if these strains represent the most efficient biotypes for the region of introduction. This could explain why several parasitoids are apparently less efficient in North America than in Europe. The tachinid *Parasetigena silvestris* (Robineau-Desvoidy) is a particularly good example. This univoltine, larval parasitoid is one of the most important natural enemies of the gypsy moth all over its geographic distribution. Several European strains were introduced into North America from 1910 on and the parasitoid was recovered only 17 years later. Since then, *P. silvestris* has become a major parasitoid of the gypsy moth in North America, but parasitism is usually lower than in most European regions. Even in Europe, there are important differences in parasitism by *P. silvestris* between regions. Of particular interest is the parasitism rate observed in the Rhine Valley in France and Germany, where collections made by Maier (1990) in the 1980's and by IIBC (M. Kenis, unpublished data) in the 1990's always provided parasitism rates by *P. silvestris* of over 60% (Table 2). In this region, outbreaks are usually of short duration and we believe that *P. silvestris* is the major and the most constant factor leading to the collapse of the outbreaks. Parasitism is usually lower in other European and Asian regions, although often higher than in North America. It is not clear why *P. silvestris* is particularly dominant in the Rhine Valley. The climate in this region might be particularly favorable for the tachinid, but it is rather similar to that of regions in France and Germany where parasitism rates are lower (Fuester et al. 1983, 1988). Other environmental factors might be more important. For instance, alternative hosts are perhaps more abundant. However, *P. silvestris* is univoltine, i.e. it does not need an alternate host to complete its cycle, and is rather monophagous. Besides the gypsy moth, the only other important host is the nun moth, *Lymantria monacha* (L.), a coniferous-feeding species which is not particularly abundant in the broadleaved forests of the Rhine Valley. The high occurrence of *P. silvestris* could also be explained by other factors, such as a low mortality due to hyperparasitoids, pathogens or predators, or good food supply for the adults, but these factors were not investigated. The possibility that the strain from the Rhine Valley represents a particularly efficient biotype is certainly worth investigating. Comparative studies could be made with different European and North American strains to determine, first, why some strains are apparently better than others, and, second, whether a European strain - that from the Rhine Valley or another region - could be more efficient in controlling North American gypsy moth populations than the introduced strain. Comparisons could be made on all traits capable of influencing the efficacy of a particular strain, i.e. fecundity, developmental responses, longevity, encapsulation resistance, host location, etc. Genetic markers could be used to determine which European biotype is established in North America and to allow the separation of the North American strain from a particular, more efficient European strain to be introduced into North America.

Table 2. Peak parasitism by *Parasetigena silvestris* observed in the Rhine Valley in France (F) and Germany (D)

Site	Year	% parasitism	
Offenburg (D)	1986	97	(Maier 1990)
Hirzfelden (F)	1992	96	(M. Kenis, unpublished data)
Mulhouse (F)	1993	63	"
Colmar (F)	1993	61	"
Offenburg (D)	1994	77	"
Bantzenheim (F)	1994	88	"
Hagenau (F)	1995	90	"

Biotypes should also be searched in the braconid *Cotesia melanoscelus* Ratzeburg, a bivoltine, solitary parasitoid which attacks first and second instars in the first generation and later instars in the second generation. It overwinters as a mature larva in a cocoon. Weseloh (1976) showed that the second generation is badly synchronized with its host because adults emerge too late, when the gypsy moth were 4th instars or larger and much less acceptable than earlier instars as hosts. The strain of *C. melanoscelus* established in North America comes from specimens collected in Sicily in 1911 (Hoy 1976). Weseloh (1976) suggests that fast developing strains could be found in other Eurasian regions and introduced into North America to improve host-parasitoid synchronization.

Conclusions

In 1989, outbreaks of the gypsy moth in seven northeastern U.S. States suddenly collapsed due to the fungal pathogen *Entomophaga maimaiga* Humber, Shimazu & Soper. In 1992, *E. maimaiga* epizootics covered most of the distribution range of the gypsy moth in North America (Hajek et al. 1993). This pathogen was first introduced from Japan to North America in 1910 and 1911 but was not recovered in the field until 1989. It is not yet clear whether the strain which recently decimated the gypsy moth populations comes from this early introduction, in which case its sudden virulence might have resulted from natural selection, or from a new, accidental introduction (Hajek et al. 1993). However, regardless of the origin of this introduction, this example shows that there is still potential for classical biological control of the gypsy moth in North America. The most promising direction appears to be a continuation of the introduction of the parasitoids *Blepharipa schineri* and *Ceranthia samarensis*, studies on egg predators, investigations of low density parasitoids in poorly studied regions, and investigation of the existence of more efficient biotypes of natural enemies already established in North America, particularly the parasitoids *Parasetigena silvestris* and *Cotesia melanoscelus*.

Acknowledgements

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Integrated Control of Species of Geometridae in Oak Forests of Romania

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ABSTRACT In this paper, we present results of experiments that were designed to evaluate biological and chemical approaches to control species of Geometridae in the oak forests of Romania. Our ultimate goal is to combine these tactics in an integrated system to manage this important group of defoliating insects.

SPECIES OF GEOMETRIDE, especially the winter moth, *Operophtera brumata* L., and *Erannis defoliaria* L., are present in most Romanian oak forests and frequently reach outbreak levels. Therefore, we are interested in developing an integrated approach to managing these pests that will be environmentally acceptable. A series of experiments were conducted on *Quercus petraea* and *Q. robur* forests that are typical of the hill region in northeast Romania. Heavy infestation of *O. brumata and E. defoliaria* occurred in this region in 1994.

Results and Discussion

Experiments with Foray 48B to control the winter moth. Studies were conducted in two sessile oak forests that contained a mixture of broad-leaves species (20-60 years old). Based on analysis of pupal and adult populations of *O. brumata*, we estimated that the population density was sufficient to cause 60-72% defoliation in that area. We applied Foray 48B at two doses (1.5 L/ha in 1.5 L/ water; 2.0 L/ha in 3.0 L/water) using an AN_2 aircraft equipped with micronaire nozzles (ULV application). Treatments were applied on April 25, 1994, when leaf expansion was optimal and under favorable meteorological conditions. We estimated that larval mortality was 90.8% in the low dose plot (1.5 L/ha) and 96% in the high dose plot (2.0 L/ha). Results are summarized in Table 1. As a result of these treatments, the outbreak never materialzed and minimal defoliation was recorded.

Ground application of microbial pesticides to control species of Geometridae. An experiment was conducted in a 20 year old oak stand that contained other broad-leaved species (hornbeam, ash) in the forest district Flaminzi in 1994. Although *O. brumata* and *E. defoliaria* were the species present in greatest abundance, *Tortrix viridana* and two other geometrids were also present. Projected defoliation in this area was 51%. Three dosages of a viral preparation from geometrid larvae, Virin-OB (I.P.B.P. Chisinau) and 6 doses of Dipel (Abbott Labs., USA) were applied on April 29-30, 1994. The results are summarized in Table 2. The level of control obtained with the Virin-OB preparation was comparable to that achieved with the bacterial preparations of Dipel 8L and Dipel ES.

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Table 1. Efficiency of aerial ULV treatments with the bacterial preparation Foray against the winter moth

Treatment	Area (ha)	Projected defoliation 1994 (%)	Mean efficiency (%)	Defoliation after treatment (%)	Probable defoliation 1995 (%)
1.5 L Foray + 1.5 L water	300	60.0	90.8	15-20	0
2.0 L Foray + 3.0 L water	110		95.8	10-15	0
2.0 L Foray + 3.0 L water	60	72.4	95.4	15-20	0

Table 2. Efficiency of ground applications of viral and bacterial preparations against Geometridae caterpillars in Forest district Flaminzi, forest Cosula, 1994

Treatment Variant (symbol. preparation.dose - l/ha. Polyhedron/ha)	Area treated (ha)	Mean efficiency (%)		Real defoliation after treatment (%)	Probable defoliation 1995 (%)
		O.b.	E.d.		
V_{11} - VIRIN - O.B. 6×10^{11} pol/ha + 100 l water	20	90.9	79.1	16	0
V_{12} - VIRIN - O.B. 9×10^{11} pol/ha + 100 l water	10	88.9	84.7	18	4 E.d.
V_{13} - VIRIN - O.B. 12×10^{11} pol/ha + 100 l water	20	86.6	88.2	16	8 C.p.
V_{21} - DIPEL - 8L - 1.0 l/ha + 100 l water	10	84.5	87.9	20	4 E.d. 23 C.p.
V_{22} - DIPEL - 8L - 1.5 l/ha + 100 l water	10	86.4	92.0	11	4 E.d. 3 E.m
V_{23} - DIPEL - 8L - 2.0 l/ha + 100 l water	10	90.3	91.9	8	0
V_{31} - DIPEL - ES - 1.0 l/ha + 100 l water	10	87.6	76.1	21	0
V_{32} - DIPEL - ES - 1.5 l/ha + 100 l water	10	81.4	84.7	15	0
V_{33} - DIPEL - ES - 2.0 l/ha + 100 l water	10	87.8	82.1	12	0
M - control (untreated)	20	-	-	50	2 O.b. 8 E.d. 4 C.p.

O.b. - *Operophtera brumata,* E.m. - *Erannis marginaria*
E.d. - *Erannis defoliaria,* C. p. - *Colotois pennaria*

Aerial application of a biodegradable pyrethroid, Sumi-Alpha, for control of geometrid species. In 1994, we evaluated an aerial application of a synthetic pyrethroid, Sumi-Alpha (Sumitomo, Japan) against species of Geometridae and *T. viridana* in a 45-60 year old *Q. petraea* forest in the hill region of Romania. The population of *O. brumata* was in the eruption phase and in the second instar at the time of application; meteorological conditions were optimal. The mean efficiency of the treatment was estimated to be 99.3% and the actual defoliation realized was 8-12% (Table 3). The populations of defoliator species were greatly reduced such that no defoliation was predicted in the treated area in 1995.

Table 3. Efficiency of aerial ULV with the biodegradable insecticide Sumi - Alpha against Geometrid caterpillars, Forest district Trusesti

Dose/L insecticide 1 ha	Area treated (ha)	Projected defoliation 1994 (%)	Mean efficiency (%)				Real defoliation after treatment (%)	Probable defoliation 1995 (%)		
			O.b.	E.d.	T.v.	X_{med}		T.v.	Geom	Total
21	700	55.5	99.7	99.6	98.5	99.3	8 - 12	0.3	0.0	0.3

T.v. - *Tortrix viridana* O.b. - *Operophtera brumata*
Geom. - Geometridae E.d. - *Erannis defoliaria*
Mixed oak forest (*Q. petraea*); larval populations in L_2-L_4 at time of application (April 22, 1994).

Evaluation of measures to stimulate the abundance of insectivorous birds. In addition to food, adequate shelter is an essential limiting factor for insectivorous birds, especially those species that nest in tree cavities (hollows). Frequently, silvicultural treatments reduce the number of trees with cavities and thus have a negative effect on insectivorous species. In this situation, it is imperative to introduce artificial nests in order to maintain optimal densities of birds, especially those that are insectivorous and sedentary (Rang and Ciornei 1991).

We conducted an experiment in a 40-80 year old oak forest in the forest district Trusesti whereby we introduced 2,000 artificial nest boxes at a density of 0.5-2.7/ha in three forests: one untreated, one treated with Sumi-Alpha, and one treated with Foray (Table 4). The data in Table 4 indicate the relationship between the dependency of occupancy of nest boxes and the abundance of defoliators on three observation dates – highest in the untreated plots and lowest in the plots with the highest treatment efficiency. In August, occupancy in the untreated plot was 69.3, 30.0 in the Sumi-Alpha plot, and 46.2 in the Foray-treated plot. Reduction in the defoliator complex as a result of the treatments caused the major nesting species (*Parus major, P. caeruleus, Passet montanus*) to abandon the artificial nests.

In the summer months, birds categorized as summer guests, in addition to *Muscicapa striata* and *Ficedula hypoleuca,* occupied the nests. Another competitor, the forest mouse, *Muscardinus avellanarius*, occupied the artificial nests, especially in the Sumi-alpha treated plot (70%).

Table 4. Comparative data regarding the occupancy of artificial nests by insectivorous birds in treated and untreated oak forests in Forest district Trusesti, 1994

Treatment/ Infestation before treatment/ Treatment efficiency	Date of nest installation	Occupying species	Number/ ex/ha before treatment 8-9.04. 1994	Percentage of occupancy (%) 8 - 9 04 1994	20 - 21 06 1994	12 - 13 08 1994
		Parrus sp.	0.68	29.0	11.8	23.1
		Passer montanus	-	14.0	11.8	15.4
		Muscicapa striata	-	-	17.6	15.4
Untreated	28.03-01.04. 1994	*Ficedula hypoleuca*	-	-	5.9	7.7
(Infestation: 25%		*Sitta europaea*	0.26	-	-	7.7
Geometridae)		**TOTAL BIRDS**	**7.07**	**43.0**	**47.1**	**69.3**
		(Muscardinus) Mice	-	-	41.2	30.7
		Empty nests	-	57.0	11.7	-
		Parrus sp.	1.44	38.7	-	10.0
Sumi-Alpha 2.0 l/hec		*Passer montanus*	0.08	12.9	12.5	20.0
		Muscicapa striata	-	-	8.4	-
(Infestation: 62% Geometridae)	28.03.1994	**TOTAL BIRDS**	**6.32**	**51.6**	**20.9**	**30.0**
		(Muscardinus) Mice	-	-	45.8	70.0
Treatment efficiency:		Wasps	-	-	8.3	-
99.3%		Empty nests	-	48.4	25.0	-
Foray -		*Parrus sp.*	1.50	16.0	14.3	23.1
1.5 - 2.0 l/hec		*Passer montanus*	-	28.0	14.2	-
(Infestation: 60% Geometridae +		*Muscicapa striata*	-	-	4.8	23.1
Tortrix viridana)	04.04.1994	*Sitta europaea*	0.30	-	4.8	-
		TOTAL BIRDS	**5.55**	**44.0**	**38.1**	**46.2**
Treatment		Mice	-	4.0	47.6	30.8
efficiency:		(Muscardinus)				7.7
90.8 - 95.8%		Bats	-	-	-	
		Empty nests	-	52.0	14.3	15.3

Actions to protect and encourage species of *Formica*. An inventory of ant colonies in *Q. petraea* and mixed oak stands from the forest district Trusesti (3,168.5 ha) demonstrates the significance of species of ants, *Formica rufa* and *F. polyctena* (Hymenoptera, Formicidae). Past research has shown that there is a direct correlation between the density of ant colonies and the occurrence of winter moth outbreaks (0.6-1.4 colonies/ha for infestations of 51-55%) (Table 5). The higher density of colonies is obviously related to the abundance of host larvae in the outbreak areas to the predaceous ants.

Table 5. The density of *Formica* colonies in oak forests infested by Geometridae, Forest district Trusesti, 1994

Location	Forest type	Age (years)	Area (ha)-	Infestation with defoliators spring 1994	Total number of colonies with normal sizes	Mean number colonies/ha
Iuresti	Mixed forest with *Q. petraea*	35-60	188.3	55.0	116	0.62
Constingeni	- " -	35-60	254.5	53.0	153	060
Mascateni	- " -	35-65	300.0	7.0	98	0.32
Blindesti	- " -	40-75	279.2	51.0	40	0.14
Soldanesti	Mixed forest with *Q. petraea* *Q. robur*	30-60	205.9	51.0	24	0.12
Vinatori	Mixed forest with *Q. petraea*	35-50	161.5	6.4	19	0.12
Saulea	- " -	35-100	441.0	25.0	33	0.07
Ionaseni stat	*Q. petraea* forest	30-80	405.8	59.0	102	0.25
Biznoasa	Mixed forest with *Q. petraea* *Q. robur*	25-45	107.2	50.0	146	1.36
Zlatunoaia	- " -	40-50	124.6	41.5	72	0.58
Fundatura	Mixed forest with *Q. petraea*	35-70	365.8	51.0	129	0.35
Dracsani	- " -	35-70	333.7	20.0	27	0.08
		TOTAL	3168.5	-	959	0.30

One major cause for the decline in the density of ant colonies is the past practice of pasturing animals in the forests. This also has a negative impact on game animals and birds because the understory habitat is destroyed. Therefore, in order to sustain an optimal density of 3-4 ant colonies/ha, which is required to maintain defoliator populations at low levels, it is necessary to protect ant colonies with various kinds of shields made of wood or wire netting. In order to reach this optimal level, we frequently transfer colonies from regions where the number is high to regions where the density has declined because of pasturing (Pascovici 1961).

The use of pheromones for monitoring populations of *O. brumata*. Between 1993-1994, we conducted studies in the forest districts of Trusesti and Flaminzi to evaluate the activity of the pheromone of *O. brumata* (3Z-6Z-9Z-1, 3, 6, 9-nonadecatetratraen) that was obtained from sources in Moldavia, Italy, and Germany. As a result of these studies, we confirmed that the pheromones were efficient in discovering adults at low densities, and in better understanding the influence of climatic factors (frost, snow) in the decrease of populations at very low densities (Figs. 1 and 2).

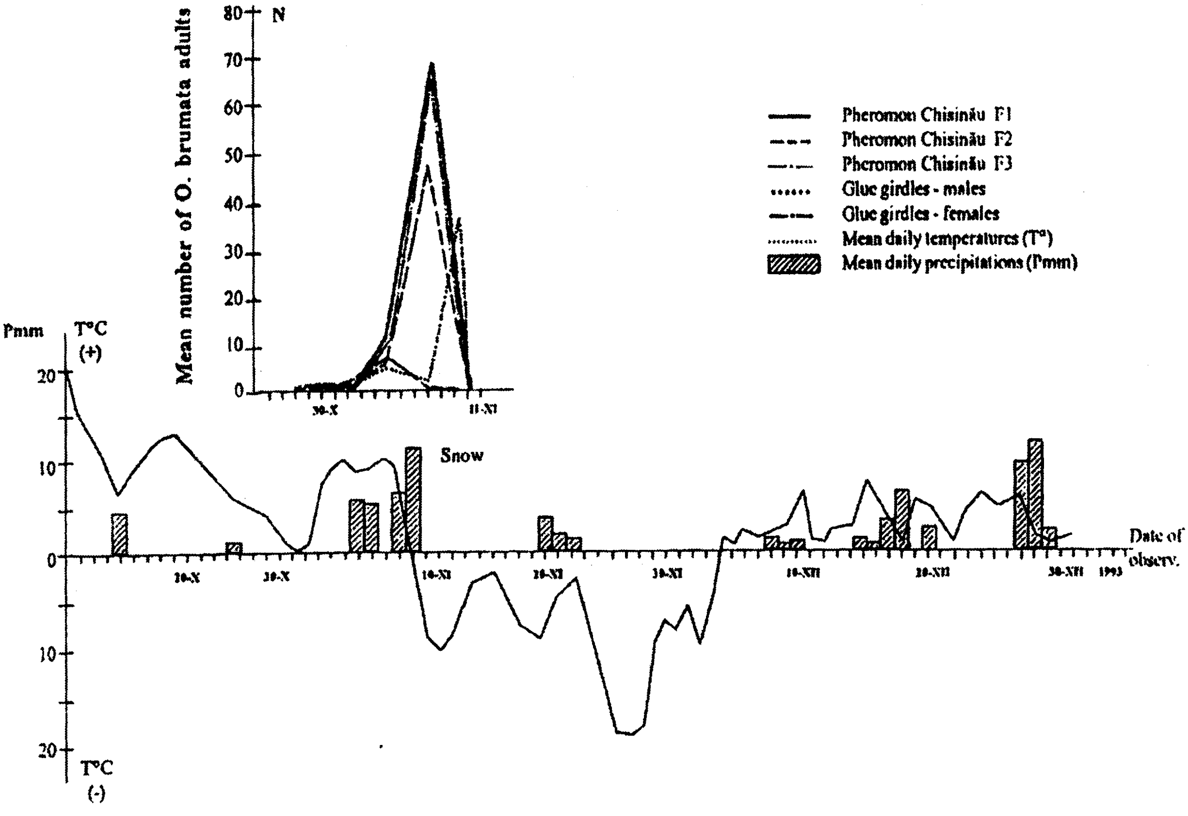

Figure 1. The flight dynamic of winter moth (O. brumata) registered by panel pheromonal traps and glue girdles correlated with the evolution of mean values of temperatures and precipitation (Forest district Trusesti, PU. III, m.u. 50A) – Meteo Station Rauseni.

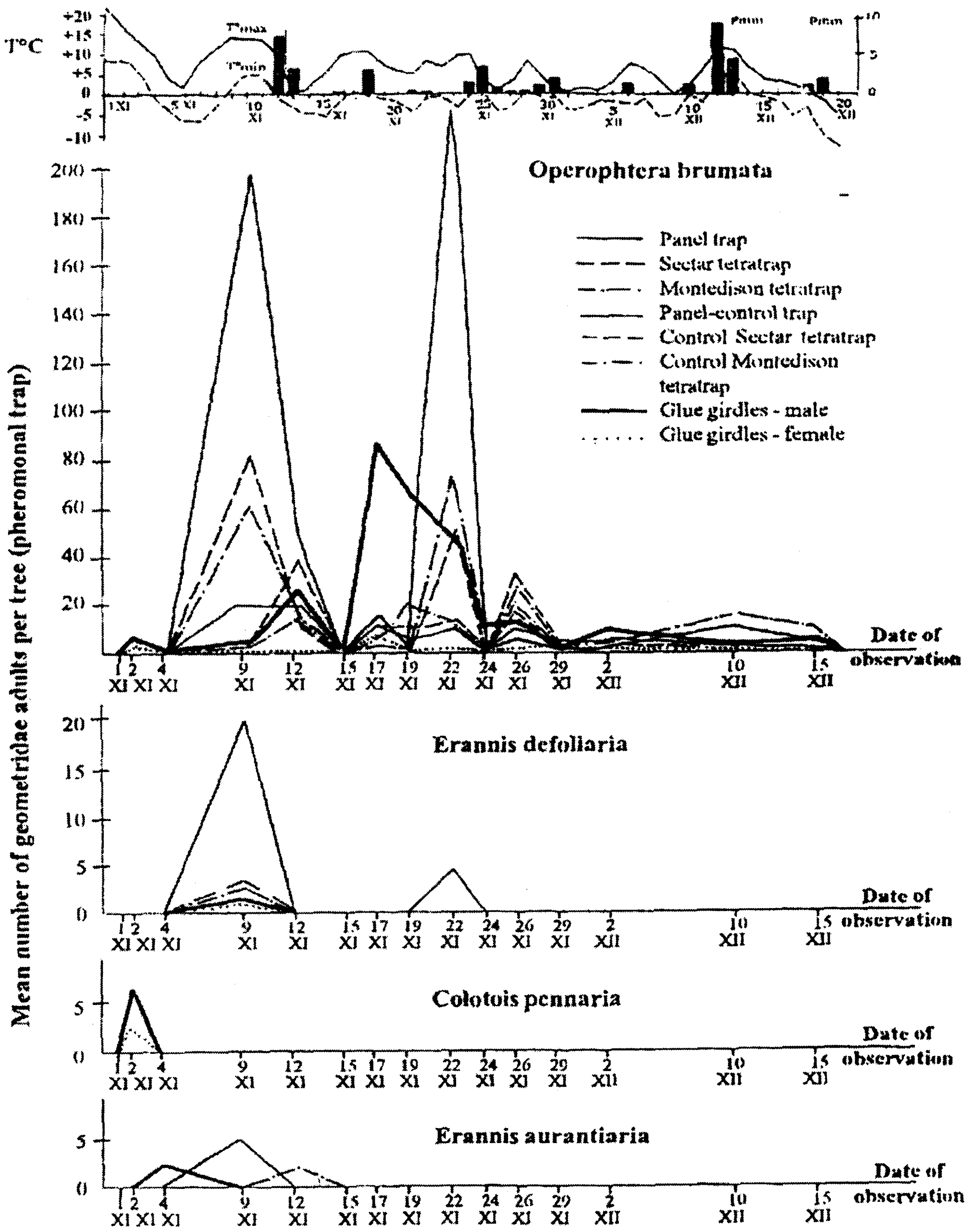

Figure 2. Flight dynamic of geometridae species using pheromonal trap and glue girdles correlated with the evolution of climatical factors (temperature; T°max T°min; precipitation – Pmm) Forest district Flaminzi – 1994.

Conclusions

The experiments that have been discussed are being integrated into a system for managing the geometrid defoliator complex in Romanian oak forests. The system has two basic components: preventive measures that apply to low-moderate density infestations, and suppressive measures that are deployed when populations are very dense and defoliation is predicted.

The preventive measures include introducing artificial nests (4-6/ha) for insectivorous birds to increase their effectiveness as predators of geometrid larvae, and protecting colonies of *Formica* in areas where pasturing is detrimental to their survival. If necessary, colonies are reintroduced from other regions in order to reach an optimum level per hectare. The use of pheromone traps for monitoring is critical to identifying areas where *O. brumata* populations are low but increasing.

When geometrid defoliator populations are high, we use aerial applications of microbial and biodegradable chemical pesticides necessary to reduce populations in the same year and prevent defoliation. We also have demonstrated the efficacy of applying ground applications of microbial pesticides such as Foray, Dipel, and Virin-OB to control geometrid populations. These methods are environmentally acceptable and fully compatible with the natural enemy complex (parasitoids, predators) that is necessary to maintain Geometrid defoliators at densities where they do not cause impacts to forest ecosystems.

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Shoot and Needle Losses in Scots Pine: Experimental Design and Techniques for Estimating Needle Biomass of Undamaged and Damaged Branches

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ABSTRACT The impact of needle and shoot losses in early and late season on growth and needle biomass of Scots pine (*Pinus sylvestris* L.) was studied in a field experiment in Central Sweden during 1991-1994. By clipping all but the current needles in June and all needles in August on 4-m trees, damage caused by the sawflies *Neodiprion sertifer* (Geoffr.) and *Diprion pini* (L.) was simulated. Parallel to that, all current shoots were clipped in early and late season to simulate shoot feeding by the common pine shoot beetle (*Tomicus piniperda* (L.)). The same treatments were applied to individual branches in whorls initiated in 1985, 1987, and 1989 of otherwise undamaged trees in the same stand. Bud formation and needle fall were recorded annually for the 300 study branches. The trees were felled in 1994, and data needed for calculations of needle weight and volume growth of stems and sample branches were recorded.

This paper describes the experimental design and techniques used to estimate the needle weights of undamaged and damaged branches at the start and end of the experiment. For most whorls, branch length explained more than 80 percent of the variation in needle biomass on undamaged sample branches. For treated branches, exponential functions were developed separately for each treatment and crown level, and these produced R^2s exceeding 0.50 in all but one case. These equations will be used to estimate needle biomass on damaged and undamaged branches at the start and end of the experiment.

KNOWLEDGE ABOUT THE impact of insect defoliation on tree growth is accumulating (for a review, see Kulman 1971, Alfaro 1991), but our understanding of the tree physiological processes involved is still far from complete, and few studies have addressed these questions (for references, see Piene and Percy 1984, Ericsson et al. 1985, Långström et al. 1990, Piene and Little 1990, Honkanen and Haukioja 1994). Understanding the links between pest population levels, the damage caused by their feeding, and the impact of the resulting defoliation on the trees, is crucial for determining proper countermeasures and forest protection strategies.

In Scandinavia, growth losses in Scots pine (*Pinus sylvestris* L.) are caused mainly by pine shoot beetles (*Tomicus piniperda* (L.) and *Tomicus minor* (Hart.); Col., Scolytidae) tunnelling the shoots or by sawfly larvae (mainly *Neodiprion sertifer* (Geoffr.) and *Diprion pini* (L.)) consuming the foliage. Shoot borers and defoliators are also found among certain groups of moths, e. g., the pine shoot moth (*Rhyacionia buoliana* (Shiff.)) and the pine looper (*Bupalus piniarius* (L.)), respectively (e. g., see Speight and Wainhouse 1989 and references therein, Eidmann and Klingström 1990). In addition, several fungal diseases cause needle

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Pages 230-246 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

losses, and on young pines, moose browsing may destroy many shoots (Eidmann and Klingström 1990).

The common pine shoot beetle (*T. piniperda*) and the lesser pine shoot beetle (*T. minor*) are bark beetles which reproduce in fresh pine timber. After oviposition, the parent beetles re-emerge from the logs in early summer and fly to pine crowns where they spend the summer tunnelling out young shoots. Later in the season when they emerge, the new generation also feeds in the shoots of living pines to become sexually mature (for details regarding the life cycle of these species, see Långström 1983). At high population densities, this shoot feeding by the beetles results in severe shoot losses followed by large growth reductions, as demonstrated in several studies (Långström and Hellqvist 1991, and references therein). Recently, *T. piniperda* has become established in North America causing damage mainly in Christmas tree plantations (Haack and Lawrence 1995).

Among the defoliators, *Neodiprion sertifer* (Geoffr.), commonly known as the European pine sawfly in Europe and North America, is the most important species on Scots pine in Scandinavia where it occasionally causes severe defoliation over vast areas (Lekander 1950, Christiansen 1970, Ehnström 1985, Juutinen and Varama 1986, Virtanen et al. 1996). By comparison, outbreaks of *Diprion pini* (L.) are less frequent and more local, but it too is a major defoliator of pine in Scandinavia (Lekander 1950, Kangas 1963, Ehnström et al. 1974, Austarå et al. 1983, Ehnström 1985). *N. sertifer* larvae feed in early season on old foliage and normally leave the developing foliage of the current year untouched. In contrast, *D. pini* larvae feed on pine needles in late season and during outbreaks they typically consume all foliage, including the current needles. Both species leave the buds intact, although some feeding on the bark of young shoots may occur, at least at high larval densities (for details on the biology of the two species, see Juutinen 1967 and Geri 1988).

It is generally agreed that stem growth losses due to needle and/or shoot losses are a result of reduced availability of photosynthates for growth in the defoliated tree. The resulting growth loss may vary considerably, depending not only on the amount of foliage lost, but also on a number of other factors (e. g., tree species, defoliation history, seasonal feeding patterns, and qualitative differences between needles eaten, such as their age class and crown position). Although little evidence is available, one can assume that factors such as stand age and site productivity may also influence defoliation effects on tree growth. Recently, Honkanen et al. (1994) proposed a unifying theory based on changing sink/source-relationships over the season that could explain the variable effects of foliage losses in different situations. However, these complex patterns of interaction are poorly understood, and little research is presently directed to this important but difficult field.

Natural episodes of defoliation seldom lend themselves to detailed impact studies, because undamaged controls for comparisons are often lacking and the full defoliation history is seldom available. As Alfaro and co-workers (1991, and references therein) have demonstrated, much useful information can be derived from stem analyses using potential growth for comparison. Controlled experiments are needed, however, if full data on foliage losses and their subsequent impacts on tree growth are to be collected, as exemplified by studies on balsam fir (Piene 1989) and Scots pine (Långström et al. 1990). The enormous amount of work involved, however, limits the number of study trees. The same applies to artificial damage studies where controlled damage levels are created by artificially removing the relevant crown elements (see Långström et al. 1990). Thus, the observation that trees have a modular structure where branches may function as more or less independent units offers the possibility of using branches as experimental units instead of whole trees (Sprugel et al. 1991, and references therein).

Project Objectives. The present study was designed to mimic the differential damage caused by shoot feeding and defoliation in early and late season, as caused by the three major pine pests mentioned above and summarized in Table 1. More specifically, we wanted to:

i) compare the impact of shoot pruning and defoliation in both early and late season on needle biomass recovery and stem growth in young Scots pines;

ii) compare the damage caused to individual branches with that of totally treated trees to ascertain if individual branches could be used to represent whole trees, and if so, which crown level was most appropriate; and

iii) measure annual needle fall to facilitate the modelling of needle dynamics on control and damaged trees (cf. Fleming and Piene 1992a,b).

Table 1. The damage patterns of the three herbivores included in this study and the treatments used to simulate their damage

Species	Feeding stage	Feeding time	Foliage Affected	Simulation Treatment	Treatment
Tomicus piniperda common pine shoot beetle	parent beetles after oviposition	June to Oct	current shoots and last year's foliage	clipping current buds and shoots in early June	EP Early Pruning
	callow adults after emergence	July to Oct	mostly current shoots	clipping current shoots in early August	LP Late Pruning
Neodiprion sertifer european pine sawfly	larvae feeding gregariously	May to July, mostly June	all foliage except the current needles	clipping all but the current needles in early June	ED Early Defoliation
Diprion pini "common pine sawfly"	larvae feeding gregariously	late July to September	all foliage	clipping all needles in early August	LD Late Defoliation

In this paper, we report on the general methodology used in the study, describe the techniques used to estimate the needle weight of undamaged and damaged branches from simple branch data, and discuss the problems involved in estimating the needle weights of branches with disturbed branch architecture.

Materials and Methods

Study Site The study was conducted at Ivantjärnsheden, Jädraås, in central Sweden, about 200 km northwest of Stockholm (61° N, 16° E, 185 m above sea level). The site was in a heath Scots pine forest, of dry dwarf shrub type, with a podzolic soil profile. For a detailed area description, see Axelsson and Bråkenhielm (1980).

Study Stand The site had been clearcut in 1971 and planted in 1972 with Scots pine seedlings of local provenance (2000 seedlings per hectare). In addition, naturally regenerated pine seedlings had developed in gaps following seedling mortality. The stand was cleaned in

1985 to ca 1500 stems per hectare, and by spring 1991, was a pure pine stand with some open patches.

Experimental Layout In 1991, *N. sertifer*, *D. pini* and *Tomicus* damage were simulated by removing all old foliage in early season, all foliage in late season, and all current shoots in both early and late season, respectively. This covered the major insect damage types causing foliage and growth losses to pine in Fennoscandia.

The study outline is based on the observation that single branches may react individually to treatments (e.g. Långström et al. 1990, Sprugel et al. 1991). By applying different damage treatments to individual branches within the same whorl (while leaving one branch as a control), the impact on branch development could be studied with less effort than the impact on whole trees. By comparing the branch development on trees with selected whorls that were artificially damaged to that of trees receiving a whole-tree treatment, the suitability of individual branches as substitutes for completely treated trees could be evaluated.

Thus, the experiment comprised the following treatments applied in 1991:

1) Control, i.e. no damage (hereafter referred to as the C-treatment);
2) Early defoliation of all needles (except the current ones developing in 1991) simulating *N. sertifer* damage (hereafter referred to as the ED-treatment);
3) Early pruning of all expanding current shoots simulating early *Tomicus* damage (hereafter referred to as the EP-treatment);
4) Late defoliation of all needles (including the current ones developing in 1991) simulating *pini* damage (hereafter referred to as the LD-treatment); and
5) Late pruning of all shoots grown out in 1991 simulating late *Tomicus* damage (hereafter referred to as the LP-treatment).

These five treatments were applied to two series of trees (Fig. 1). First, 10 trees were treated entirely with each one of the above treatments (whole-tree-treatment, hereafter referred to as the WTT series). Second, individual branches in whorls initiated in 1989, 1987 and 1985 on 10 trees were treated (branch-scale-treatment, hereafter referred to as the BST series). In the latter case, one randomly selected main branch per whorl received each one of the above treatments; the other branches on the tree were left intact.

Selection of Experimental Trees. On 21 May 1991, 75 similar looking, open-grown, experimental trees were selected in the study stand using the following criteria: DBH range of 40-60 mm (mean 52 mm ±6 mm SD), tree height 3-4 m (350 ±24 cm), "normal" height growth in 1988-90 (105 ±18 cm), 8-10 live whorls, at least 3 age classes of needles and no less than 4 main branches in the 1989, 1987 and 1985 whorls.

Of these trees, 13 trees (10 "ordinary" plus 3 "spare" trees) were randomly selected for the BST series from the 32 trees having five or more main branches in each of the 1989, 1987 and 1985 whorls. Within each of these whorls, treatments were randomly assigned to the main branches starting with the north-facing one and proceeding clockwise. Branches shorter than half the length of the well developed ones were not selected. Discarded branches on these whorls, and all other branches on these trees, were left untouched.

Of the remaining 62 trees, 50 were randomly allocated to the WTT series (10 trees per treatment) and measured for height and DBH. Another 10 trees were randomly selected for destructive needle biomass sampling.

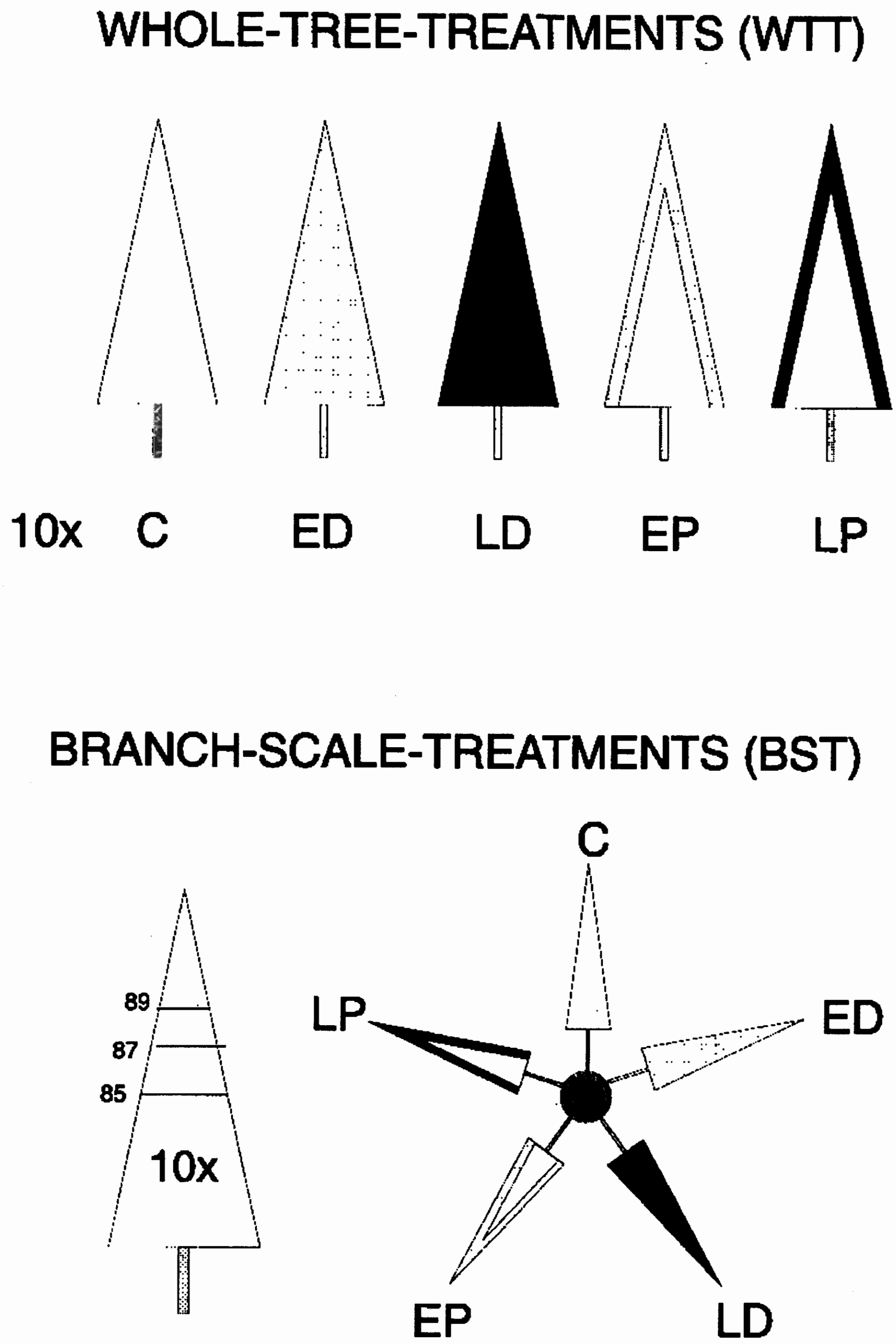

Figure 1. Schematic description of the experimental design. In the whole-tree-treatment: series, n=10 entire trees were each treated as follows: C=control; ED=early defoliation; EP=early pruning; LD=late defoliation; LP=late pruning. Individual branches in the 1989, 1987 and 1985 whorls of the 10 trees in the branch-scale-treatment series were correspondingly treated, with one main branch per whorl receiving one of the five treatments described above. The remaining branches on these trees were left unharmed.

Clipping and Pruning Starting on 2 June, all ED- and EP-trees in the whole-tree-treatment (WTT) series were pruned and/or clipped, respectively. During that week, all needles or currently expanding buds were removed in the upper crown (whorls 1990-1985) on the ED- and EP-trees, respectively. This included the needles/buds on the main stem. Needles were cut with scissors at the base of the needle pair leaving the base of the fascicle intact, and shoots were cut in the 1990 internode as close to the node as possible, i.e. within 1 cm of the bud base. The following week, all remaining needles or buds were cut in a second damage step.

The ED- and EP-branches in the branch-scale-treatment (BST) series were defoliated or clipped in a corresponding manner. During the first week, all needles or buds were taken in the outer half of the branches, i.e. from positions 1-2, 1-3 and 1-4 in the 1989, 1987 and 1985 whorls, respectively (cf. Fig. 2; see also Flower-Ellis et al. 1976, Långström 1980 for shoot labelling and branch architecture). All remaining needles or shoots were clipped in the next week.

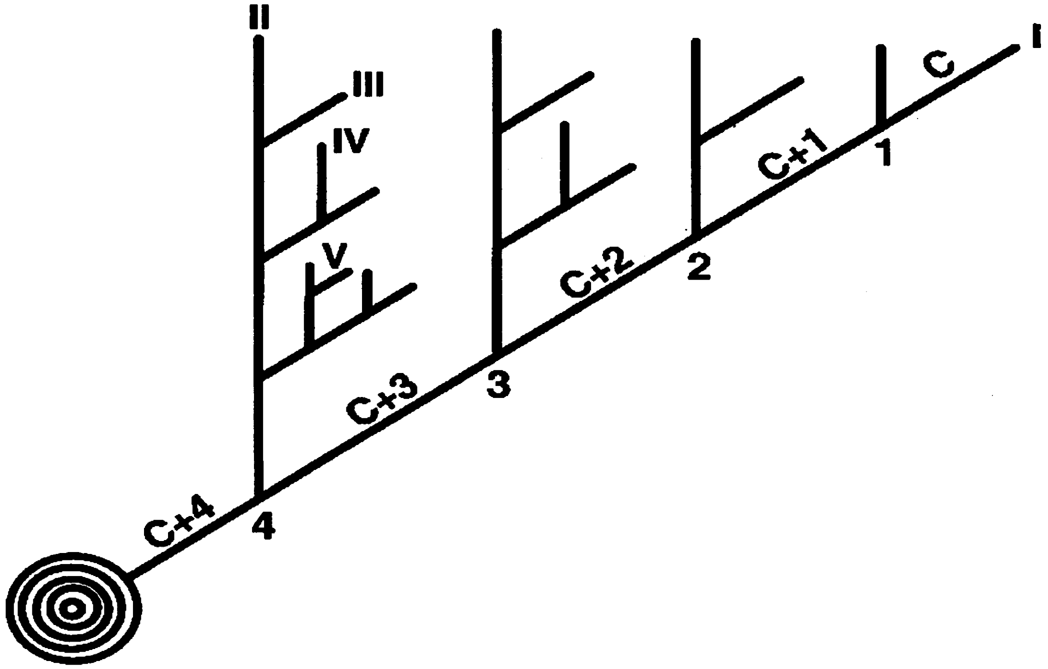

Figure 2. Schematic description of the branch architecture of a 5-yr-old Scots pine branch (Flower-Ellis et al, 1976; Långström, 1980). Roman numerals refer to the branch axis order: I=main axis or first-order branch, II=side branch or second-order branch axis, III, IV and V=third-, fourth- and fifth-order branch axes, respectively. Arabic numerals refer to the branch nodes, i.e. the forking positions on the branch axes according to the age of the side branch (measures of internodal distances equal annual shoot length increments). Shoot age is given as C for current year's growth, C+1 is last year's growth etc. The same labelling applies for needle age classes, but needles older than C+3 are rare in young Scots pine, since they normally drop after their fourth season.

The elongation of current shoots was intensive during the period of clipping and pruning, and was not completed by June 14th when the early season treatments were completed.

Similarly, starting on August 13th, the late season defoliation and/or pruning was done on the LD- and LP-branches, respectively, for both the BST and the WTT trees. Hence, needles and current shoots were cut in two steps in the late season treatments: upper crown or outer branch first, lower crown/inner branch second. At this time, shoot elongation and bud formation were completed, so the defoliation and pruning treatment included the current foliage. On August 30th, when the treatments were finished, the needle age class born in 1988 (i.e., the C+3 needles, Fig. 2), which was bound to fall that autumn, had started to turn yellow on some of the trees.

Sampling Branches for Initial Needle Weight To estimate the initial needle weight present before the treatments were applied, sample branches were taken for needle biomass estimates in late May. From the 10 trees randomly selected for this purpose, one branch in each whorl was sampled. Alternating between whorls and trees, small and large sample branches were taken in order to provide the size variation needed for computation of needle weight functions. This procedure was repeated on 19-20 August when a new branch from each tree and whorl was taken in order to estimate the needle biomass present between the 1991 needle flush and the expected needle fall in autumn. All sample branches were labelled and taken to the laboratory, and processed as explained below.

Needle Fall and Bud Mapping To estimate yearly changes in needle weights in different treatments, needle fall was estimated annually for each age class present on the study branches on the 1989, 1987 and 1985 whorls in both the BST and WTT series of trees. Altogether this was 300 branches. The technique developed by Piene (1989) was modified for Scots pine and a visual estimation of needle fall was conducted. This involved classifying needle fall as 0, 1-20, 21-40, 41-60, 61-80, 81-99 and 100 percent on selected side branches (i.e. second order branch axes) of each study branch.

Parallel with the annual needle fall estimates, we also mapped all developing buds on the 300 study branches. Beginning in spring 1991, the branch architecture of the study branches in the C-, ED- and LD-treatments of both tree series was delineated on branch maps showing the forking and the number of shoots. Each autumn, these maps and similar ones constructed for the pruning treatments in autumn 1991, were updated to include the current shoots, their buds, and notes on their health and appearance. More details on these techniques will be provided in a forthcoming paper on foliage dynamics (Piene et al. in prep.).

Tree and Branch Vitality In late September 1991, all study trees were checked for tree and branch mortality. In trees subjected to branch-scale-treatments (BST), only the experimental branches were checked. In the WTT series all branches were inspected. Dead branches were noted by whorl and marked depending on whether they had died in 1991 or were obviously dead in 1990 or earlier. Dead branches below the last green branch were ignored. We also measured the length of all branches that died in 1991 along the main axis to facilitate estimation of lost needle biomass.

In autumn 1992 and 1993, branches were distinguished according to whether they were dead, dying (no new needles, the remaining ones unhealthy and yellowish), weakened (no current buds, little but healthy foliage) or vital.

Harvesting Procedures Harvesting started on 15 August 1994, when annual growth and budsetting were completed, but before the oldest needle age class (1991) had dropped. The study branches of the 1985, 1987 and 1989 whorls were cut from the BST trees and taken to the laboratory for examination. First, all shoots and buds developed in 1994 were counted and added to the bud maps. Needle survival was then visually estimated as in previous years. Later, needle weights were determined and branches were sampled for volume estimates (see below).

The corresponding sample branches of the trees subjected to whole-tree-treatment (WTT) were treated as above. In addition, all branches in each whorl of the WTT trees were cut off and measured in the field for their annual growth in length. The current vitality status of each of these branches was then recorded as dead, dying, weakened or vital. With the exception of the control trees, one branch per whorl (and each of the entire 1985, 1987 and 1989 study whorls) was sampled for biomass determinations (see below). On whorls containing different size classes of branches, one sample branch was taken from each class.

After all branches were removed from the main stem, data for volume estimates were collected as described below. The leader needles were collected and taken to the laboratory and treated like other needle samples (see below). Field work was completed by 7 September.

Estimation of Initial and Final Needle Weights All branches collected in 1991 and 1994 for needle biomass determinations were treated as follows: First, all needle-bearing shoots (except those on the main axis) were cut and collected separately for each branch and needle age class. Then, the lengths of all internodes were measured along the main branch axes. Finally, the needles of the main axes were sorted by age class. All needle samples were dried for 24 h at 80°C, normally starting on the day of harvest. Then, the needles were separated from their shoot axes, re-dried and weighed to the nearest 0.01 g.

Using these data, relationships between branch length and needle biomass will be established for different whorls. Knowing the number of branches in each whorl and their length before shoot elongation in 1991, the total needle weight prior to treatment can be calculated for each tree in the WTT series as well as for the individual study branches in the branch-scale-treatment (BST) series. The final needle biomass present at harvest in 1994 will be reconstructed for the whole trees in a way analogous to that described above, but using the sample branches in 1994.

The reconstruction of needle weights by age class over time for the different treatments will be done by combining the initial and final needle weight estimates with the needle fall data. These procedures will be detailed in another context.

Stem and Branch Volume Estimation When all branches were removed from the main stem, the annual height growth of the stem was measured and discs were cut in the middle of each stem internode down to 1 m. Discs were also cut at DBH (i.e. 1.3 m), at 0.7 m and at the base of the stem (i.e. 0.1 m). During needle sampling discs were cut from each of the experimental branches in the 1989, 1987 and 1985 whorls of the two series of trees. These branch discs were cut in the middle of each internode along the main branch axis and at the base of the branch. All stem and branch discs were labelled, bagged and frozen immediately. All stem and branch discs were mailed to Canada by express mail, where they were kept frozen until they were analyzed.

Ring widths of the stem and branch discs were measured to the nearest 0.01 mm along two average diameters approximately perpendicular to each other. Branch and stem volumes were calculated for each year by sectioning using annual ring widths and internode lengths according to Smalian's formula. A cone was used to estimate top volume. Further details on these procedures are given in Piene et al. (in prep.).

Statistical Methods Statistical models were developed to estimate the dry weight of all needles on treated branches at the start (1991) and end (1994) of the experiment. For brevity, this description of model development is focused on the most complex set of these models, which deals with the damaged branches in 1994. The same general approach was used in developing models for undamaged branches in 1991 and 1994.

The first step in this approach was to search for appropriate models for damaged branches. In this search, scatterplots of the total needle dry weight (g) in 1994 were plotted against branch age, length and growth. These plots suggested that, depending on the treatment, total needle dry weight was sometimes linearly and sometimes logarithmically related to branch length. Because of these logarithmic relationships, and the fact that needle weight is necessarily positive, we fitted linear models in log (Y) where Y represents the dependent or response variable, total needle dry weight.

These logarithmically transformed regression models were not used to estimate Y directly, however, because they predict geometric means. The best predictors of needle dry weight on branches where this variable was not measured are the predicted arithmetic means which tend to be under-estimated by their geometric counterparts (Sokal and Rohlf 1981). (Even back-transformation with correction can produce bias if the untransformed variable is not lognormally distributed.)

The logarithmically transformed-regression models were used to provide initial parameter estimates for fitting nonlinear models of the form,

$$\mathrm{E}(Y) = \exp(b_0 + b_1X_1 + b_2X_2 + b_3X_3 + \ldots.). \tag{1}$$

Here $\mathrm{E}(Y)$ is the expected or predicted average value of Y, the total needle dry weight (g) on the branch. The b_i, $i \geq 0$, are parameters to be estimated, and the X_j, $j > 0$, are independent variables.

To reduce the potential problems associated with multicollinearity among independent variables, many of these variables were standardized (Devore 1982) by subtracting the sample average from each observed value and dividing the result by the sample standard deviation. These variables are listed in Table 2. In addition, pairs of remaining, highly correlated ($r > 0.95$), independent variables were eliminated by excluding one, usually the less recently changed, variable from the analysis. For instance, since the length of a branch at the end of the 1994 growing season (length94) was usually highly correlated with its 1993 length (length93), the latter variable was often omitted when fitting equation (1).

Technically, the process of fitting equation (1) was one of recursive model building using a pseudo Gauss-Newton algorithm for nonlinear least squares estimation (Ralston 1983). We removed parameters with estimates not significantly different from zero ($P < 0.05$) according to the partial F-test (Draper and Smith 1981) and refitted these reduced models. This procedure was continued until only parameters with statistically significant estimates remained. Residual distributions and residuals plotted against predictions were examined to verify that the regression assumptions were adequately satisfied.

Table 2. Standardized independent variables which describe branch characteristics. These variables were standardized by subtracting the sample mean from each observation and dividing the result by the sample standard deviation

Observed Variable	Unit of Measurement	Variable Name	Sample Size	Sample Mean	Sample Standard deviation	Sample Minimum	Sample Maximum
age	year	age	425	5.11	3.12	0	13
length in 1988	cm	length88	194	43.2	21.0	3	115
length in 1989	cm	length89	243	52.4	22.9	4	125
length in 1990	cm	length90	280	57.1	24.8	7	130
length in 1991	cm	length91	292	58.9	26.1	1	134
length in 1992	cm	length92	340	56.9	30.5	1	135
length in 1993	cm	length93	393	58.9	32.2	1	137
length in 1994	cm	length94	422	62.0	33.1	2	138
growth in 1989	cm	growth89	194	16.8	5.49	4	32
growth in 1990	cm	growth90	243	10.8	5.54	0	29
growth in 1991	cm	growth91	280	3.93	5.02	0	20
growth in 1992	cm	growth92	291	6.04	6.01	0	36
growth in 1993	cm	growth93	339	9.47	7.58	0	46
growth in 1994	cm	growth94	393	6.58	5.56	0	37

Results and Discussion

Needle Biomass of Undamaged Branches Using the sample branch data from 1991, needle biomass was regressed on branch length for each whorl as well as groups of whorls representing different crown fractions. Linear regressions explained much of the data for individual whorls or groups of whorls in the upper crown ($R^2 > 0.80$, data not shown), but were less successful in the lower part of the crown ($R^2 = 0.50 - 0.70$, data not shown). There was no difference in branch length - needle weight relationships between the two cohorts of branches taken in June and August, respectively. Hence, these cohorts were pooled. By using the experimental branches (harvested in 1994) from the 1989, 1987 and 1985 whorls of the whole-tree-treatment trees as tests, we found that the best fits occurred when using regressions derived for 3-whorl-groups in 1991 ($R^2 = 0.768$, data not shown). Thus, a satisfactory estimate of the needle biomass of any branch at the start of the experiment can be calculated.

Knowing the number of branches per whorl and their lengths, the needle biomass present on the experimental trees at the beginning of the experiment can thus be reconstructed. Similarly, these equations can also be used to calculate the needle biomass of the control trees at harvest in 1994. Thus, the estimation of the needle biomass of undamaged branches and trees is a straightforward procedure. We are currently investigating the possibility that these estimates could be further improved by fitting non-linear equations to the data (as was done for the damaged branches).

Needle Biomass of Damaged Branches Initial analyses of the data sets indicated that the equations developed for undamaged branches were not appropriate for estimating the needle weights of damaged ones. It also seemed prudent to develop different equations for each treatment.

In fitting equation (1) to the data for damaged branches, our goal was purely to derive models for estimating the 1994 needle biomass on those damaged branches which had not been sampled for this variable. At this stage, no attempt had been made to compare treatments directly in terms of their 1994 needle biomass. In fact, there are more appropriate formulations than equation (1) for making such comparisons. Nonetheless, fitting equation (1) does help to draw out trends in the data.

Figure 3, for instance, illustrates our attempt to fit equation (1) to all the data from the early pruning treatment. The result is a surface of predicted mean needle biomasses which depend on the age and length of the branch in 1994 (Fig. 3c). Because the fitted points (Fig. 3b) are drawn from this surface of predicted means, trends in the data are often clearer in the patterns of these fitted points than in the raw data (Fig. 3a). Thus, Figure 3b suggests that in the early pruning treatment, on average, needle biomass was greatest on branches of intermediate age. In addition, Figure 3b indicates that for branches of a given age, longer branches usually had greater needle biomass in this treatment.

While estimated surfaces (Fig. 3c) illustrate trends in the data, they can also be misleading. For instance, Figures 3a and b show that much of the fitted surface is extrapolated. In all treatments, the observations lie along a diagonal in the length94 x age plane: young branches are short, old branches are long. There are no old and short or young and long branches.

Parameter estimates corresponding to Figure 3 and associated statistics can be found at the top of Table 3. This table summarizes the parameter of equation (1) for estimating needle biomass on damaged branches in all treatments. The table is sectioned according to the ages of the branches being considered (age=0 represents branches initiated in 1994). The R^2 reported in the table is Kvalseth's (1985) recommended coefficient of determination. Because non-linear approximation methods were required to fit the models (Ralston 1983), the reported statistics should be viewed as asymptotic approximations (Gallant 1975).

Table 3 shows that equation (1) did not provide a good fit simultaneously to all data from the late defoliation treatment ($R^2 = 0.30$). One possible reason for this was that the independent variables common to all branches were limited to branch length in 1994 and branch age. This is because, by definition, branches initiated in 1994 can have no length measurements from previous years, and hence have only their age (0) and their 1994 length (or growth).

One possible solution to this difficulty was to fit equation (1) separately to branches of different ages. The last three sections of Table 3 summarize the fits using this approach. The age groupings listed (0, 1-5, and 6 and older) provided the best series of fits in terms of R^2 and SEE. There was no requirement that similar groupings apply to all treatments, so in this sense the results are noteworthy.

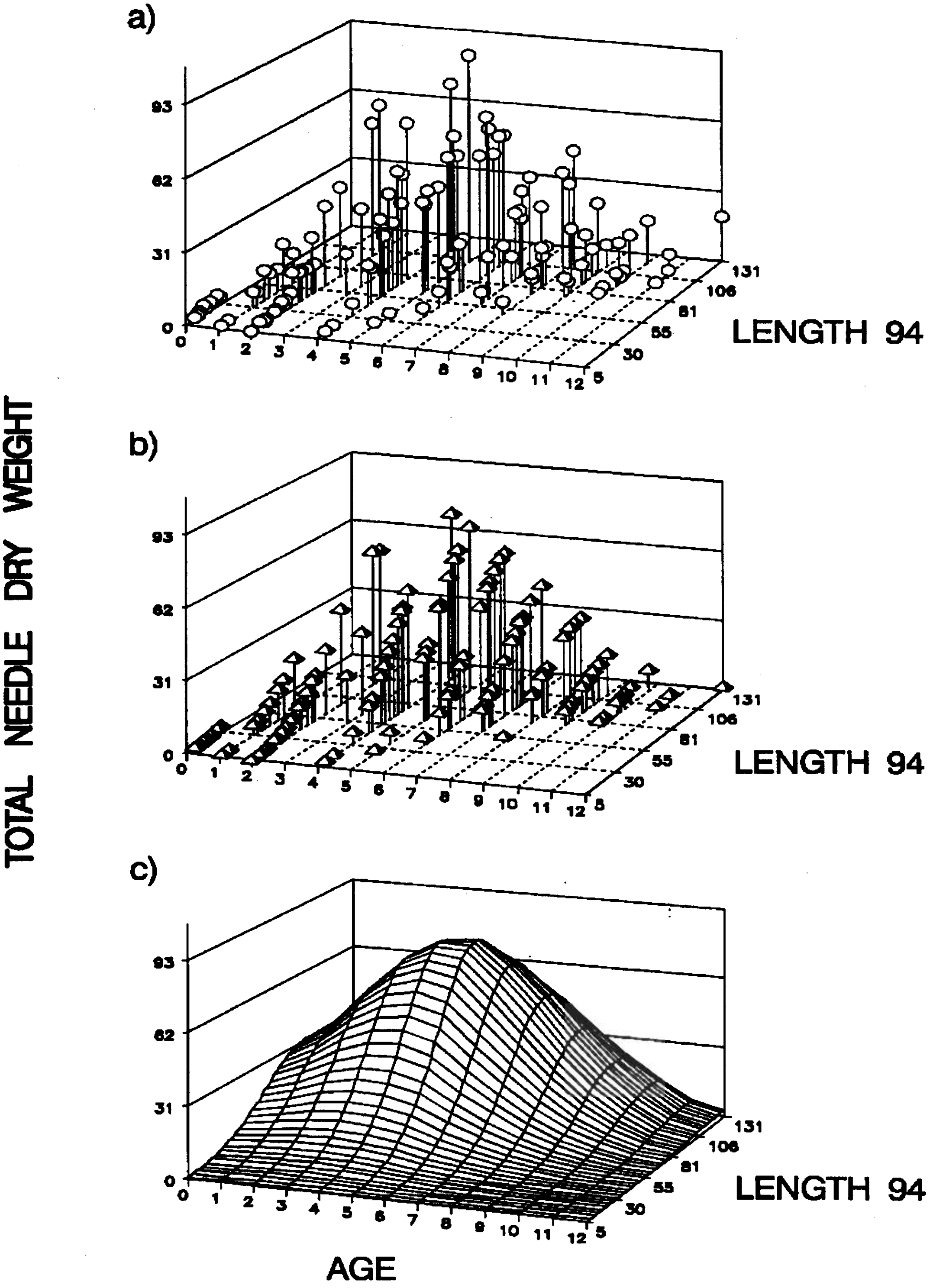

Figure 3. The relationship between total needle dry weight (g), branch length (cm), and branch age (years) in 1994 in the early pruning (EP) treatment: a) observations, b) corresponding model predictions, and c) the model's predictive surface.

Table 3. Fit statistics and parameter estimates (with standard errors, SE) for non-linear regressions of equation (1). The dependent variable is total needle dry weight (g), n is the sample size, and SEE is the standard error of the estimate. See text for further explanation

Treatment	Branch Ages	R^2	SEE	n	Independent Variables	Parameter Estimate	(SE)
early pruning	0-12	.88	7.35	128	intercept	3.27	(0.060)
					age	-0.79	(0.099)
					age^2	-0.61	(0.060)
					length94*age	0.31	(0.093)
					length94	1.51	(0.138)
					length94^2	-0.54	(0.087)
early defoliation	0-12	.70	9.03	100	intercept	-6.72	(0.982)
					age	-0.77	(0.098)
					age^2	-0.14	(0.071)
					ln(length94)	2.40	(0.227)
late defoliation	0-13	.30	8.22	42	intercept	-7.32	(3.207)
					age	-0.83	(0.281)
					ln(length94)	2.34	(0.749)
late pruning	0-11	.64	11.5	119	intercept	-2.36	(0.744)
					ln(age)	-0.48	(0.209)
					age^2	-0.27	(0.075)
					ln(length94)	1.56	(0.218)
early pruning	0	.54	0.90	10	intercept	-1.74	(1.087)
					ln(length94)	0.96	(0.348)
early defoliation	0	.79	0.81	10	intercept	-1.96	(0.715)
					ln(length94)	1.10	(0.240)
late defoliation	0	** insufficient data **					
late pruning	0	.90	0.47	8	intercept	5.26	(0.623)
					length94	3.18	(0.483)
early pruning	1-5	.95	5.42	65	intercept	-14.2	(2.73)
					age	-1.51	(0.418)
					ln(growth94*age)	1.44	(0.368)
					length94	-0.81	(0.272)
					ln(growth94)	-1.87	(0.448)
					ln(length94)	3.96	(0.648)
early defoliation	1-5	.85	6.70	48	intercept	-3.70	(0.716)
					growth94*age	0.90	(0.243)
					ln(growth94*age)	-0.57	(0.087)
					growth94	1.01	(0.197)
					ln(growth94)	2.18	(0.189)
late defoliation	1-5	.87	2.74	15	intercept	4.64	(0.692)
					ln(growth94*age)	-0.71	(0.230)
					length94	3.16	(0.546)
					length94^2	-12.6	(2.39)
					length93^2	12.6	(2.52)
late pruning	1-5	.89	4.76	60	intercept	13.0	(1.59)
					ln(age)	-5.55	(0.927)
					age^2	-3.46	(0.563)
					length94	0.98	(0.108)
					length94^2	-0.57	(0.117)

Table 3 cont'd

early pruning	6-12	.79	8.45	53	intercept	3.49	(0.179)
					growth94*age	1.39	(0.245)
					length94*age	-1.62	(0.315)
					length89*age	1.30	(0.329)
					length94	0.94	(0.175)
early defoliation	6-12	.72	8.81	42	intercept	-15.2	(2.74)
					age	-1.80	(0.303)
					ln(length94)	4.43	(0.649)
					growth90	-0.45	(0.153)
late defoliation	6-13	.56	7.68	26	intercept	-6.56	(2.067)
					ln(growth92)	4.90	(1.020)
					$growth92^2$	6.79	(2.389)
late pruning	6-11	.68	11.8	50	intercept	-7.28	(2.020)
					growth94*age	0.70	(0.148)
					length88*age	-0.40	(0.108)
					ln(length94)	2.62	(0.470)
					ln(growth93)	-0.54	(0.115)

Conclusions

Different statistical models were developed to estimate the dry weight of needles on branches subjected to various damage treatments. In some cases (e.g., early pruning) a single model provided a reasonable fit to all the data. In other cases (e.g., late defoliation) it was advantageous to develop different models for different groups of branch ages. The optimal grouping of branch ages (0, 1-5, and 6 years of age and older) was the same for all damage treatments. These models (Table 3) will be used to reconstruct the needle biomasses on damaged branches of experimental trees at the end of the experiment (i.e., in 1994). Corresponding models are in their final stages of development for reconstructing the needle biomasses of all (undamaged) branches at the start of the experiment (i.e., in 1991) and on the control trees at the end of the experiment.

The experimental design and techniques used to simulate damage caused by pine sawflies and pine shoot beetles will be discussed in detail in forthcoming papers. Here it may suffice to notice that shoot clipping produces similar growth effects as the beetle's feeding activity (Långström et al. 1990). Similarly, Lyytikäinen (1992) found no difference in larval performance when sawfly larvae were exposed to naturally and artificially defoliated trees. Thus, the defoliation and pruning treatments should fairly well represent the natural situations they are supposed to mimic. As this study was done on one site only, it is worth mentioning that another study using the same single-branch-concept was running parallel to this one during 1992-1996 in another site. Branches of Scots and lodgepole pine (*Pinus contorta* var. *latifolia)* were exposed to pruning, defoliation and both, and needle biomass and branch growth were followed over time. Thus, this second study will serve as a kind of replication in time and space to the present one.

Further exploration of the data collected includes preparation of a number of papers addressing the issues raised under the study objectives. One paper will ascertain if individual branches could be used to represent whole trees (Piene et al. in prep.); another will compare the performance of comparable branches of SBT- and WTT-trees (Långström et al. in prep.).

The main work will be to reconstruct and match needle biomass and stem growth dynamics in the different treatments. Finally, these processes will be modelled.

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Spruce Budworm Defoliation-Foliage Production: Differences Between White Spruce and Balsam Fir

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ABSTRACT Foliage production was compared between white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) following defoliation by the spruce budworm (*Choristoneura fumiferana* (Clem.)). After severe defoliation by spruce budworm, including bud destruction, both white spruce and balsam fir react with a prolific epicormic shoot production. When spruce budworm defoliation is low to moderate with no bud destruction, white spruce still react with a prolific shoot production, but no such shoot production occurs in balsam fir. The implications that this difference in shoot growth has on volume growth are discussed. Also, a hypothesis is presented which states that white spruce, balsam fir and the spruce budworm have, through evolution, developed individual adaptive strategies that ensure coexistence and future growth and survival.

MUCH ATTENTION HAS been given to the mechanisms of woody plant defenses against insect attacks (Mattson et al. 1988, Baranchikov et al. 1991). Insect feeding may reduce plant tissue quality which, in turn, may result in reduced insect performance either shortly after or in the years following the injury (induced resistance). In particular, this has been observed for deciduous species, and conifers may have a limited capacity for induced resistance (Neuvonen and Niemelä 1991). However, insect damage does not always induce resource decline (Haukioja et al. 1990). In fact, it may improve the food resource, for example, when it results in increased shoot production and foliage quality (Piene and Percy 1984, Piene 1989).

The objective of this report is to discuss shoot production in white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.) in relation to their growth performance following defoliation by the spruce budworm (*Choristoneura fumiferana* (Clem.). Furthermore, it presents the hypothesis that white spruce, balsam fir and spruce budworm have, through evolution, developed individual adaptive strategies that ensure coexistence and future growth and survival.

Bud Formation. In general, there are two foliation systems in conifers: (1) the normal development of lateral buds and buds originating from the terminal bud unit; and (2) epicormic or adventitious bud development, resulting from stress or changing tree conditions that could range from improved light conditions from silvicultural operations to severe insect attacks. Epicormic shoots originate from preformed suppressed buds that are formed in continuity with the apical meristem and show the presence of a vascular trace to the primary xylem. These buds are distinguished from adventitious buds which totally lack such a trace (for a discussion see Bryan and Lanner 1981).

In balsam fir, these developing buds are epicormic in origin (Stone 1953). In white spruce, they are also most likely of epicormic origin, as adventitious buds are relatively uncommon in conifers (Stone 1953, Brown 1971).

Pages 247-252 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Shoot Production - High Spruce Budworm Densities. Although white spruce is less susceptible to spruce budworm defoliation than balsam fir (Greenbank 1963, Thomas 1983), under extremely high spruce budworm densities, bud destruction will occur. White spruce compensate for this with prolific epicormic shoot production the following year. Under normal circumstances, with no further severe insect attacks, this ensures rapid tree recovery (Piene, unpublished data).

Similarly, balsam fir responds vigorously to bud destruction with prolific epicormic shoot production. Complete defoliation of all age classes of needles of balsam fir during a 2-year period, followed by yearly protection by insecticide spraying, showed that 3 years into the recovery period, the number of shoots per centimeter of branch length was significantly higher than on undefoliated trees (Piene 1989). As a result, foliage weight per tree was similar to that of undefoliated trees (Fig. 1), although there were only three needle age classes present for the defoliated trees as opposed to the normal eight for the undefoliated ones. This rapid foliage recovery continued and 5 years after the protection started, there was no significant difference in growth rates between defoliated and undefoliated trees (Piene 1989).

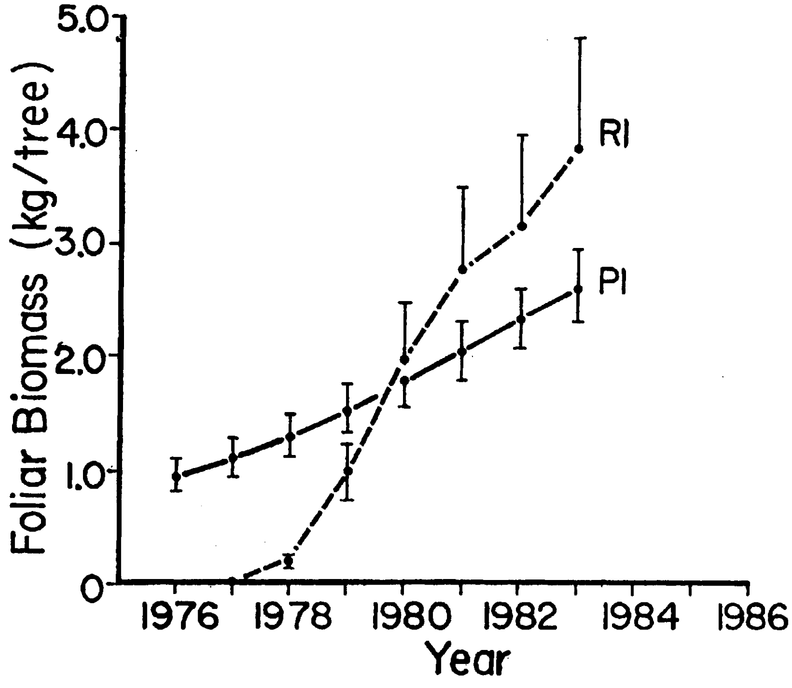

Figure 1. Changes in total foliar biomass per tree for undefoliated (P1, n=21) trees, and for trees (R1, n=16) that were completely defoliated of all age classes during 1976-77, and subsequently protected thereafter (adapted from Piene 1989). The vertical bars represent SE above and (or) below the means (p=0.05).

Based on the previous discussion, white spruce and balsam fir react similarly to severe defoliation by the spruce budworm that includes bud destruction, with prolific epicormic shoot production. Although these epicormic shoots appear mainly around the branch nodes for white spruce, they can appear anywhere along the branch for balsam fir (Piene, unpublished data).

Shoot Production - Low to Moderate Spruce Budworm Densities. When spruce budworm defoliation is relatively low and does not include bud destruction, the response to foliage loss differs dramatically between white spruce and balsam fir. White spruce does not require bud destruction to trigger the development of epicormic shoots and is extremely sensitive to losses of current-year needles. In fact, on undefoliated trees, each year there is some development of epicormic shoots (Piene, unpublished data), presumably due to changing environmental factors such as local light conditions. This extreme sensitivity to needle loss is demonstrated in an experiment where plantation white spruce were artificially defoliated. A loss of 50% of the current-year foliage resulted in an increase in shoot production of about 40%, primarily from the release of lateral buds (Piene, unpublished data). In contrast, balsam fir is not very sensitive to needle loss of current foliage when buds are not destroyed, and no significant amounts of epicormic shoots develop (Piene and Little 1990).

These differences in sensitivity to needle loss between white spruce and balsam fir when spruce budworm populations are relatively low with no bud destruction are demonstrated in Figure 2. Although a loss of about two age classes of needles during a 2-year period resulted in a growth reduction of about 20% for white spruce, the growth reduction for balsam fir was much more severe, amounting to about 50%. The white spruce compensated for the foliage loss by prolific epicormic shoot production in the second year of defoliation (Piene 1991), which reduced the growth loss in comparison to balsam fir where no such compensation occurred.

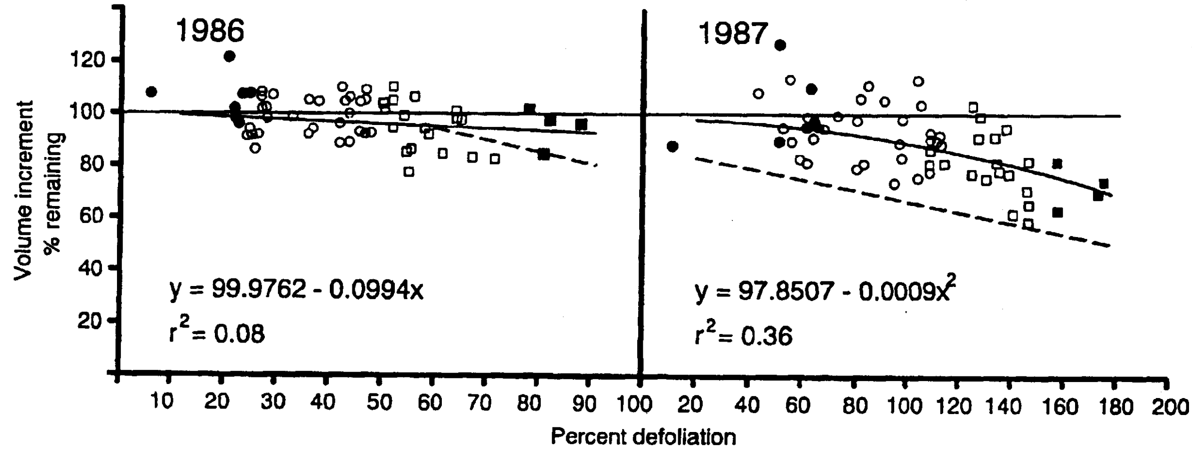

Figure 2. Relationships between percent volume increment remaining in 1986 and 1987 and percent defoliation of current-year foliage for plantation-grown white spruce. Different symbols indicate 25% classes of defoliation in 1986. Defoliation in 1987 is accumulated defoliation (defoliation in 1986 + 1987). The solid line at 100% indicates no change in volume increment. The other solid lines indicate the regression lines for white spruce, while the broken lines show the relationships for balsam fir (from Piene 1991).

Conclusion

In eastern North America, spruce in mixture with balsam fir covers large tracts of forest land, with white spruce as the most common spruce species (Gordon 1985). Periodically, the spruce budworm has severely damaged this forest, and outbreaks have been documented to have occurred since the early 1700s (Royama 1984). White spruce and balsam fir have probably been in coexistence with spruce budworm for thousands of years.

I hypothesize that white spruce, balsam fir and the spruce budworm have, through evolution, each developed individual strategies to ensure coexistence and survival. Regardless of strategy, replacing foliage lost due to defoliation is of the highest priority for a tree for future survival (Ericsson et al. 1980). During especially severe spruce budworm outbreaks, both white spruce and balsam fir experience bud destruction and, as discussed previously, both species respond with a prolific epicormic shoot production that compensates for the previous year's foliage loss. Bud destruction is also common in balsam fir, with subsequent release of epicormic buds, when spruce budworm populations are at more normal levels (Piene, unpublished). However, I contend that, for white spruce, bud destruction is relatively uncommon. Therefore, to replace lost foliage, white spruce has developed the ability to release epicormic buds even in response to small losses of current-year foliage, thus maintaining or perhaps even increasing the foliage complement (Piene, unpublished).

The spruce budworm, on the other hand, may benefit from increased nutrient levels in the needles of the epicormic shoots (Piene and Percy 1984), thus maintaining vigorous population levels (Royama 1992). As the spruce budworm outbreak continues, white spruce, balsam fir and the spruce budworm are, in a sense, benefiting from each other's existence. However, as defoliation continues, balsam fir and white spruce become weakened. This is probably due to a low shoot production, thus decreasing the amount of "food" available to the tree, in combination with a decrease in nutrient uptake caused by rootlet mortality (Redmond 1959). Eventually, the amount of "food" produced is so low that it cannot meet the requirement for tree maintenance, and the tree dies. This is particularly true for balsam fir, which is more vulnerable than white spruce (Blais 1981).

This difference is probably due to a combination of differences in foliage production and to feeding rates on older foliage. While backfeeding on older age classes is common on balsam fir, it is rarer on white spruce because the older age class foliage is almost unpalatable to the spruce budworm (Thomas 1983).

After about 6 to 10 years, the spruce budworm declines to endemic levels (Royama, pers. comm.). However, due to the difference in vulnerability between white spruce and balsam fir, a much larger percentage of the seed-bearing balsam fir than white spruce has been killed by the spruce budworm. Although balsam fir has much better seedling establishment characteristics than white spruce, the longer lived white spruce present a continued seed source that ensures a mixture of white spruce and balsam fir in the new regenerating stand.

Therefore, the spruce budworm is also an essential factor in maintaining the white spruce in the future stand (Gordon 1985). Thus, the white spruce-balsam fir ecosystem is maintained, and presents a readily available food source for the next spruce budworm outbreak.

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The Role of Parasitoids in the Population Dynamics of Forest Lepidoptera

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ABSTRACT Using new methods of time series analysis, I show that population fluctuations of three forest caterpillar species seem to be strongly influenced, if not dominated, by interactions with insect parasitoids, and conclude that parasitoids may play a more significant role in the dynamics of forest Lepidoptera than is generally recognized.

SOME FOREST LEPIDOPTERA exhibit remarkable variations in abundance, sometimes going through 10,000-fold changes in density during population increases and decreases, (e.g., the larch budmoth, *Zeiraphera diniana*) (Baltensweiler et al. 1977, Berryman 1996). Many other forest caterpillars fluctuate with much less variability, remaining at sparse densities for indefinite periods of time.

Foliage-feeding Lepidoptera are known to be attacked by numerous insect parasitoids in the families Ichneumonidae, Braconidae, Eulophidae and Chalcidae (Hymenoptera) as well as Tachinidae and Sarcophagidae (Diptera). The larch budmoth, for example, is attacked by 94 species of parasitoids (Baltensweiler et al. 1977). The question I wish to address in this paper is: what role do parasitoids play in the fluctuations, or lack thereof, of forest caterpillar populations? I will approach this question by reference to studies on three forest defoliators.

CASE 1: The blackheaded budworm, *Acleris variana* (Tortricidae). Morris (1959) analyzed 11 years of data on the density of blackheaded budworm caterpillars and their larval parasitoids (Fig. 1), and concluded that the key factor in the population dynamics of this insect was a suite of larval parasitoids. Although key factor analysis has been discredited recently (Royama 1996), and although McNamee (1979) has proposed an alternative hypothesis for blackheaded budworm dynamics, I was forced to agree with Morris (Berryman 1986, 1991a). My conclusions are based on a reanalysis of the budworm-parasitoid data using some new methods of time series analysis (Royama 1977, 1992, Berryman 1991a, 1992, 1994, Berryman and Millstein 1994, Turchin 1990).

Time series analysis of population counts over a number of years looks for correlations between the rate of increase of the average individual, $R = \ln N_t - \ln N_{t-1}$, and population density N_{t-d}. In other words, we perform a simple regression on the model

$$R = a + bN_{t-d} \qquad (1)$$

where d is the dominant lag in the density dependent feedback response (Berryman 1992), or on the multiple regression on the model

Pages 253-260 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.

$$R = a + b_1 N_{t-1} + b_2 N_{t-2} + \dots\dots\dots b_d N_{t-d} \tag{2}$$

where d is now the maximum dimension of the feedback structure (Turchin 1990) and densities may be transformed into logarithms (Royama 1977, 1992). The dimension is rarely greater than 2 in biological data.

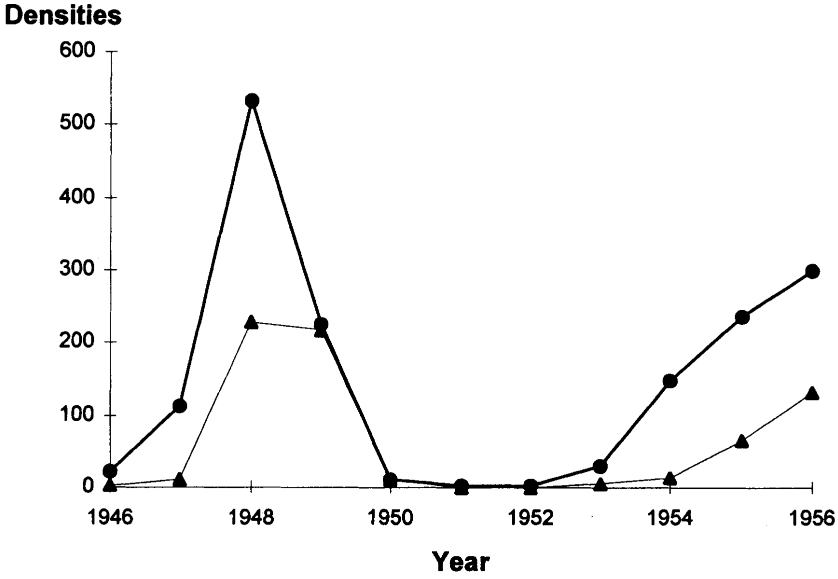

Figure 1. Numbers of blackheaded budworm larvae per 100 m^2 of balsam fir foliage; ● = total larvae, ▲ = parasitized larvae (after Morris 1959).

In the case of the blackheaded budworm, the dynamics are strongly affected by "second order" feedback (d=2), or delayed density dependence (Turchin 1990, Berryman 1986, 1991a, 1992, Berryman and Millstein 1994). What this means is that the survival and/or reproduction of the budworm in one year is dependent on larval density in the previous year. To obtain such an effect, one needs to have a negative feedback mechanism that operates with a delay of the same relative time scale as the budworm. There seem to be two plausible explanations for this second order feedback effect:

1. *A foliage effect.* Second order feedback can be created if the quality of foliage is affected by defoliation in the previous year (the "delayed induced defense" hypothesis [Haukioja et al. 1988, Baltensweiler and Fischlin 1988]) or if high caterpillar densities and/or food shortages in one year affect the survival and/or fecundity of the next generation via physiological (the "maternal effect" hypothesis [Rossiter 1994, Ginzburg and Taneyhill 1994]) or genetical (the "genetic polymorphism" hypothesis [Chitty 1967]) mechanisms. However, blackheaded budworm populations decline before the host plant (balsam fir) is seriously defoliated and food shortage becomes an important limiting factor (Morris 1959, Miller 1966). Hence, it seems unlikely that the second order feedback is due to foliage effects.
2. *A parasitoid effect.* Many parasitoids, especially those which are relatively specific, have generation spans similar to those of their lepidopteran hosts. This, together with the fact that parasitoids often exhibit strong numerical responses to host density, can give rise to delayed

negative feedback. The numerical response of parasitoids can be measured by fitting the equation (Berryman 1991a, 1994)

$$R_p = \ln P_t - \ln P_{t-1} = A_p - C_p \frac{P_{t-1}}{N_{t-1}} \qquad (3)$$

to time series data, where R_p is the realized per-capita rate of change of the parasitoid population from one generation to the next, P_t is the density of the parasitoid population, N_t is the density of the host population, A_p is the maximum rate of change of the parasitoid when host density is infinitely large, and C_p is the impact of the parasitoid on its host. Fitting this model to data on the density of budworms and larval parasitoids explains 91% of the variation in R_p, demonstrating that the parasitoids have a very strong numerical response.

We can also estimate the effect of the parasitoid on the rate of change of the budworm by fitting the equation (Berryman 1992, 1994)

$$R_n = \ln N_t - \ln N_{t-1} = A_n - B_n N_{t-1} - C_n \frac{P_{t-1}}{N_{t-1}} \qquad (4)$$

in which the parameters A_n and C_n have similar meaning as for the parasitoids and B_n reflects the effects of first order feedback due to competition for food, functional responses of predators, and so on. Equation (4) explains 85% of the budworm population changes and, of this, 76% is explained by parasitism alone (partial correlation 82%). Equations (3) and (4) can now be used together to simulate budworm-parasitoid dynamics, and we see that the model predicts the 6-8 year cycles of abundance seen in the data (Fig. 2). These results, together with the analyses of Morris (1959), Berryman (1986, 1991a, 1992) and Turchin (1990), strongly suggest that parasitoids are largely responsible for density fluctuations in budworm populations.

CASE 2: The spruce needleminer, *Epinotia tedella* (Tortricidae). Munster-Swendsen (1991) analyzed 20 years of data on the spruce needleminer inhabiting a Danish spruce plantation (Fig. 3), and used these data to construct a detailed simulation model of the interactions between needleminer, host-tree, parasitoids, predators, diseases and weather (Munster-Swendsen 1985). This model faithfully recreated the dynamics observed in this and other plantations. By deleting variables from his model, Munster-Swendsen found that parasitoids were the major factors regulating populations of this needleminer. This conclusion is further supported by the fact that strong second order effects are observed in spruce needleminer data, and parasitoids have a strong numerical response, with equation (3) explaining 81% of the variation in parasitoid rates of change (Berryman and Munster-Swendsen 1994).

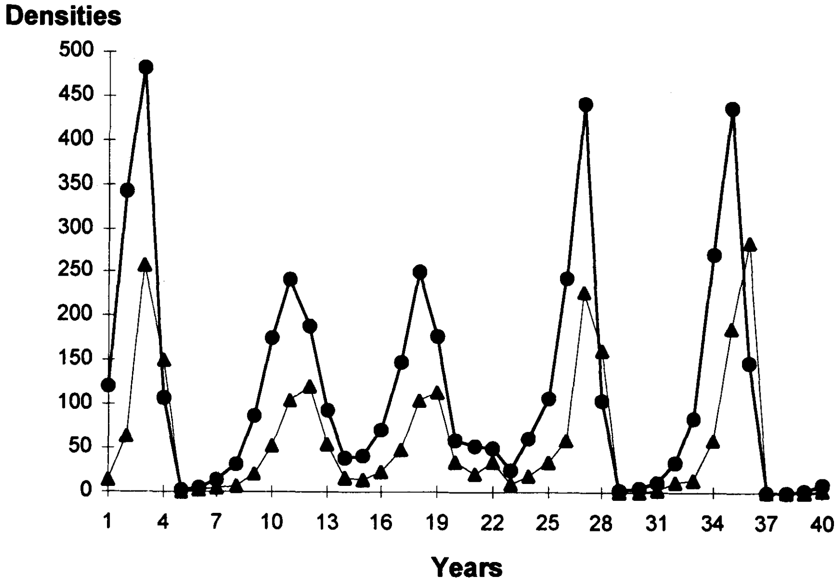

Figure 2. Simulation with the two species model [equations (3) and (4)] with parameters estimated from the data in figure 1: ● = total larvae, ▲ = parasitized larvae $A_p = 2.442, C_p = 5.535, A_n = 2.152, B_n = 0.003, C_n = 4.131,$ with some random variability added to the computed R-values (after Berryman 1991a).

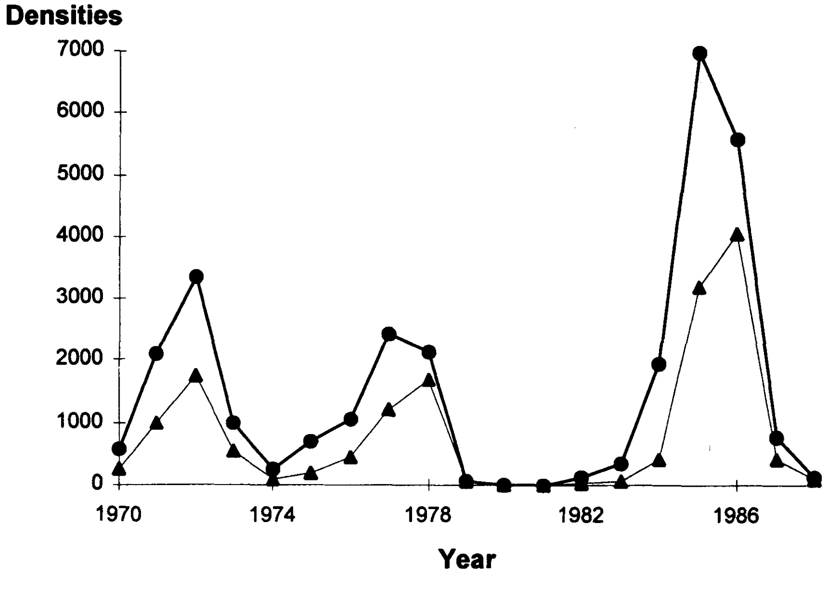

Figure 3. Numbers of spruce needleminer and parasitoid larvae per 10 m^2 of spruce foliage [from Munster-Swendsen (1991) and personal communication]. ● = total larvae, ▲ = parasitized larvae

Like the blackheaded budworm, spruce needleminers rarely cause severe defoliation to their host trees. Parasitoid density also has a strong negative effect on needleminer rates of change, explaining 76% of the variation. Simulation experiments show that models using fits to equations (3) and (4) also recreate the 9-10 year oscillations seen in needleminer populations.

One of the interesting things that emerged from needleminer population studies was the phenomenon called pseudoparasitism (Munster-Swendsen 1994). Munster-Swendsen found that "reduction in fecundity" was a key factor in needleminer population fluctuations, and that direct mortality caused by parasitoids was insufficient to explain the decline of needleminer populations. This lead him to discover that parasitoids often sting, but fail to oviposit in their hosts, particularly when parasitoid densities were high (possibly due to interference between parasitoids). Needleminers which were pseudoparasitized developed to adults but were infertile (Brown and Kainoh 1992), thereby explaining, simultaneously, the "reduction in fecundity" effect and the strong suppressive effect of parasitoids. These results may cause us to reconsider the role that parasitoids play in the population dynamics of other forest defoliators.

CASE 3: The gypsy moth, *Lymantria dispar* (Lymantriidae). Sisojevic (1979) collected 26 years of data on the density of gypsy moths and their tachinid parasitoids in the former Yugoslavia (Fig. 4). The data show a strong second order effect (Montgomery and Wallner 1988, Turchin 1990, Berryman 1991b), but in this case defoliation of the host plant sometimes occurs. However, experimental supplementation of gypsy moth populations during the low density phase prevented defoliation, suggesting that some other factor, probably parasitoids, was able to respond and suppress the prey population before defoliation could occur (Maksimovic et al. 1970).

On the other hand, the gypsy moth dynamics are not quite so simple. Berryman (1991b) found that second order effects dominated the time series for the first 16 years but first order feedback became prevalent in the final 10 years. In addition, multivoltine generalist parasitoids were observed to be more common during this time, while univoltine specialists were most abundant during the first period (Fig. 4). This suggests that the dynamics of gypsy moth populations in southern Europe are largely determined by the relative dominance of tachinid generalists, which generate first order dynamics, and tachinid specialists which generate second order dynamics.

Berryman (1991b) also found strong second order effects in the North American gypsy moth time series following its collapse from very high densities, and concluded that gypsy moth populations had been controlled by introduced parasitoids, an idea that has generated some controversy (Liebhold and Elkinton 1991, Berryman 1991c). However, stocking experiments by Gould et al. (1990) strongly suggest that generalist tachinid parasitoids can suppress incipient gypsy moth outbreaks by rapid (first order) spatial density dependent responses. These results suggest that North American gypsy moth populations are being regulated by similar mechanisms as those in Europe.

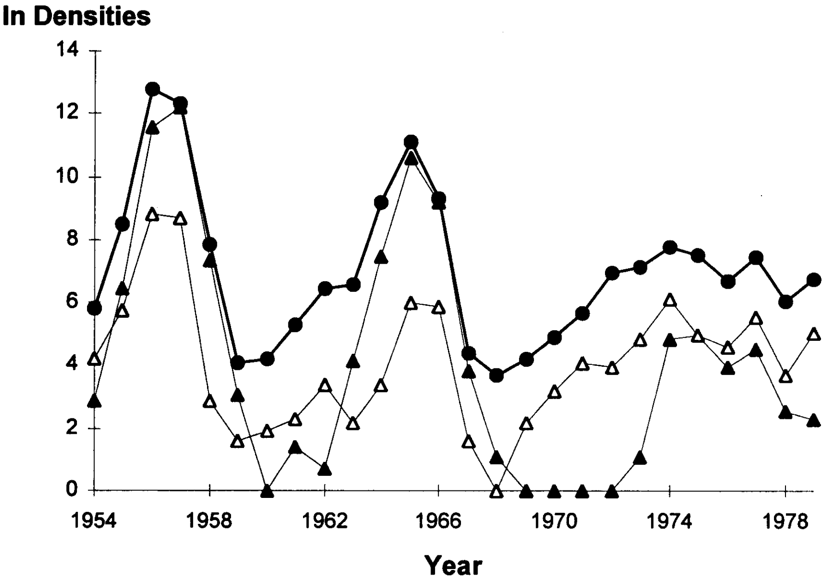

Figure 4. Numbers of gypsy moth egg masses per ha (●) and percentage parasitism by specific (▲) and general (Δ) tachinid parasitoids (after Sisojevic 1979).

Conclusions

I have discussed three cases where parasitoids seem to be a major force in the observed population fluctuations of foliage-feeding forest Lepidoptera. If time had permitted I could have included other examples and cited cases of successful biological control of forest caterpillars by parasitoids to support this contention (see, Berryman 1996). My general conclusion is that parasitoids frequently play a more significant role in the dynamics of forest Lepidoptera than they are sometimes given credit for. Of particular importance is the recent discovery of pseudoparasitism (Brown and Kainoh 1992, Munster-Swendsen 1994) which suggests that the effect of parasites on the dynamics of their hosts may be greater than is generally believed (particularly in Tortricids), and may also explain the reduction in fecundity often observed during the decline of caterpillar outbreaks. This should not be taken to mean that I believe other factors (e.g., food quantity/quality and virus epizootics) are not important in specific cases or at certain times in the examples cited above. Parasitoids, however, seem to be a more consistent and persistent force in the dynamics of many defoliator populations, regardless of the other forces that may be involved.

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Effects of Silvicultural Management on Gypsy Moth Dynamics and Impact: An Eight-Year Study

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ABSTRACT A long-term study initiated in 1989 at the West Virginia University Forest contrasted the effects of silvicultural treatments on the development of gypsy moth (*Lymantria dispar* L.) outbreaks and their impacts. The area is a relatively susceptible *Quercus* spp./mixed hardwood forest. Egg mass densities, survivorship, and mortality from natural enemies differed little between stands that were treated silviculturally and those that were not. However, stands that were thinned had less overstory mortality than unthinned stands despite incurring comparable levels of defoliation.

THE GYPSY MOTH (*Lymantria dispar* L.) is a polyphagous insect first introduced into North America in the late 1860s. Since that time, its range has expanded steadily from the northeastern United States to large areas of commercial forests in the Appalachian Mountains. Outbreaks are likely to be intense and substantially affect forest resources in those areas. While it is possible to reduce defoliation levels by applying pesticides aerially, other approaches to managing gypsy moth are needed because of the expense and ecological impact of pesticides on the environment. Several silvicultural approaches to managing gypsy moth populations have been proposed over the last 100 years (Fiske 1913, Clement and Munro 1917, Behre 1939, Bess et al. 1947, Gottschalk 1993). All have emphasized the use of sanitation thinning to reduce or eliminate host species preferred by the gypsy moth. Theoretically, this technique would lower stand susceptibility (defoliation potential). Gottschalk (1993) also proposed the use of presalvage thinning to remove low-vigor host trees to reduce stand vulnerability (likelihood of mortality following defoliation).

Of the relatively few studies that have examined the effectiveness of silvicultural manipulations in reducing stand susceptibility and vulnerability, most have focused on the effects of thinning on gypsy moth impacts with respect to forest stand structure and composition. In addition, there is a need to understand how silvicultural manipulations may influence the dynamics of gypsy moth populations. The objectives of this study were to test the effects of both presalvage and sanitation thinning on gypsy moth dynamics. Specifically, we tested how thinnings affected changes in egg mass density, patterns of within-generation survivorship, and the amount of mortality caused by various gypsy moth parasitoids and pathogens. We also evaluated the resulting forest vegetation following thinnings and the long-term impact of gypsy moth populations.

Pages 261-268 in M.L. McManus and A.M. Liebhold, editors. 1998. Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247.

Materials and Methods

The study area was located at the West Virginia University Forest (WVUF) in Monongalia and Preston Counties. In 1989, 16 stands (average size 10.5 ha) that reflected a range of overstory types were established on the WVUF. Some stands were mixed hardwood, with only 15% oak (*Quercus* spp.) in the overstory, while others were mixed oak, with more than 80% of the basal area in oak species. Each stand was paired with an adjacent stand bearing similar vegetation and site characteristics. In the winter of 1989-90, one stand of each pair was selected for thinning. In stands where oak accounted for a low proportion of stand basal area (mostly less than 50%), a sanitation thinning was applied. The primary objectives when marking trees were to reduce total stand basal area and preferentially remove host-tree species preferred by the gypsy moth (Gottschalk 1993). In stands where oak accounted for a higher proportion of stand basal area (greater than 50%), presalvage thinning was applied. The principal objective was to remove trees in poor condition regardless of species or their preference by gypsy moth larvae (Gottschalk 1993).

Gypsy moth sampling. Gypsy moth populations were sampled before thinning and each year thereafter until 1996 by counting all egg masses in 0.01-ha (1/40-acre) plots in each stand (Liebhold et al. 1994). Within each stand, plots were located in a grid with 100 m between sampling points. Each stand had 10 to 19 permanent plots depending on stand size.

In stands where larval densities were sufficiently high, larvae were collected weekly to quantify mortality due to parasitism and disease. The first larval sample was timed to coincide with larval hatch and the last sample was taken when pupation began. When available, 100 larvae were collected each week at five sampling locations within each stand. Early instars were collected by sampling foliage of saplings and seedlings; late instars and pupae were collected from tree boles and also from burlap bands that were placed around trees.

Larvae were placed in individual 30 ml plastic cups containing artificial diet. The cups were placed in an outdoor insectary located on the WVUF so that temperature and phenological development were approximately the same as that for field populations. Each cup was checked weekly until eclosion. The presence of parasitoids in each cup was recorded and cadavers were inspected microscopically for viral polyocclusion bodies or fungal spores. The maximum percent mortality among collections was used as the estimate of mortality occurring for each agent in the field. Peak percentage mortality is the best measure of parasitoid and disease impact under the sampling plan used in this study (Gould et al. 1989).

Because mortality caused by various gypsy moth parasitoids and pathogens is density dependent (Elkinton and Liebhold 1990), we wanted to evaluate the effect of thinning on mortality using an analysis that accounted for variation in host density. Stepwise regression (Draper and Smith 1981) was used to model peak mortality (transformed using an arcsine-square root transformation) as a linear function of: (1) N_t, gypsy moth density [log(x+1)] at the beginning of the current generation; and (2) N_{t-1}, gypsy moth density [log(x+1)] at the beginning of the prior generation. Each of these independent variables was successively added to the model; the probability associated with the *F* statistic ($P < 0.05$) for each independent variable was used as the criterion for entering and retaining each term in the model. These selected variables were included as covariates in an analysis of variance where we assumed a randomized complete-block design (Steel and Torrie 1980). Peak percent mortality was the response, N_t and N_{t-1} were included as covariates (only if they were significant in the stepwise regression), and treatment (thinning) and block were the effects.

Vegetation sampling. Overstory vegetation was sampled in 1989 prior to silvicultural treatments, and each year thereafter. Measurements were taken on overstory vegetation on each of 20 0.04-ha (0.1-acre) plots in the 16 stands. All overstory vegetation (dbh ≥ 6.3 cm) in each plot was identified as to species and measured. Defoliation estimates were taken on each overstory tree. The percentage of foliage removed was estimated visually and the estimates weighted by the diameter of the defoliated tree.

Results and Discussion

In this study, eight distinct causes of larval mortality were identified across all stands (Table 1). Unidentifiable causes, however, accounted for the majority of gypsy moth larval mortality in each year except 1991. Not all mortality agents were recovered in all stands.

Table 1. Peak percent mortality each year from mortality agents of gypsy moth, based on weekly collections of larvae and pupae

Item	1990	1991	1992	1993	1994
Unidentified	71.0	47.5	86.8	91.1	90.1
NPV	34.7	86.3	51.4	41.5	17.6
Entomophaga maimaiga	0	0	5.7	36.7	2.0
Parasetigena silvestris	1.1	19.8	25.2	30.3	36.2
Cotesia melanoscela	0	1.7	11.6	28.7	19.8
Blepharipa pratensis	22.7	13.4	20.3	8.4	[a]
Brachymeria intermedia	3.4	19.8	2.9	3.0	[a]
Compsilura concinnata	1.0	16.2	6.9	5.6	16.8
Phobocampe unicincta	0	0	6.8	3.0	9.2

[a] Incomplete data

The relationship between parasitism and host density varied considerably among parasitoid species (Table 2). Parasitism by *Brachymeria intermedia*, *Compsilura concinnata*, *Cotesia melanoscela*, and *Parasetigena silvestris* was positively related to density in the current generation, N_t, and parasitism by *Blepharipa pratensis* was inversely related to N_t, reflecting the delayed density dependence of these parasitoids.

Parasitism by *C. concinnata*, *C. melanoscela*, and *P. silvestris* was inversely related to host density in the previous generation, N_{t-1}. These patterns are mostly in agreement with previous studies (Elkinton and Liebhold 1990, Williams et al. 1992, 1993).

Mortality caused by the nuclearpolyhedrosis virus (NPV) was highest in 1991 but only in defoliated stands where it caused populations to decline in subsequent years. Overall, virus mortality was positively related to both density in the current and previous generation (Table 2), and generally concurs with existing knowledge of NPV epizootiology (Doane 1970, Woods et al. 1991). By contrast, *Entomophaga maimaiga* caused considerable mortality in 1993 but much less mortality in 1992 and 1994, and no mortality prior to 1992. Mortality caused by *E. maimaiga* was first discovered in North America in New England in

1989. By 1992, this pathogen apparently expanded its range to encompass nearly the entire range of the gypsy moth (Hajek et al. 1995). Thus, its absence in our samples from 1989 to 1991 can be explained by its general absence from the region during that period.

Table 2. Results of stepwise regression of peak mortality on egg mass density (N_t) and lag egg mass density (N_{t-1})

Dependent variable	Independent variable[a]	Estimate	Probability of $\alpha > F$
Blepharipa pratensis	N_t	-0.070	0.047
	N_{t-1}	0.12	0.002
Brachymeria intermedia	N_t	0.14	0.0006
Compsilura concinnata	N_t	0.12	0.0001
	N_{t-1}	-0.077	0.006
Cotesia melanoscela	N_t	0.12	0.003
	N_{t-1}	-0.20	0.0001
Phobocampe unicincta	N_{t-1}	-0.061	0.002
Parasetigena silvestris	N_t	0.10	0.012
	N_{t-1}	-0.20	0.0001
NPV	N_t	0.16	0.003
	N_{t-1}	0.13	0.009
unknown	N_{t-1}	-0.14	0.0001

[a] N_t = egg mass density at the beginning of the same generation [log(1 + egg mass/ha)], N_{t-1} = egg mass density at the beginning of the previous generation [log(1 + egg mass/ha)].

Rates of parasitism by *P. silvestris* and *C. melanoscela* generally increased from 1989 through 1994. Perhaps this is related to the increasing population densities of gypsy moth over this period. Another cause of the increase in parasitism rates is that they tend to be low in newly established populations along the expanding population front; range expansion by parasitoids tends to lag behind the expansion of host gypsy moth populations (Ticehurst et al. 1978).

When gypsy moth larval mortality between thinned and unthinned stands was compared using a paired *t*-test (Sokal and Rohlf 1981), we found parasitism by *B. intermedia* and *C. melanoscela* significantly higher in thinned stands, and mortality caused by NPV significantly lower in thinned stands (Table 3). However, the results in Table 2 indicate that mortality is often closely associated with gypsy moth densities. Therefore, the differences in mortality rates may be due to differences in gypsy moth densities between thinned and unthinned stands. As a result, it was necessary to assess the significance of thinning on mortality rates using an analysis of covariance, where gypsy moth density and/or lagged density were used as covariates. The least squares means in Table 3 adjust mortality rates based on the known relationship(s) with gypsy moth density. None of the least squares means indicated a significant effect on thinning. Thus, the adjusted analysis indicated that thinning had no effect on mortality rates.

Table 3. Unadjusted means and least squares means (adjusted for covariates listed in Table 1) for transformed peak percent mortality

Dependent variable	Unadjusted mean		Least squares mean	
	unthinned	thinned	unthinned	thinned
Blepharipa pratensis	0.291	0.306	0.270	0.327
Brachymeria intermedia	0.092	0.150*	0.088	0.154
Compsilura concinnata	0.238	0.213	0.232	0.236
Cotesia melanoscela	0.261	0.271*	0.243	0.309
Phobocampe unicincta	0.054	0.093	0.098	0.075
Parasetigena silvestris	0.334	0.385	0.357	0.370
NPV	0.631	0.549*	0.555	0.583
unknown	0.973	1.00	0.994	1.01

* Significant at $\alpha = 0.05$.

Figure 1 shows the temporal pattern of gypsy moth dynamics, defoliation, and overstory mortality for paired thinned/unthinned stands with high egg mass densities. Populations of gypsy moth increased rapidly from 1989 to 1990 and egg mass density (Fig. 1a) and defoliation (Fig. 1b) were greatest in 1991. Live basal area (Fig. 1c) began to decline in 1991 and overstory mortality was greatest between 1991 and 1992. Both egg mass density and defoliation appeared to be greater in unthinned than thinned stands, but the differences were not statistically significant. It is possible that differences were not observed because gypsy moth densities were already at outbreak levels. Following 2 years of defoliation in these stands, populations collapsed to low densities such that it probably would be difficult to detect differences in densities due to thinning (Fig. 1). However, it is also apparent that thinned stands experienced less overstory mortality than their unthinned counterparts.

Since we detected a decrease in gypsy moth densities following thinning in only two of eight thinned stands, it is difficult to conclude that thinning caused a reduction in densities. However, numerous studies have reported that outbreak frequency is closely related to the proportion of stand basal area represented by host-tree species preferred by the gypsy moth (Bess et al. 1947, Houston and Valentine 1977, Herrick and Gansner 1986). Perhaps we did not observe a more dramatic decrease in gypsy moth densities in thinned stands because the proportion of basal area in preferred species was not reduced greatly in any of the stands following thinning. Nevertheless, our results suggest that any reduction in gypsy moth density caused by thinning is most likely not the result of differential response by natural enemies but rather is due to another factor, for example, mortality occurring during dispersal and/or effects on fecundity. Despite demonstration of an apparent lack of effect on gypsy moth populations caused by thinning, there was a distinct difference in overstory mortality between the thinned and unthinned stands.

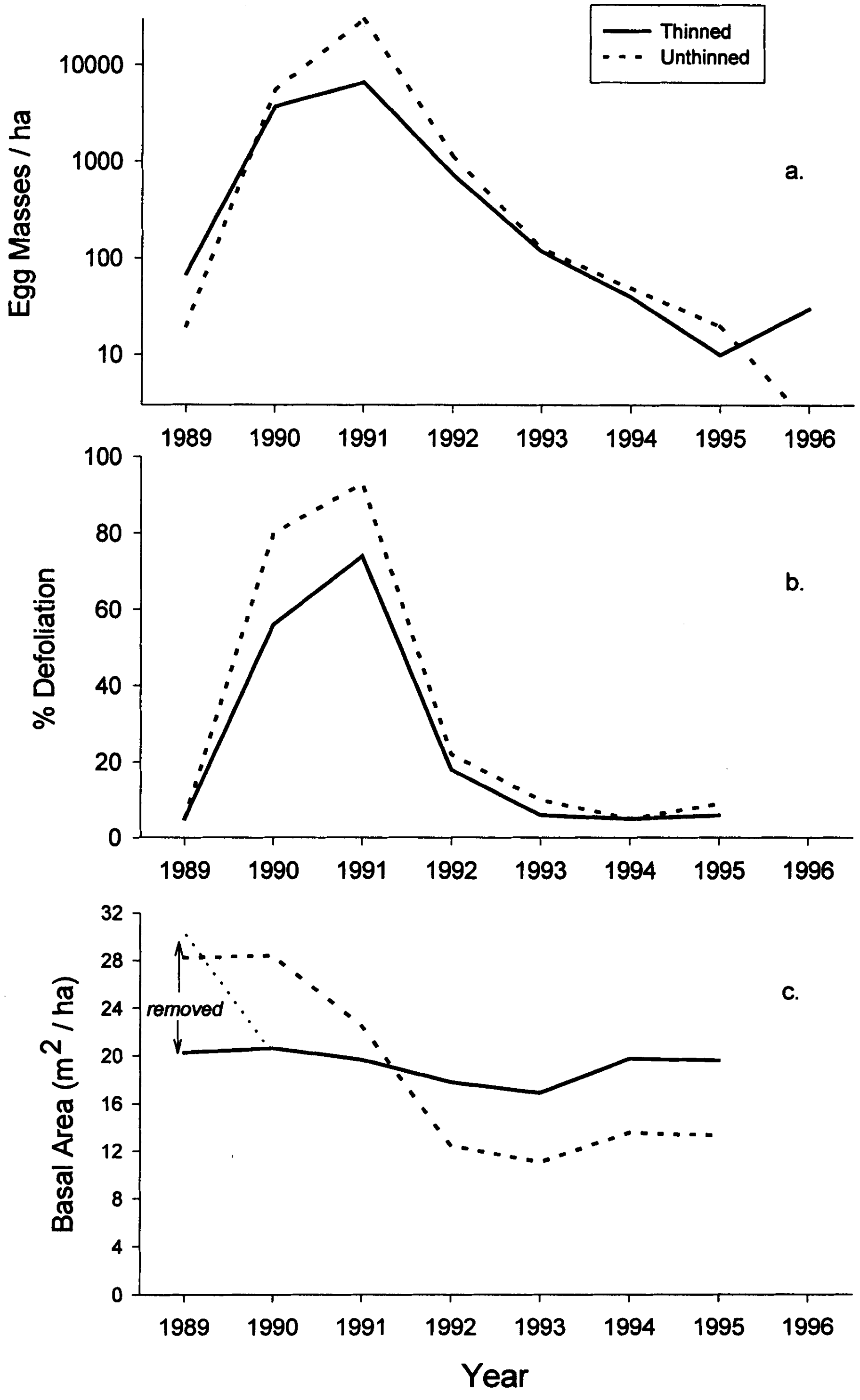

Figure 1. (a) Gypsy moth egg mass density from 1989 to 1996: (b) defoliation estimates of overstory trees from 1989 to 1995; (c) live basal area in defoliated stands; the amount of basal area removed in the silvicultural thinning is represented by the length of the arrow and small dashed line at the 1989 mark.

Conclusion

In this study we were unable to determine that thinning significantly altered rates of gypsy moth mortality caused by specific parasitoids or pathogens. Similarly, Grushecky (1995) found no effect of silvicultural thinning on predation of gypsy moth life stages. Thus, it seems unlikely that these silvicultural operations can reduce the frequency or intensity of gypsy moth outbreaks by enhancing the activity of natural enemies. However, the lack of a detectable effect of thinning on the action of these natural enemies does not preclude the feasibility of using silvicultural approaches to manage gypsy moth populations. Our data provide evidence that thinning may help to reduce mortality, though it may actually increase defoliation in certain situations.

Silvicultural manipulations are more likely to affect stand susceptibility simply by reducing the total or relative amount of host foliage (Gottschalk 1993) than by affecting gypsy moth populations directly. Moreover, silvicultural manipulations can be useful tools in gypsy moth management by removing and utilizing trees that are likely to die as a result of defoliation (i.e., those with poor crowns).

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The System of Gypsy Moth Population Regulation in the Slovak Republic

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ABSTRACT The gypsy moth is a very important pest in oak forests of the Slovak Republic and has a 6-8 year outbreak cycle. Frequency and abundance of pathogens, parasitoids and unknown mortality agents were observed during the last two outbreak periods. Currently, we are conducting research on the development of a pheromone monitoring system and on the use of microbial pesticides such as *Bacillus thuringiensis* and nuclearpolyhedrosis virus to augment the natural bioregulation of the gypsy moth. Using this scientific information, an experimental model of gypsy moth control was developed that emphasizes the use of ecological methods to control gypsy moth populations in Slovakia before outbreaks develop. The main objective of the new strategy is to minimize the incidence of defoliation caused by gypsy moth. The term "advance control", or "control in advance" is introduced to define actions that are taken to manage populations at a time when pest populations are low but have an increasing trend in abundance. The steps involved in this process and the parameters that were used for making decisions are discussed.

THE GYPSY MOTH, *Lymantria dispar* L., causes significant damage in the oak forests of Slovakia. The periodicity of outbreaks is 6-8 years and the area infested can vary significantly (Fig. 1). The impact of pathogens, predators and unknown mortality agents on the pest population density differs during various outbreak stages, however, the role of predators has not been examined. *Bacillus thuringiensis* (*Bt*) and nuclearpolyhedrosis virus (NPV) products were used as an artificial component of the natural bioregulation complex. The dosage and method of application was determined based on the population density of the pest. We utilized data collected from pheromone traps over a 12-year period to monitor the densities of gypsy moth populations.

The development of a strategy for regulating the abundance of defoliators such as the gypsy moth is similar to that employed in most integrated pest management (IPM) systems. The aim of the system is to utilize ecologically and economically acceptable measures during the period of progradation to maintain pest populations below an economic threshold.

This model of integrated oak protection against leaf-eating insects is based on two basic activities: (a) determine precisely when the first indication of population increase above a threshold level occurs; and (b) Take appropriate actions to maintain populations below a predetermined economic threshold. Monitoring, prognosis and population regulation are processes that are integral to the principles of forest protection.

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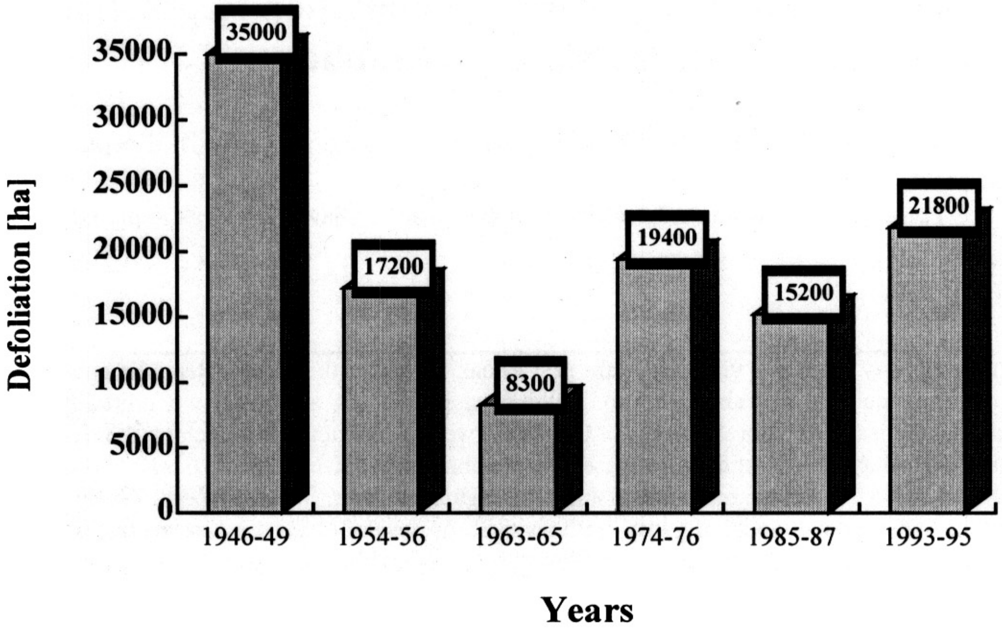

Figure 1. The area damaged by gypsy moth in the Slovak Republic during outbreak periods.

Material and Methods

In 1992 we initiated an experimental study to evaluate preventive treatments before population densities began to increase. The experimental area chosen was an oak forest in the forest district (FD) Cifáre, which is historically a primary focus for *L. dispar* outbreaks.

Within the FD, a relatively self-contained forest complex consisting of 110 ha in a locality referred to as Kovácová was used for this experiment. At that time, estimates of the density of *L. dispar* populations throughout the FD Cifáre indicated that a slight increase in trend was occurring, which is indicative of an impending mass outbreak of this species.

The experimental plot was treated with half of the normal dose of *Bacillus thuringiensis*, Foray 48 B (2 l/ha = 25 BIU), using a ULV aerial application with Micronair 4000 atomizers. For comparison, forest stands in the forest regions (FR) Mochovce, Nevidzany, and Pata, which also are primary foci for *L. dispar* outbreaks, were left untreated. During 1990-1994 the population trends of *L. dispar* were monitored using a modified Turcek method on both the experimental and comparison plots (Turcek 1956). The efficacy of the preoutbreak application of *Bt* was determined by comparing the results of monitoring *L. dispar* densities on the experimental and control plots for several years after the applications. These applications were referred to as "advance control," or “control in advance.” We introduced the term “advance control” to define pro-active (preventive) measures that are initiated at a time when background populations of *L. dispar* begin to show an increasing trend, which normally indicates that an outbreak is imminent.

Results

Mortality agents affecting gypsy moth populations. During the last ten years, research activity in Slovakia has focused on entomopathogens and the complex of parasitoids that attack the gypsy moth, and their impact on population densities of the pest under Central European conditions. The results of this research are very encouraging.

Observations during periods of two gypsy moth outbreaks confirmed that the natural bioregulation complex has a major influence on gypsy moth abundance. The intensity of the effect of the natural bioregulative complex varies depending upon the phase of gradation of the pest.

Laboratory and field observations demonstrated that mortality caused by natural enemies ranged from 79.1% to 97.3% while the population was increasing, from 86.2% to 99.7% during the outbreak phase, and from 83.6% to 85.1% during the period in which the population declined. Entomopathogenic microorganisms and undetermined factors affected pest abundance most significantly. The contribution of both of these factors to overall mortality was 70.6% during the endemic period, 52.7% during increasing populations, 66.8% during the outbreak phase, and 68.3 % during the period in which the population declined. The highest mortality of gypsy moth in natural conditions was caused primarily by the nuclearpolyhedrosis virus (*Borrelina reprimens* Holmes). Several species of entomopathogenic bacteria caused mortality of early larval stages of the pest, however, presence of natural mortality caused by *Bacillus thuringiensis* was rarely observed. Several microsporidia were recovered, namely the genera *Nosema, Thelohania* and *Pleistophora.* Fungi were rarely encountered as a primary cause of natural mortality in gypsy moth populations. Mixed infections occurred very frequently and these usually consisted of virus and Microsporidia (Table 1).

Table 1. Species of gypsy moth pathogens recovered in the Slovak Republic

Family and species	Family and species
VIRUS:	**BACTERIA:**
Borrelina reprimens (Holmes)	*Bacillus thuringiensis* (Berliner)
Smithia rotunda (Bergold)	*Pseudomonas aeroginosa* (Schroeter)
PROTOZOA:	**FUNGI:**
Vairimorpha sp	*Beauveria bassiana* (Balsamo)
Nosema serbica (Weiser)	*Spicaria farinosa* (Dicks)
Thelohania disparis (Timofejeva)	
Pleistophora schubergi (Zwolfer)	

The effect of parasitoids was substantially lower, especially during advanced phases of the outbreak. The amount of gypsy moth mortality caused by parasitoids in different population phases was as follows: 29.4% (latency), 47.3% (gradation), 33.2% (culmination), and 31.7% (regression/decline). The main families of parasitoids recovered were Braconidae and Tachinidae. The Braconids were prevalent when the populations were in the endemic and outbreak phases, while the Tachinids were prevalent in all other population phases. *Cotesia melanoscelus* (Ratz.), *Glyptapanteles liparidis* (Bouche), *Parasetigena silvestris* (R.-D.) *and*

Blepharipa pratensis (Meigen) were confirmed as the principal species that were recovered (Table 2).

Table 2. Species of gypsy moth parasites observed in the Slovak Republic

Family and species	Years of outbreak		
	1972-1974	1985-1987	1992-1994
Braconidae			
Cotesia melanoscelus	x	xxx	xxx
Glyptapanteles porthetriae	xx		x
Glyptapanteles liparidis	xx	xx	xx
Meteorus versicolor			x
Ichneumonidae			
Apechtis compunctor			x
Hyposoter tricoloripes			x
Hyposoter sp.			x
Iseropus inguisitor		x	
Iseropus instigator		x	x
Iseropus turionelae		x	
Lymantrichneumon disparis			x
Phobocampe unicincta (=Hyposoter disparis)	x	x	xx
Phobocampe sp. (P. lymantriae, P. pulchella)			xx
Pimpla hypochondriaca			x
Theronia atalantae		x	x
Campoplex sp.		x	
Casinaria sp.			x
Chalcididae			
Brachymeria intermedia		x	x
Monodontomerus sp.			x
Tachinidae			
Blepharipa pratensis	xxx		xxx
Blepharipa schineri			x
Blondelia nigripes	xxx	x	
Carcelia gnava			x
Compsilura concinnata	xx	xx	x
Parasetigena silvestris	xxx	xxx	xxx
Pales pavida			x

Table 2 cont'd

Exorista larvarum			x
Zenillia libatrix	x	x	x
Drino incospicua			x
Sarcophagidae			
Agria affinis		x	
Kramerea schuetzei		x	
Muscina stabulans	x		
Pseudosarcophaga affinis	x		

x - occurrence, xx - important, xxx - very important

Bioregulation of gypsy moth population density. Before *L. dispar* populations enter the progression phase, our primary objective is to take appropriate actions necessary to suppress populations so that they will not enter the outbreak phase. We began to estimate the abundance of gypsy moth egg masses in the Kovácová area of FD Cifáre in 1990 after the pheromone monitoring system indicated that the trend in populations was increasing from latency to a base level. Based on the estimate of egg masses per tree in the fall of 1991, we initiated a program to apply *Bt* (Foray 48 FC) aerially in the spring of 1992.

We applied *Bt* at a dose of 2 liters/ha (25 BIU), which is 50% of the standard dose recommended, and achieved 79.8 % mortality within two weeks after treatment. No actions were prescribed for the other focal sites in the FRs Mochovce, Nevidzany, and Pata, where gypsy moth population densities were comparable. Observations on all populations were recorded in subsequent years.

While the population density in the experimental (treated) area of Kovácová has remained at a base level (less than 0.28 egg masses per tree), outbreaks developed in the three comparison sites. In the FR Nevidzany, the egg mass density increased from 0.29 per tree in the fall of 1992 to 3.07 per tree in the fall of 1993. It was necessary to apply chemical pesticides in both young and mature stands in order to prevent severe defoliation.

The situation in FR Mochovce was even more difficult. The number of egg masses per tree, which was similar to that found in FR Kovácová in 1991, increased dramatically to 25.24 in the fall of 1992, making it necessary for us to aerially apply pesticides over an extensive area in the spring of 1993. Despite these efforts, heavy residual populations required treatment again in 1994.

In the FR Pata, where egg mass densities were lower in 1991 than in Kovácová, the population increased to 5.64 egg masses per tree in the fall of 1992, which required that we apply pesticides in the spring of 1993 to prevent damage from occurring. Despite our efforts, severe defoliation occurred in young stands in this FR when the stands were reinvaded by windblown larvae from mature stands in the adjacent area. The changes in egg mass densities over time that occurred in these plots are summarized in Table 3.

We reached two conclusions from these results: (1) it is necessary to maintain *L. dispar* abundance at base levels to prevent serious impacts that affect the health of oak forests; and (2) this goal can be achieved by implementing an early detection system based on the use of pheromone traps and egg mass surveys, correct diagnosis of increasing trends of *L. dispar* abundance from latency to a base level, and pre-emptive treatments to prevent the increase of populations to the progradation phase.

Table 3. Changes in the abundance of gypsy moth populations based on the mean egg masses per tree and control forest regions

Locality	Years					
(FR)	1990	1991	1992	1993	1994	1995
Kovácová ☒	0.060	0.09	0.14	0.28	0.054	0.11
Mochovce þ	0.005	0.08	25.24	1.74	0.0	0.0
Nevidzany þ	0.000	0.04	0.29	3.07	0.0	0.0
Pata þ	0.005	0.05	5.64	0.04	0.002	0.002

☒ - Locality where the model of efficient bioregulation of gypsy moth population density was used

þ - Control plots

We have referred to this process as "advance control" or "control in advance." The most critical factor in this process is the decision to take action when populations are still very low, because as demonstrated in the three comparison areas, gypsy moth populations are capable of expanding to outbreak levels in a single generation, thus there is little room for error.

The model of efficient bioregulation of gypsy moth population density. In order to maintain gypsy moth populations at endemic levels, we have developed a model for bioregulation of populations that allows us to supplement the actions of the natural enemy complex by using ecologically acceptable artificial means. The model consists of the following steps:

1) A systematic monitoring grid of pheromone traps is deployed in historically primary outbreak areas (foci) beginning in the third year after the collapse of the last outbreak. The grid consists of 16 pheromone traps spaced 50 m apart in a 4 x 4 configuration.

(a) If less than 60 male moths per trap are caught within the grid, no further action is necessary and the monitoring grid is activated again in the following year;

(b) If more than 60 moths per trap are caught within the grid, proceed to Step 2;

2) Estimates of the density of the gypsy moth population in the area are made using a modification of the Turcek method (Turcek 1956), whereby the number of egg masses are counted on the boles of 300 trees within the area of the monitoring grid.

(a) If the abundance of egg masses is estimated to be below 0.05 per tree, no action is required and the monitoring grid is activated again in the following year (Step 1).

(b) If the abundance of egg masses is estimated to be between 0.05 and 0.20 per tree, proceed to Step 3.

(c) If the density of egg masses exceeds 0.20 per tree, this indicates that the population is increasing rapidly and is beyond the point where bioregulation is feasible. This population will be scheduled for treatment in the following spring. Chemical pesticides will be applied aerially to prevent defoliation from occurring.

3) The probability of increased abundance of the gypsy moth population is estimated based on weather conditions in the preceding years.

(a) If it has been less than 4 years since the collapse of the last outbreak in the area, and hot, dry weather, which is favorable to gypsy moth populations, did not occur in the spring (April-May) of the last two years, no further action is recommended. The monitoring grid is restored in the following year (Step 1).

(b) If it has been 4 or more years since the collapse of the last outbreak, and if favorable weather (hot, dry) did occur in the spring of the two preceding years, proceed to Step 4.

4) Application of microbial pesticides and the criteria that are considered for their use.

Only two microbial pesticides are recommended for use in this pre-emptive strategy: commercial preparations of *Bt*, and the gypsy moth NPV. In most of the area designated for treatment, one-half of the standard dose of *Bt* (20-30 BIU/ha) is applied using ultra low volume (ULV) technology to reduce the density of populations to a base level. In environmentally sensitive areas, however, where rare or sensitive lepidopteran species occur, a full dose of the NPV is applied (5×10^{11} - 1×10^{12} POBs/ha).

The timing of application of both products is critical since neither *Bt* nor the NPV have a long period of residual activity. Spraying is usually conducted when larvae are in the second instar and leaves of preferred host tree species are about two-thirds expanded. Preferably, the ambient temperature should exceed 12°C, so that most larvae are actively feeding.

The selection of forest stands for treatment is based on the following criteria listed in descending order:

1) Forest stands where silvicultural treatments or reforestation efforts have occurred.
2) Oak stands where oak wilt is present.
3) Young oak stands in any condition.
4) Conifer stands.
5) Oak stands containing mast crops that require protection.
6) Stands containing other tree species that are healthy or have mast crops.
7) Any forest stand that is within 300 m of orchards or vineyards.

Discussion

This article describes a new and novel strategy for managing the gypsy moth in Slovakia whereby artificial bioregulation tactics (microbial pesticides) are prescribed when gypsy moth populations are still at a base or endemic level to prevent them from entering a progressive phase of increase. This system is referred to as "advanced control" and is dependent upon the use of an intensive monitoring network of pheromone traps in gypsy moth focal areas.

This system differs from the approach to managing gypsy moth populations that is described in Doane and McManus (1981), where pesticides are used to suppress populations when defoliation is imminent. It is important to recognize that there are differences in the status of the gypsy moth in the U.S. and in Slovakia, and in the characteristics of the forest in the two locations. In the eastern U.S., the gypsy moth is established in over 16 states, but for varying lengths of time. The insect has been present in New England forests for over 80 years, however, the gypsy moth is a relative newcomer to the states of Virginia and West Virginia to the south, and to Ohio and Michigan to the west. The gypsy moth is distributed in about 50% of the potentially susceptible oak forests of the U.S. Throughout this region, where the gypsy moth occurs, there are large areas of contiguous susceptible forests containing many species of oaks (*Quercus*). Thus, when outbreaks do develop, the potential for defoliation is massive, as exhibited in 1981 when over 5 million ha were defoliated.

In Slovakia, where the gypsy moth has existed for centuries, oak forests occur as discrete parcels that may be widely separated by farmland or conifer forests. Therefore, there are more opportunities to implement integrated management strategies on specific areas that are less than 100-200 ha. Results from early studies in Slovakia and other countries in Central Europe led us to believe that we needed a new strategy to address defoliating insects such as the gypsy moth. During the last two gypsy moth outbreaks in Slovakia, populations increased rapidly in mature oak stands and then young larvae were dispersed by wind into adjacent oak plantations or conifer stands before any control actions could be initiated. In this situation, the only practical alternative that is available is to use chemical contact pesticides in order to prevent severe impacts from occurring. We needed to develop a strategy where we could address the gypsy moth problem in a preventive manner, utilize the benefits of the extensive natural enemy complex, and minimize the undesirable utilization of chemical contact pesticides.

Our bioregulation model is based on utilization of a pheromone-based monitoring system that detects changes in the abundance of gypsy moth populations at a base level (less than 60 male moths per trap). This information triggers the need for egg mass surveys only when there are indications that populations are increasing from latency. Taking into account the estimates of population density from egg mass surveys, and our knowledge and experience with spring weather conditions that are conducive to increases in the abundance of populations, we can make decisions about the feasibility of applying microbial controls that will supplement natural bioregulation processes. The important aspect of this process is that populations are treated at very low densities, which prevents them from progressing to outbreak status.

Our recent experiences with this strategy in the FD Cifáre suggests that it has been successful in preventing outbreaks from developing. We propose to identify further forested areas that serve as gypsy moth foci so that our monitoring system can be expanded. We also suggest that this model system can be modified to address other defoliator problems that are common to Slovakia and neighboring countries.

Acknowledgments

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Pheromone Monitoring of the Larch Bud Moth, *Zeiraphera diniana*, in the Swiss Alps

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ABSTRACT Pheromone monitoring helped to detect specific differences in pheromone communication, moth size and flight activity between two host races of *Zeiraphera diniana*. The host race on larch is bigger than the one on cembran pine and flies mainly at night. However, since response polymorphism of the males to pheromones was too rare in the course of the population cycle and since it was not consistently linked with the variable color polymorphism, assortative mating of the black colourmorphs cannot be the driving force of the cycle in the trough phase.

THE LARCH BUD moth is perhaps the most clear-cut case in the world of a truly cyclic moth (Ginzburg and Taneyhill 1994). Due to its regular devastation of the larch forests around the tourist resorts in the Engadine valley at 8-9 years intervals, control of this lepidopteran pest was demanded immediately after World War II. Therefore, a larval census was established in 1949 covering an area of 6000 ha of subalpine larch-cembran pine forest. Since then 5 population cycles were observed, several large-scale control operations were attempted, and more than 100 scientific papers published. The knowledge obtained led to the conclusion that control operations will be neither ecologically nor economically justifiable. In contrast, the study of the larch bud moth system revealed itself as very rewarding from a scientific point of view. It yields not only an outstanding example for ecosystem research (Baltensweiler 1996) but also an intriguing case for sympatric speciation of host races on either the deciduous larch or the evergreen conifers (Emelianov et al. 1995). Morphologically these host races are distinguishable only in their 5th larval instar, but they differ considerably in their development rates and surprisingly also in their pheromone communication (Baltensweiler et al. 1978; Guerin et al. 1984). All these traits are polymorphic and are well reflected in the offsprings of crossings between the host races. Interestingly enough, the extreme black larch form predominates at the peak of the population cycle on larch whereas intermediate colourforms prevail during the trough of the cycle (Baltensweiler 1993).

The host race on larch employs the trans-11-tetradecenyl acetate (larch form LF/ *E*11-14:Ac) whereas the host races on evergreens, i.e. cembran pine and Norway spruce, make use of the trans-9-dodecenyl acetate (AF / *E*9-12:Ac). Priesner (1979) discovered among the progeny of an AF x LF crossing F1-males which showed the same maximum EAG response to both the *E*9-12:Ac and *E*11-14:Ac. Subsequently, 'response' types were based on the relative effectiveness of the pheromone components *E*9-12:Ac vs. *E*11-14:Ac. Nine response types were distinguished, ranging from ≥ 100 / 1 to 1 / ≥ 100 and including 7 potential intermediary responses (30/1 to 1/30) (Priesner and Baltensweiler 1987a). This response polymorphism appeared to be the logical counterpart to the findings that the females produce in their glands these substances in variable ratios (Guerin et al. 1984).

Pages 278-291 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.

Therefore, the specificity of male attraction to synthetic sex lures and the response type of the relevant males captured, as measured by electroantennogram (EAG) measurements (Priesner and Baltensweiler 1987b), was studied by means of a standard series of 35 different lures, made up of varying combinations of the two pheromones.

In this paper the use of pheromone monitoring is exemplified with regard to the evaluation of two hypotheses, which were proposed to explain the immediate sequence of one cycle after the other:

1) The findings that the dark phenotype is an expression of a recessive gene in the homozygote (Baltensweiler 1993) and that both sexes exhibit a pheromone polymorphism led to the hypothesis that a correlation between colourmorph and pheromone type provides the basis for assortative mating between the different fitness types which occur at different stages of the cycle (Guerin et al. 1984).

2) Correlation between traits such as early emergence, large size (Stearns 1989) and black colourmorph could account for an increased fitness whereby subsequent assortative mating among the largest individuals would result in population increase.

Materials and Methods

Standard Series of Lures and Trap Model. The standard series of lures consisted of 5 doses of pure *E*11-14:Ac and *E*9-12:Ac respectively and 25 binary mixtures of these substances (Fig.1). Each lure was represented by just one trap. For the sake of interpretation, the traps were combined into three groups; two groups of 15 traps each with the predominance of either substance, and the intermediate group of 5 traps with equal doses of the two substances. In 1985 we reduced the number of lures to 8 combinations (Fig. 1), but each lure was replicated 4 or 5 times.

The synthetic pheromone substances (*E*11-14:Ac; *E*9-12:Ac) and their blends on rubber caps as well as traps were provided by H. Arn, Swiss Federal Research Station for Agriculture, CH-8820 Wädenswil, Switzerland.

The Tetra Trap (Arn et al. 1979) were hung on lower branches approx. 2 m above ground on either larch or cembran pine. The catching surface, an exchangeable sheet of carton covered with Tangle Trap (Tanglefoot Company, Grand Rapids, Michigan, USA) measured 155x90 mm.

The marking and recapture experiment. A standard series exposed in the mixed larch-cembran pine forest God god, S-chanf was used from the 23.8.-9.9.1982 to test the consistency of attraction: The tetra traps # 1, 8, 5 (Fig. 1) were not equipped with the adhesive carton, instead powdery dyes of different colours were filled into the trap to let attracted males mark themselves and leave the trap again at their will.

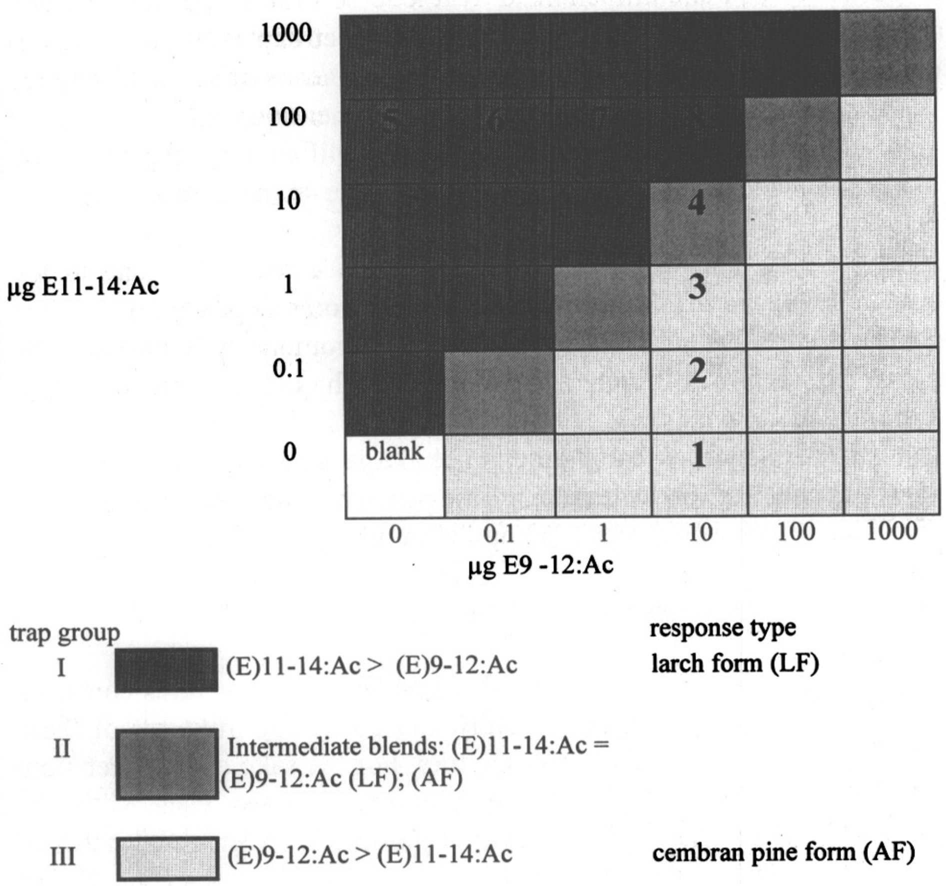


Figure 1. Trapping design 1981/1985-1989: 1 - 8.

Test sites. The test sites were chosen in the Engadine valley in either pure larch forests, mixed larch-cembran pine forests and a pure cembran pine forest:

pure larch forest:	1981:	Ardez, God San Steivan; 1500 m a.s.l.
	1982:	Sils, Crappa, 1850 m a.s.l.
pure cembran pine forest:	1981:	S-charl, Praditschöl, 2100 m a.s.l.
mixed larch-cembran pine	1981:	S-chanf, God god, 2050 m a.s.l.
forest:	1982:	Pontresina, Val Bernina, 1900 m a.s.l.

Results

Pheromone Polymorphism as measured by EAG Analysis. More than 1800 males from field populations of either pure or mixed host forests or F1-hybrids of 3 host races were analyzed (Priesner and Baltensweiler 1987a,b, Baltensweiler and Priesner 1988). Whenever feasible we ascertained also the correlation between the larval colour type and the response type.

Table 1 lists the catches for the three sites and the lure groups I-III, weighted according to the number of traps per group. The catch in Ardez clearly reflects the expectations, the small proportion of males found on lure group I is considered as being due to accidental or disoriented attraction of LF moths. Rather a surprise was the large proportion of LF males caught in the pure cembran pine forest of S-charl on trap group III. These males are thought to be immigrants from larch forests at lower altitudes. Obviously, these data are not sufficient to allocate the catch to its proper host race, additional criteria such as the pheromone response type of the males need to be known.

Table 1. Percentage of catch for 3 groups of pheromone compounds in 3 sites (July-October 1981)

			number moths		
			Ardez	S-charl	S-chanf
group	lures µg	n traps	4720	4304	2302
I	*E*9-12:Ac > *E*11-14:Ac	15	1.72	24.88	37.05
II	*E*9-12:Ac = *E*11-14:Ac	5	24.60	28.16	47.90
III	*E*9-12:Ac < *E*11-14:Ac	15	73.68	46.96	15.90

Ardez: pure larch forest;
S-charl: pure cembran pine forest;
S-chanf: mixed larch-cembran pine forest.
(n moths weighted for 15 traps/group)

The marking and recapture experiment was considered to provide some information about the consistency of the orientation to a specific lure. The recapture of males marked in traps #1 and 4 is shown in figure 2a,b. The recaptures are rather evenly distributed all over the traps of lure group I and II, as an exception a few moths were attracted to trap *E*9-12:Ac/*E*11-14:Ac 100/1000µg in lure group III. Because there were very few males in trap 0/10µg caught and marked and only 3 recaptures in traps 0/100 and 0/1000 µg recorded, no table is provided. This poor result is considered to be due to the deterrent effect of defoliated larch trees present at the site.

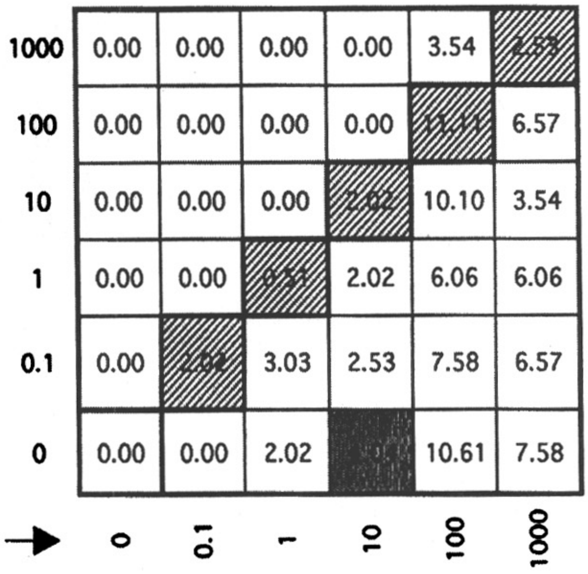
In 1985 we resumed the same experimental idea, however, the number of lures was reduced to 8 (Fig. 1). and the traps were exposed in only two sites, i.e. the pure larch forest of Sils and the mixed larch-cembran pine forest of Pontresina. Among the male response types we distinguished only between 'pure' ≥100 /1 and 'pure' 1/ ≥100 responses, i.e. between AF or LF males. At that time the population cycle was at its minimum density and we continued the monitoring until 1989 when the first local defoliation in Sils signaled the beginning of the peak phase. Figures 3a, 3c show the percentage of total catch/lure (defined by trap# 1-8; Fig. 1) and Fig 3b,d represent the absolute numbers of either the AF or the LF response types per lure for the years 1986-1989 and the two sites.

0	0	0	0	7	5
0	0	0	0	22	13
0	0	0	4	20	7
0	0	1	4	12	12
0	4	6	5	15	13
0	0	4	8	21	15

■ dye

fig. 2a

n=198

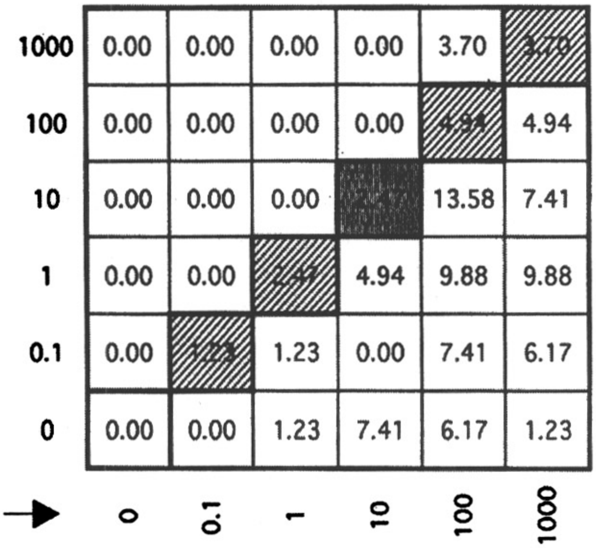


E11-14:Ac μg ↑ / E9-12:Ac μg →	0	0.1	1	10	100	1000
1000	0.00	0.00	0.00	0.00	3.54	2.53
100	0.00	0.00	0.00	0.00	11.11	6.57
10	0.00	0.00	0.00	2.02	10.10	3.54
1	0.00	0.00	0.51	2.02	6.06	6.06
0.1	0.00	2.02	3.03	2.53	7.58	6.57
0	0.00	0.00	2.02	[illegible]	10.61	7.58

0	0	0	0	3	3
0	0	0	0	4	4
0	0	0	2	11	6
0	0	2	4	8	8
0	1	1	0	6	5
0	0	1	6	5	1

fig. 2b

n=81



E11-14:Ac μg ↑ / E9-12:Ac μg →	0	0.1	1	10	100	1000
1000	0.00	0.00	0.00	0.00	3.70	3.70
100	0.00	0.00	0.00	0.00	4.94	4.94
10	0.00	0.00	0.00	2.47	13.58	7.41
1	0.00	0.00	2.47	4.94	9.88	9.88
0.1	0.00	1.23	1.23	0.00	7.41	6.17
0	0.00	0.00	1.23	7.41	6.17	1.23

Figure 2. **Mark-recapture experiment percentage recapture. Traps exposed on Cembran Pine 23.8.-9.9.1982, S-chanf, God god.**

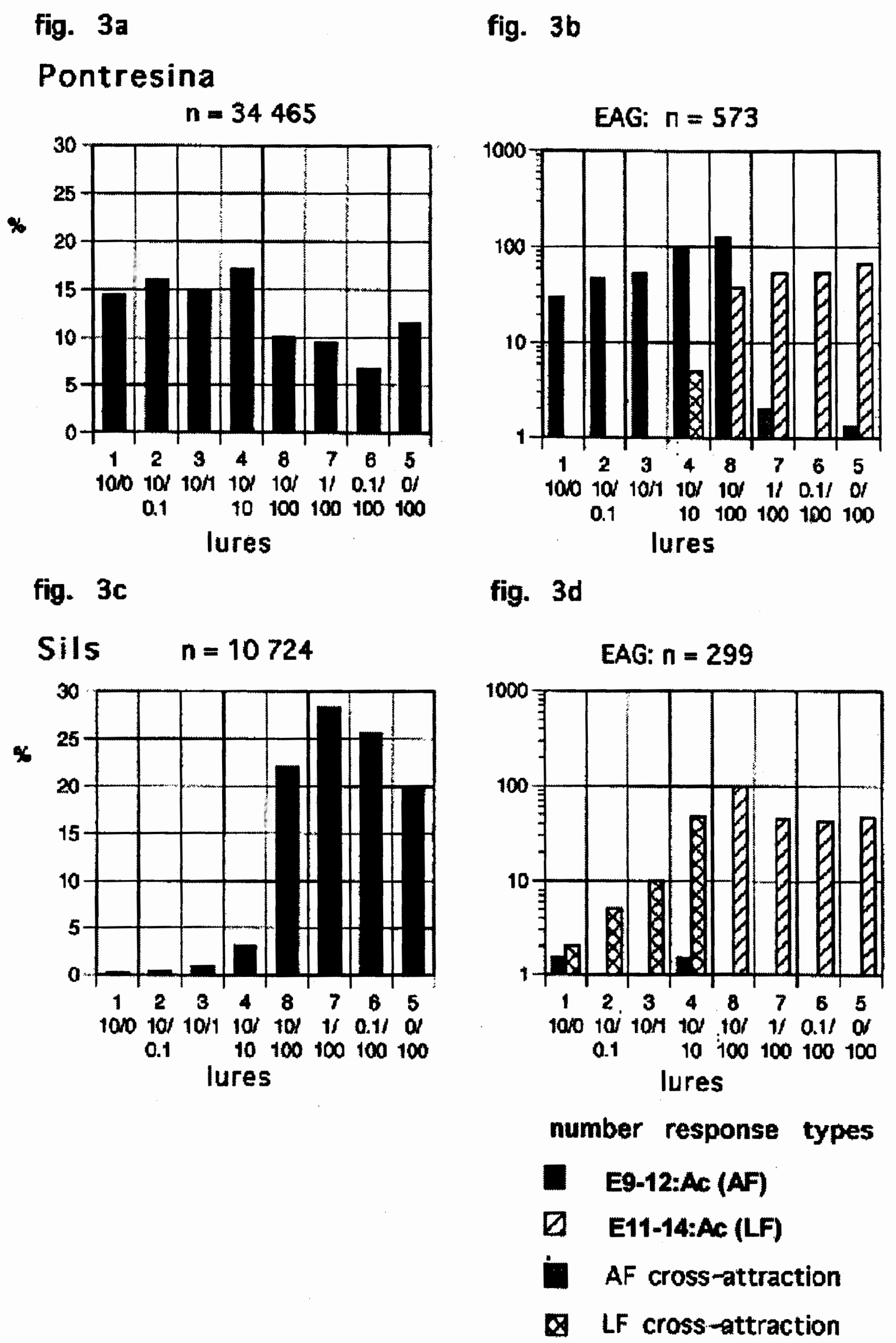


Figure 3. Percentage of total catch in 5 generations 1985-1989 per tetra trap #1-8 (Fig. 1) (Fig. 3a,c) Number of 'pure' response types per trap# 1-8 (Fig. 3b,d). (*E*9-12:Ac/*E*11-14:Ac =100/1 'pure' AF male); (*E*9-12:Ac/*E*11-14:Ac 1/=100 'pure' LF male); Fig. 3a,b: Pontresina: larch-cembran pine forest; Fig. 3c,d: Sils: pure larch forest.

In combination with the EAG response type of captured males it was found that the attraction to the single chemicals is highly selective. The pure *E*9-12:Ac source (trap 10/0 id.

trap#1) attracts almost only AF and the pure *E*11-14:Ac source (trap 0/100 id. trap #5) with one exception only LF males. Traps baited with compound mixtures, on the other hand, usually contained individuals of both host races, whereby the AF tolerated a larger amount of *E*11-14:Ac added to its own pheromone than the LF (Pontresina: trap 10/100 id. trap #8). Thus, an admixture of an equal amount of *E*9-12:Ac to *E*11-14:Ac (trap 10/10 id. trap #4) significantly reduced the attraction of LF males and higher ratios of *E*9-12:Ac/*E*11-14:Ac almost prevented attraction.

Five out of 103 EAG-analyzed moths caught in Pontresina on the 10/10 lure revealed themselves as LF males (4.8%) and none were found on traps#1-3, whereas 3 moths out of 177 analyzed individuals from the traps #5-7 were AF males (1.7%). Considering the biased collection of moths for EAG analysis from the trap 10/10 (id. trap#4), absolute cross-attraction would be even smaller.

In Sils we discovered only 2 *E*9-12:Ac response types out of a total of 299 EAG-analyses. Of the 297 LF, 64 or 21.5% were collected from the traps 1-4, however since the total catch on these traps amounted to 476 or 4.4% of the total, i.e. 10 724 moths, the bias is even more obvious. Whether this surprisingly large proportion of LF-moths being attracted to traps with greater amounts of *E*9-12:Ac represents oriented flight and should be termed 'cross-attraction' is open to speculation. Since the total catch on dummy traps amounts to 20 individuals only, i.e. approximately the same quantity as on trap #1 (id. 10/0), the increasing quantity of moths on traps #2-4 reflects the trend of increasing probability of oriented flight.

Another interesting result is seen in figure. 4, where from 1985 to 1989 the absolute number of moths per day and trap groups #1-4 and #8 is decreasing, whereas in contrast the absolute population of LF is increasing. Two interpretations are possible, either the discrimination by the LF improves or else the proportion of response types tolerating larger amounts of *E*9-12:Ac decreases. Because we did not continue the detailed analysis initiated by Priesner, this second interpretation cannot be confirmed.

The Size Criterion. Visual observation of the trap cartons revealed an obvious and consistent difference in size between the host races, the AF being ~1 mm smaller than the LF. However since size was also considered to be an important criterion for fitness within the hostrace, the length of most of the moths from the front of the head to the tip of was measured.

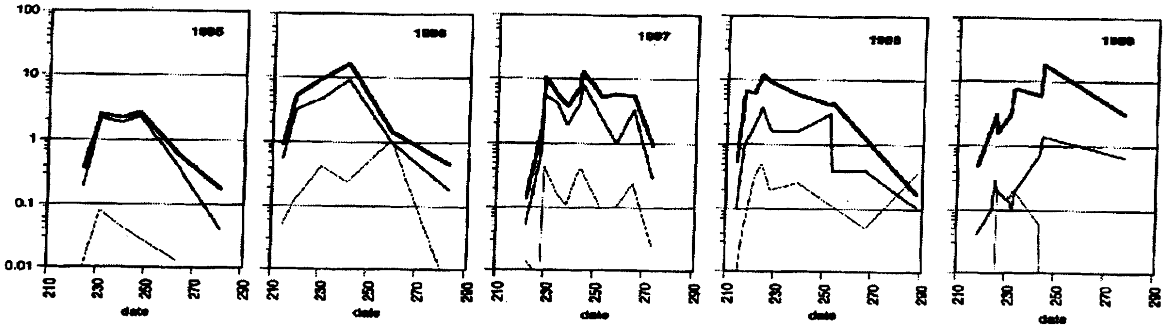


Figure 4. Density of *Z. diniana* moths per day and trap group, Sils 1985-1989.
Trap #1-4: —— 100 μE9 - 12Ac; 0-10 μE11 - 14Ac
Trap #8: ▬ 10 μE9 - 12Ac; 100 μE11 - 14Ac
Trap #5-7 ▬▬ 0-1 μE9 - 12Ac; 100 μE11 - 14Ac

LF populations show in general a typical leptokurtic size distribution (Fig. 5) with a maximum falling into the two size classes 9.76-10.00 and 10.01-10.25 mm in the course of the 5 years 1985-1989. Size distributions of AF populations are of the platykurtic type, their maxima ranging from 9.01-9.25 mm to 9.51-9.75. Lure group II which attracts both host races exhibits either a platykurtic or in the extreme case, such as in 1986, a bimodal distribution.

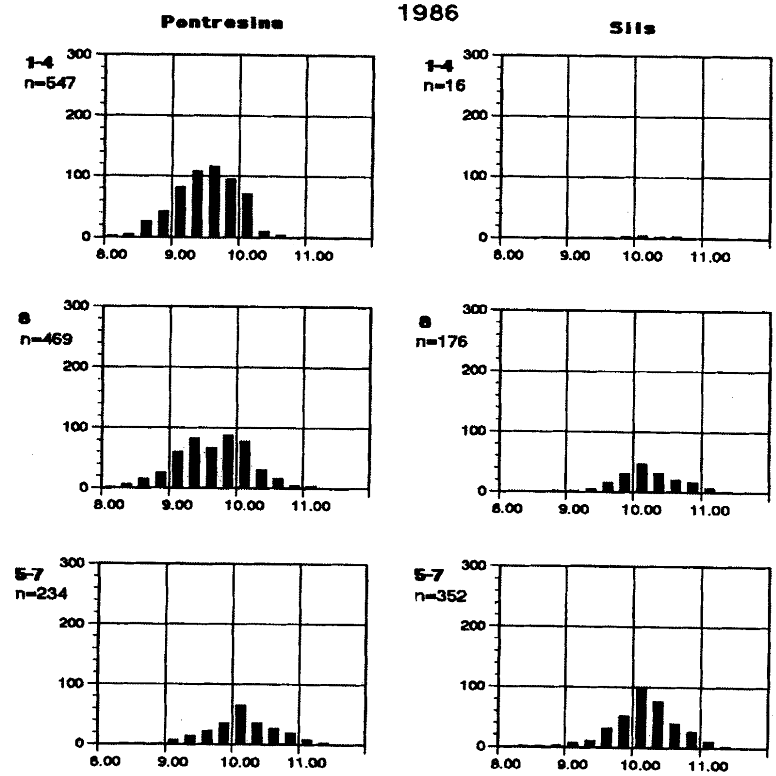


Figure 5. Frequency distribution of moth size in generation 1986.
trap groups #1-4, 8, 5-7, (class size: 0.25 mm)
Pontresina: larch-cembran pine forest
Sils: pure larch forest

Diurnal Flight Activity. In 1982 the standard series design was used in the mixed larch-cembran pine forest God god to evaluate the flight behaviour of the two host races. Between August 12th. and September 9th the traps were inspected intermittently at 12 hour intervals. In order to account for the activity threshold of the moths at approx. 7°C, the nights were grouped according to their temperature (weather station Bever):

day, n= 16;	1300:17.52 ±0.88 °C;
warm night, n=7:	1900:14.51 ±0.77 °C; 0001: 8.20 ±0.88 °C,
cold night, n=7:	1900:11.63 ±0.75 °C; 0001: 4.40 ±0.99 °C

Figure 6 clearly reveals the differences in diurnal flight behaviour but also a seasonal trend in the moth flight. At the beginning of the flight season moths of both host races fly mainly during warm nights, but in the middle of the flight season, the cembran pine form is, in contrast to the larch form, mainly day-active. This behaviour, however, is rather variable since also the LF may become day-active after cold nights or towards the end of the flight season in October.

Discussion and Conclusions

The efforts involved to determine male pheromone polymorphism with EAG analysis is considerable. When we realized that the response polymorphism proved to be too rare in field populations that it could be of any importance at the level of population dynamics (Baltensweiler and Priesner 1988), we restricted the analysis 1985-1989 to the determination of either the 'pure' ≥100 /1 or the 'pure' 1/ ≥100 response type, i.e. the correctness of attraction. Because of the rareness of male polymorphism and the fact that colour morphs and response types were not consistently correlated, led us to accept that hypothesis 1, i.e. assortative mating among black fitness types mediated by pheromone communication cannot not be valid.

As to hypothesis 2, it is postulated that fast development, which leads to early emergence and large size, are important criteria for superior fitness. These criteria, which all apply to the dark LF, would then cause synchronisation and, hence, favour assortative mating among them. This reasoning should express itself by the catch of the largest moths at the beginning of the annual moth flight of the 4 generations 1985-1988 which lead up to the peak of a cycle in 1989. It does not, however, necessarily presuppose a pheromone polymorphism.

Figure 7 shows the variation of moth size in the Sils population for the lure groups I-III, which all are made up of LF response types (Fig. 3b). Obviously the trend of decreasing moth size in the course of the annual moth flight is not confirmed. This postulated decrease in size, however, is reflected by the course of moth size on lure 10/100 (id. trap#8) in Pontresina (Fig. 8). But this trend stems from the fact that both host races are attracted to this trap, the large LF as well as the smaller and later emerging AF, which is well disclosed by its bimodal size distribution (Fig. 5). Hypothesis 2 could only be accepted if this phenomenon would be corroborated for the population attracted to lure group I, which is not the case.

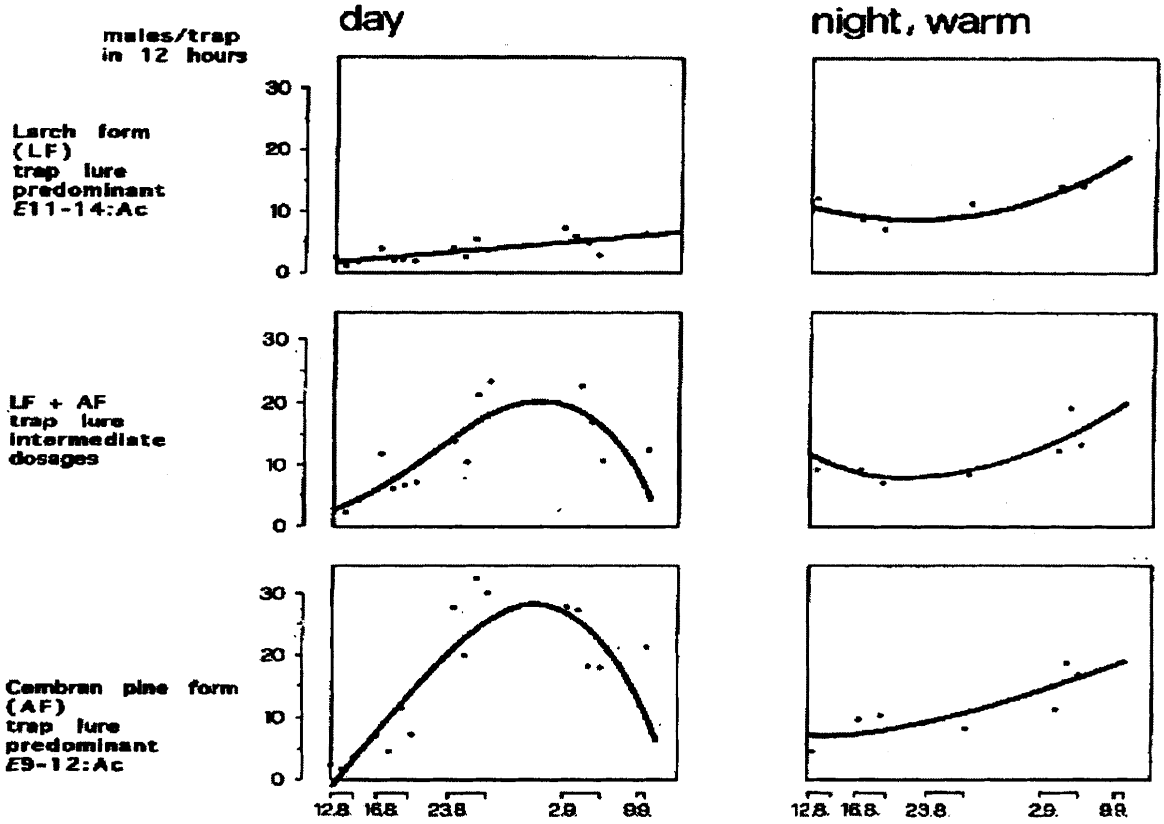


Figure 6. Flight behaviour of the two host races of *Z. diniana* as revealed by their attraction to parapheromone blends. S-chanf God god: 12.8.-9.9. 1982. traps exposed on cembran pine

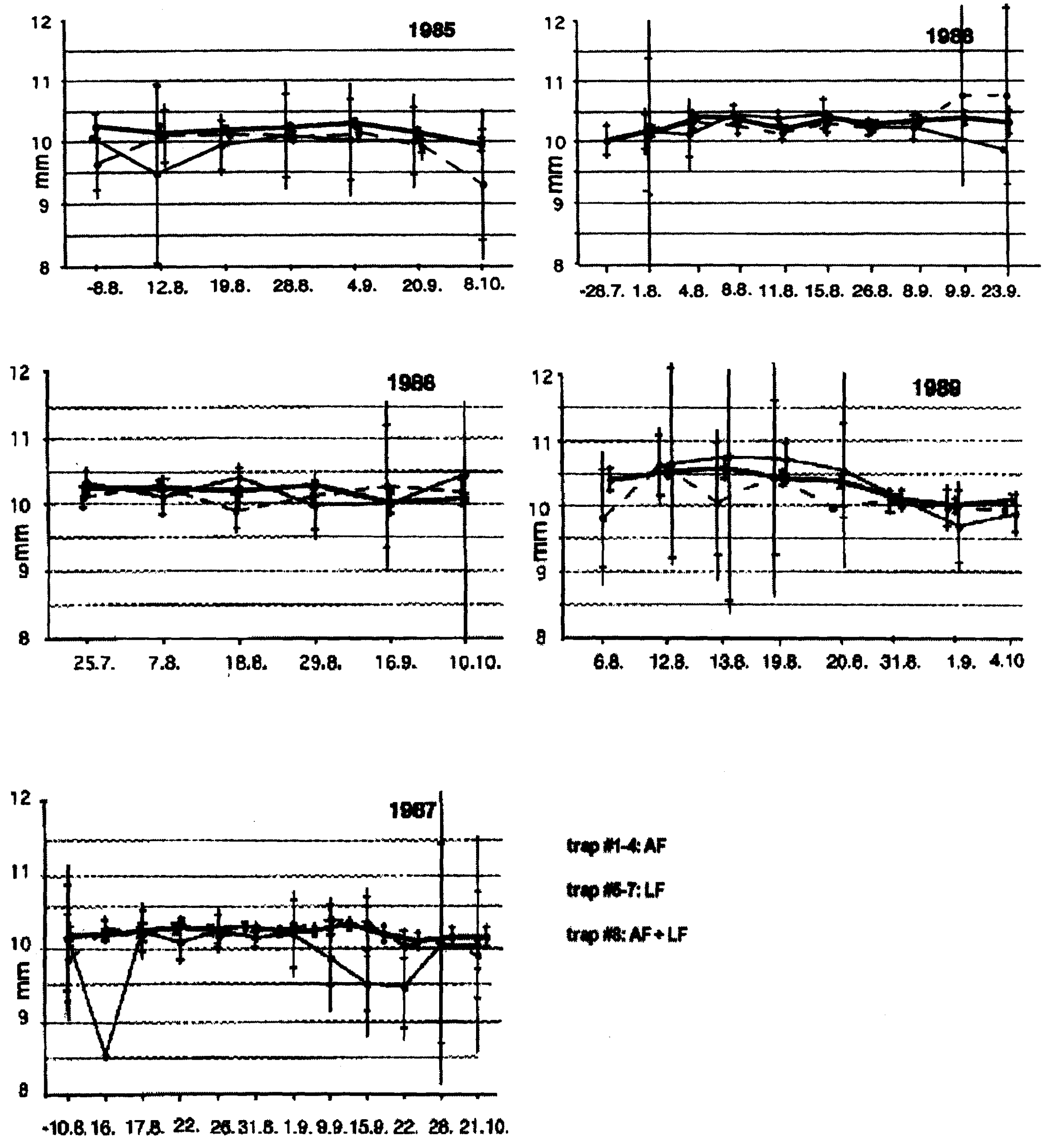


Figure 7. Moth size in the course of the flight season 1985-88 in Sils.

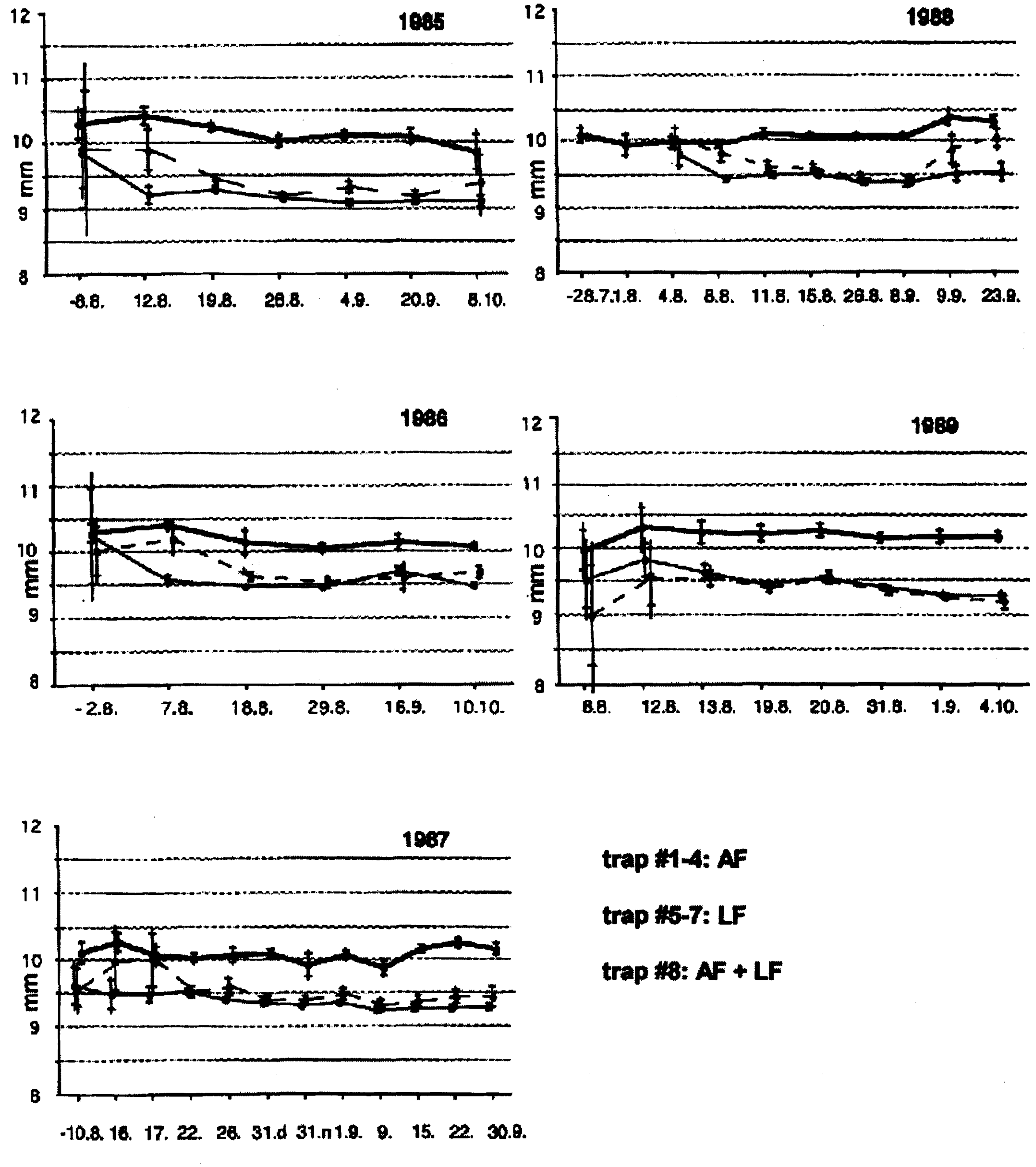


Figure 8. Moth size in the course of the flight season in Pontresina 1985.

Thus pheromone monitoring of the two host races provided much new information, but it could not contribute to the question of the driving force of the cycle at its minimum density. Whether allozyme and/or DNA analysis might help to elucidate this problem will need more research.

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