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FOREST INSECT GUILDS: PATTERNS OF INTERACTION WITH HOST TREES

Edited by:

YURI N. BARANCHIKOV
WILLIAM J. MATTSON
FRED P. HAIN
THOMAS L. PAYNE

Abakan, Siberia, U.S.S.R.
August 13-17, 1989

COVER

The insects on the cover are all European dendrophilous species: *Nymphalis polychloros* (Nymphalidae), *Cimbex femorata* (Cimbicidae), and *Dasyneura rozkovi* (Cecidomyiidae). Mr. Victor Bakhtin (Krasnoyarsk, U.S.S.R.) was the artist.

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PREFACE

This proceedings is the result of a symposium held in Abakan, Siberia, U.S.S.R., August 13-17, 1989. It was organized under the guidelines of the International Union of Forestry Research Organizations. Five IUFRO Working Parties convened to achieve this exchange: S2.07-01 (Seed and Cone Insects), S2.07-05 (Bark Beetles), S2.07-06 (Population Dynamics), S2.07-08 (Gall Midges), and S2.05-06 (Mechanisms of Tree Resistance to Insects).

The papers are arranged in three sections according to their subject matter: 1) general or theoretical papers, 2) highly mobile, external phytophages, and 3) poorly mobile, internal phytophages. The breakdown by external and internal feeding strategy was done to recognize that therein lies a fundamental dichotomy between the kinds of defenses employed by trees against these two broad classes of feeders. This is not to imply, however, that within each general class there are not still substantial guild-to-guild differences in plant defenses. There are. This was the subject of the symposium.

This publication is the result of a joint effort between the Northeastern Forest Experiment Station and the North Central Forest Experiment Station, USDA Forest Service. It is symbolic of their strong support for IUFRO goals of facilitating worldwide research on the significant problems facing forest resource managers.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the V.N. Sukachev Institute of Forest and Wood, Siberian Branch of the U.S.S.R. Academy of Science, and the U.S.S.R. State Committee for Forests. Without their unflagging commitment this symposium could not have materialized. In particular, Dr. A. Isaev, Minister of State Forests, provided crucial sponsorship.

We also thank Mrs. Svetlana Pusir for her very significant technical assistance.

Over the course of more than one year, many people helped to bring this printed volume to fruition. To them, we are especially indebted because they donated substantial time from their busy schedules. We recognize them in alphabetical order: Bruce A. Birr, Robert A. Haack, Robert K. Lawrence, and William A. Main. In addition, we thank Marilyn Brouwer and Robin Bolig for their exacting efforts in the technical editing and computer formatting of the entire volume.

Finally, we thank the INRA Station de Zoologie Forestiere, Ardon-45160 Olivet, France, for providing work space and support while editorial chores (of WJM) were being executed.

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HOST-PLANT SPECIALIZATION IN NEEDLE-EATING INSECTS OF SWEDEN

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INTRODUCTION

It has been suggested that the enormous diversity of phytochemicals within the plant kingdom makes it impossible for one and the same insect species to exploit all plant species (Dethier 1954, Fraenkel 1959). Not surprisingly, the number and diversity of host plants utilized by different phytophagous insects are highly variable, and the specific selective pressures acting on them are still poorly understood (Bernays and Graham 1988, Strong 1988). Many hypotheses have been proposed to explain variations in host specificity among phytophagous insects. For example, there are those based on plant traits: plant defenses (Ehrlich and Raven 1964), plant apparency (Feeny 1976, Rhoades and Cates 1976), plant abundance (Root 1973), plant nutritional value (Mattson and Scriber 1987); those based on insect traits: degree of intimacy with the host plant (Mattson et al. 1988), neuronal capacity of the insect (Levins and MacArthur 1969) and finally those based on natural enemies' traits, e.g. the impact of generalist predators (Bernays and Graham 1988).

In this paper we examine the predictions resulting from hypotheses based on plant characteristics and insect intimacy. We have used the data available in the literature on host ranges of Swedish needle-eating insects reported to feed on the three major conifer species native to Sweden: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and juniper (*Juniperus communis*). These species account for almost all of Sweden's coniferous flora.

HYPOTHESES EXPLAINING HOST-PLANT SPECIALIZATION

According to the plant apparency hypothesis, differences in tissue chemistry exist between long-lived perennial plants that are easily discovered by insects (apparent) and annual ephemerals that are more difficult to discover (unapparent) (Feeny 1976, Rhoades and Cates 1976). Supposedly, apparent plants contain relatively large amounts of unspecific allelochemicals of low toxicity, high in molecular weight (e.g. tannins), whereas unapparent plants contain small amounts of specific, highly toxic allelochemicals with a low molecular weight (e.g. glucosinolates). These groups of allelochemicals have been called quantitative and qualitative, respectively, by Feeny (1976). Owing to these differences, polyphagous insects are associated mainly with apparent plants and monophagous insects mainly with unapparent plants. Being long-lived and large, conifers meet all the criteria of apparent plants. Hence one can predict that a majority of insects feeding on conifers will be polyphagous. However the apparency hypothesis further predicts that the types of allelochemicals will vary among tissues within a plant depending on tissue apparency. Analogous to between-species variation, apparent tissue (usually perennial), containing unspecific allelochemicals, and unapparent tissue (usually short-lived), containing more specific allelochemicals, should favor polyphagy and monophagy, respectively.

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According to the nutrition hypothesis, folivores that feed on nutrient-impoverished plants will have evolved special behavioral adaptations and digestive and metabolic systems that allow them to sequester nutrients from very dilute mediums (Mattson and Scriber 1987). Such adaptations should not in principle prevent them from also feeding on nutrient rich diets. Hence they have the capacity to be polyphagous if other factors are not limiting. Because the conifer species in this study tend to be adapted to nutrient poor sites, and characteristically have low concentrations of N in their needles (Tamm 1955), one might predict then that their phytophagous insects should tend to be polyphagous other things being equal. In fact, Holloway and Hebert (1979) reported that many species of macrolepidoptera feeding on conifers seem to be less specific in their choice of hosts than species feeding on Angiosperms.

According to the Host Intimacy Hypothesis, host specialization by insects will be proportional to the amount of time and body surface area which is spent in direct contact with living tissues of the host plant (Mattson et al. 1988). The rationale is that high intimacy requires highly elaborate behavioral, physiological, and temporal adaptations with a host plant and that increasing intimacy will therefore impose concomitant specialization. Hence the intimacy hypothesis predicts that intimate species such as leaf miners should tend toward monophagy whereas nonintimate species such as free feeding Lepidoptera should tend toward polyphagy.

METHOD AND DEFINITIONS

Information about food plants utilized by each insect species was obtained from Escherich (1931), Nordström et al. (1941), Schwenke (1974, 1978, 1982), Winter (1983), and Ehnström (pers. comm.) but the appendices provide further details. Only insects reported to occur on juniper (Cupressaceae), Scots pine (Pinaceae), and Norway spruce (Pinaceae) have been included. Most of the literature data concern insect occurrence at the plant species level, but in some cases information at the genus level has also been included.

Host-plant specialization is defined according to Cates (1980): insects are considered to be monophagous (Mono) if they utilize one or several plant species within a single genus, oligophagous (Olig) if they feed on two or more genera within one plant family or closely related families, or polyphagous (Poly) if they feed on plants from two or more families (i.e. at least one conifer and some angiosperm). Insect species feeding on one genus within the Pinaceae plus juniper, and insects feeding on two or more genera within the Pinaceae plus juniper, denoted MonoJ and OligJ respectively in the appendices, are included in the oligophagous group elsewhere. Chemistry and morphology are more similar between the two conifer families than between conifers and angiosperms (Thomas 1970), justifying our inclusion of insects denoted MonoJ and OligJ in the oligophagous group.

With respect to numbers of insect species associated with various host plants, a good correspondence has been found between faunal lists derived from the literature and data based on extensive field sampling (Southwood et al. 1982, Niemelä and Neuvonen 1983). Thus the coarse division of host range used in this study probably reflects actual conditions.

Needles were classified as either young or old. The young included buds and current-year needles; the old group included needles $\geq$ 1 year of age.

RESULTS

Detailed information concerning the host plants utilized by individual insect species as well as their host ranges, needle-age utilization, and feeding modes are presented in Appendices A-D.

No obvious trend in the degree of host-plant specialization is apparent when all insect species are considered (Table 1). However, the degree of specialization varies distinctly among feeding and taxonomic insect groups. Mining microlepidopterans are mainly monophagous ($X^2 = 13.38$, $p < 0.01$, df = 2). The absolute monophagy among the sawflies is notable. Chewing micro- and macrolepidopterans are predominantly polyphagous, the microlepidopterans, however, not significantly so ($X^2 = 5.76$, $p > 0.05$, df = 2, and $X^2 = 14.92$, $p < .001$, df = 2, respectively). Beetles are mainly oligophagous.

Table 1. Numbers of mono-, oligo-, and polyphagous species within different insect groups on Swedish conifers

Insect group	Monophagous	Oligophagous	Polyphagous
Microlepidoptera			
Chewing	2	5	10
Mining	13	6	0
Others	7	4	3
Macrolepidoptera	2	16	21
Hymenoptera			
Symphyta	28	0	0
Coleoptera			
Larvae	1	3	0
Adults	2	9	6
All chewing spp.	33	33	37
Total	55	43	40

Table 2. Degree of host-plant specialization among chewing insects as related to their needle-age (young vs. old) utilization on Swedish conifers (based on 14 Lepidoptera, one sawfly, and four Coleoptera species)

Host range	Young needles	Old needles
Monophagous	0	1
Oligophagous	5	5
Polyphagous	5	3

No association was found between the degree of host-plant specialization and needle-age utilization in chewing insect species (Table 2).

The oligophagous group predominates on all three conifers, comprising ca. 45 percent of the total number of insect species on each of them (Fig. 1). The relative proportions of monophagous and polyphagous insects differ between the tree species. Juniper, with its high proportion of monophages and low proportion of polyphages, differs significantly from both spruce and pine ($X^2 = 9.59$, $p < 0.01$, df = 2, and $X^2 = 6.15$, $p < 0.05$, df = 2, respectively). Although spruce and pine do not differ significantly, the proportion of monophages is slightly higher on pine.

DISCUSSION

All conifer species studied must be regarded as highly apparent to insects searching for ovipositional sites and low in nutritive value. According to the apparency and nutrition hypotheses, insects feeding on these tree species should tend toward polyphagy. Our data show no such trend when all insect species are considered. On the contrary, less than one third (29 percent) are polyphagous (Table 1). However, such a crude comparison might be too superficial. A more realistic assessment might be achieved by comparing our results with the proportion of monophagous and polyphagous insect species in studies including less apparent and more nutritious plants. This is possible only with specific insect groups (see below). Juniper differs from both spruce and pine, furthermore, in having relatively more monophagous insect species (Fig. 1). However, differences between the three conifer species with respect to apparency and nutritional value appear to be small. Ideally, any attempt to explain host-plant specialization based on plant characteristics should at least take variation in feeding habits among insect feeding guilds into account. The selection pressure on the insect varies depending on the plant traits encountered during feeding. Although this fact was earlier pointed out by Feeny (1976), among others, it has often been ignored. For example, insects feeding internally, such as mining insects, might be able to avoid some plant allelochemicals that are compartmentalized in the plant (Feeny 1970, 1976, Cornell 1989). On the other hand, they might expose themselves more to rapidly inducible defenses, such as phytoalexins. Although the nutrition

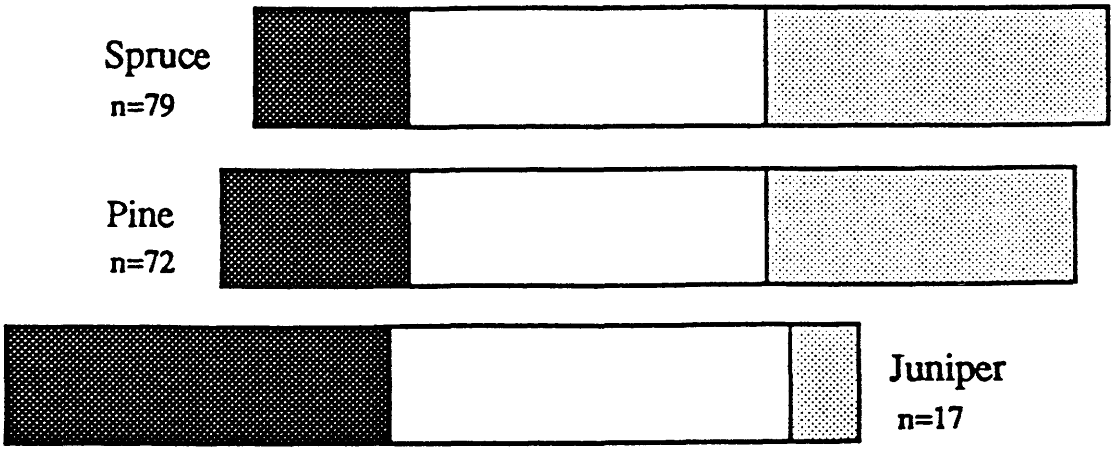

Figure 1. Relative proportions (%) of mono-▓, oligo-□, and polyphagous ░ insect species on each of the three conifer species. Each bar equals 100%. n = number of insect species.

hypothesis was developed based on free-living Lepidoptera, other groups might be more sensitive to variation in nutrient concentrations. In the following, therefore, we have broken down our data into feeding guilds.

Mining Microlepidopterans

The fact that the main defense compounds in conifers (terpenes) are concentrated in clearly defined resin ducts (Bennett 1954) may have important consequences for mining insects. For example, one needle-mining microlepidopteran (*Exoteleia pinifoliella*) utilizes only pine species whose needles have very few resin ducts, all of which are small. Thus this species appears to be avoiding the resinous defense of the host (Bennett 1954). Mining insects seem to be very specialized, irrespective of which food plants they utilize (Hering 1951, Claridge and Wilson 1982, Price 1983). This implies that the degree of host-plant specialization is determined by selective pressures other than those proposed by the apparency hypothesis. The intimate relationship between mining insects and their hosts can probably best explain the narrow host ranges of mining insects. For example, the need to adapt to the anatomy and phenology of the plant may determine the range of hosts that a miner can potentially exploit (Hering 1951). However, the high degree of specialization might actually be an artifact produced as a result of poor investigation of most mining insects (Connor et al. 1980, Powell 1980).

Chewing Insects

Generally, insects feeding externally on leaves and needles come into minimal contact with their host's chemical defense. Among the chewing insects in this study, however, the monophagous species constitute as large a proportion as the polyphagous species when compared over all conifer species (32 percent and 36 percent, respectively).

However, most of the monophagous species are sawflies (Table 1) and sawflies are predominantly monophagous, regardless of which type of plants they utilize (Hodkinson and Hughes 1982, Shaw 1984). Neither the apparency nor the nutrition hypothesis predicts this monophagy. In contrast, the intimacy hypothesis does because conifer-feeding sawflies insert their eggs into the needles of their host, and needle morphology is an important factor in determining oviposition success (Ghent 1959). The ability of females to find needles suitable for oviposition should therefore be strongly selected for. A behavioral adaptation of this kind could be a major reason for the prevalence of monophagy among needle-eating sawflies (Futuyma and Peterson 1985). Moreover, several conifer sawflies have evolved the ability to "detoxify" the defensive compounds produced by their hosts (Eisner et al. 1974, Larsson et al. 1986) and furthermore to use these substances in their own defense against natural enemies (Eisner et al. 1974, Morrow et al. 1976, Boevé and Pasteels 1985). This may be another reason why sawflies on conifers are so specialized. Thus the intimacy hypothesis is partially supported in the sawfly case.

The predominance of polyphagy among chewing Lepidoptera accords with the predictions of all three hypotheses. In two other studies including insects feeding on less apparent, more nutritious plants, the proportion of polyphagous species was reported to be 54 percent and 32 percent (Holloway and Hebert 1979, Hodkinson and Hughes 1982, respectively), whereas in this study it was 52 percent. According to both the apparency and the nutrition hypotheses, however, one would expect relatively more polyphagous insect species on conifers than on plants of lower apparency and higher nutritional value. Thus one out of two comparisons with other studies supports these hypotheses. In principal, a species may behave as a generalist either because every individual is generalistic or because the species consists of specialized individuals or subpopulations (Van Valen and Grant 1970, Jaenike 1978, Singer 1983). For herbivorous insects there are many examples of specialization among individuals and populations (Knerer and Atwood 1973, Fox and Morrow 1981, Singer 1983, Futuyma and Peterson 1985, Ng 1988). *Lasiocampa quercus* provides one such example in this study (Appendix B). Until more data have been accumulated on the nature of polyphagy in herbivorous insects, any general conclusion would seem premature. Nevertheless, it is possible that "true polyphagy" (i.e. generalistic individuals) is a rare phenomenon. For example, the cost of multiple detoxification systems might be too great for individual insects (Karowe 1989).

Needle-Age and Degree of Specialization

According to the apparency hypothesis, young tissue should be protected by qualitative defenses and thus there should be selection for specialization among insects feeding on such tissue. However, there is no correlation between needle-age utilized and degree of host-plant specialization in our data (Table 2). Results from studies of insects on deciduous trees support the apparency hypothesis (Cates 1980, Niemelä 1983). This difference between conifers and deciduous trees with respect to degree of specialization and utilized tissue-age could be due to the fact that young needles develop more slowly than young deciduous leaves. Hence the absence of a correlation between needle-age and degree of specialization could be due to small differences in apparency between young and old needles. Still, there is evidence showing that young needles of jack pine (*Pinus banksiana*) and Scots pine contain a resin acid that repels sawflies normally feeding on old needles (Ikeda et al. 1977 and Niemelä et al. 1982, respectively). It has yet to be determined whether other needle-eating insects are repelled by the same substances (Buratti et al. 1990).

CONCLUSIONS

The applicability of the examined hypotheses to Swedish needle-eating insects can be summarized in the following way. 1) Polyphagy predominates among chewing lepidopterans, thereby supporting all three hypotheses. However, the many examples of specialized individuals among polyphagous insects and the comparison of our results with those obtained in studies of macrolepidopterans on other plant species weaken this support. 2) The absolute monophagy among sawflies supports the intimacy hypothesis and may be attributable to the oviposition behavior of the female and the detoxification ability of the larvae. 3) Although data on the mining insects also supports the intimacy hypothesis, the impact of generalistic predators cannot be ruled out. 4) No correlation was found between utilized needle-age and host-plant specialization, possibly because small differences in apparency exist between young and old needles.

The data presented here supply very little support for the apparency and nutrition hypotheses. In their defense, we readily acknowledge that they were never developed as explanations for host specialization by phytophagous insects. For this reason, then, they are too general as we have presented them. They treat herbivorous insects as a uniform group and do not distinguish between feeding guilds. It has become more and more apparent that insect feeding guilds must be treated separately if we are adequately to understand plant-insect interactions (Mattson et al. 1988, Cornell 1989, Larsson 1989). The intimacy hypothesis, which distinguishes between insect feeding guilds, is the hypothesis given most support by the data obtained in our survey of the literature.

SUMMARY

The degree of host-plant specialization in needle-eating butterflies and moths (Lepidoptera), sawflies (Hymenoptera, Symphyta), and beetles (Coleoptera) occurring in Sweden has been examined based on data in the literature.

No general trend was found when all insects were considered. However, a closer examination of certain feeding guilds revealed that 1) polyphagy is predominant among chewing Lepidoptera,

2) monophagy among the mining microlepidoptera and all sawfly species, and 3) oligophagy among beetles.

No correlation was found between utilized needle-age and degree of host-plant specialization.

A comparison of the relative numbers of monophagous, oligophagous, and polyphagous insect species on the three common conifers (i.e. Scots pine, Norway spruce, and juniper) in Sweden showed that the frequencies of oligophagy are similar for each of the conifer species. However, the proportion of monophagous species was found to be significantly greater in juniper than in pine and spruce.

These results are discussed with reference to hypotheses concerning patterns of host specificity in herbivorous insects based on plant characteristics.

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APPENDIX A

Host-plant utilization, host range, utilized tissue-age, and feeding mode of microlepidoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Gustafsson (1979); reference not provided.

Family Species	Host plants[1]	Host range[2]	Tissue age[3]	Feeding mode[4]	References
Yponomeutidae					
Argyresthia abdominalis Zell.	Jun	Mono	?	M	1,2
A. arceuthina Zell.	Jun	Mono	?	BM	1,2
A. aurulentella Stt.	Jun	Mono	?	M	1,2
A. dilectella Zell.	Jun	Mono	?	M	1,2
A. fundella F.v. Rösl.	Pic,(Abi)	Olig	Y+O	M	2,4,5
A. glabratella Zell.	Pic	Mono	Y	M	1,4
Blastotere bergiella Ratz.	Pic	Mono	Y	M	4
Cedestis gysseleniella Zell.	Pin,(Abi)	Olig	O	M	1,4,6
C. subfasciella Steph.	Pin	Mono	O	M	1,4,6,7
Ocnerostoma friesei Svensson	Pin	Mono	?	M	1,7
O. piniariella Zell.	PIN,Jun	OligJ	?	M	1,4,7,10
Gelechiidae					
Dichomeris juniperella L.	Jun	Mono	?	C	1
D. marginella F.	Jun	Mono	O?	C	1,3
Exoteleia dodocella L.	Pin	Mono	Y(O)	M	1,4,10,11
Momphidae					
Batrachedra pinicolella Zell.	Pic,Pin	Olig	?	M	1,3
Tortricidae					
Acleris abietana Hb.	PIN	Olig	Y+O	C	1,4,8,12
A. hyemana Haw.	PIN,D	Poly	?	C	1,8
Aphelia paleana Hb.	Pic,H	Poly	?	?	1,8
A. viburnana Den. & Schiff.	PIN,D,H	Poly	Y	C	1,4,8
Archips oporana L.	PIN,Jun	Olig	Y+O	C	1,4,6,12
A. podana Scop.	PIN,D	Poly	Y+O	C	1,4,12
A. rosana L.	Pic,D,H	Poly	?	C	1,4,5,10
Blastesthia posticana Zett.	Pin	Mono	Y	M	1,4,10
B. turionella L.	Pin,H	Poly	Y	M	1,4
Clepsis senecionana Hb.	PIN,H	Poly	?	M	1
Cnephasia incertana Treit.	PIN,H	Poly	?	M→C?	4,8
Epinotia caprana F.	Pin,D	Poly	?	C	1,8
E. fraternana Haw.	PIN	Olig	O	M	1,4,8
E. nanana Treit.	Pic	Mono	O	M	1,4,10
E. nigricana H.-S.	Abi,(Pic)	Olig	Y	BM	1,4
E. pygmaeana Hb.	Pic,(Abi)	Olig	Y(O)	M→C	1,4
E. rubiginosana H.-S.	Pin	Mono	?	M→C	1,8,10

APPENDIX A continued

Family Species	Host plants[1]	Host range[2]	Tissue age[3]	Feeding mode[4]	References
E. subsequana Haw.	Abi,Pic	Olig	Y	M	1,4
E. tedella Cl.	Pic	Mono	(Y)O	M	1,4,13
Olethreutus lacunana Den. & Schiff.	Pic,D,H	Poly	?	C	1,4,8
Pandemis cinnamomeana Treit.	PIN,D,H	Poly	Y+O	C	1,3,4,12
Philedone gerningana Den. & Schiff.	Pic,D,H	Poly	?	C	1,3,8
Philedomides lunana Thnbg.	PIN,D,H	Poly	?	C	1,8
Ptycholoma lecheana L.	Pic,D	Poly	?	C	1,4
Rhyacionia buoliana Den. & Schiff.	Pin	Mono	Y(O)	M(BM)	1,4,14
R. duplana Hb.	Pin	Mono	Y	BM	1,4
R. pinicolana Doubl.	Pin	Mono	Y	BM	1,4
R. pinivorana Zell.	Pin	Mono	Y	BM	1,4
Spilonota laricana Hein.	Lar,(Pic)	Olig	Y	C→M	1,4
Zeiraphera diniana Guen.	Pic,Pin	Ol*	Y	C(BM)	1,4,10
Z. ratzeburgiana Ratz.	PIN	Olig	Y	C(BM)	1,4
Cochylidae					
Aethes rutilana Hb.	Jun	Mono	?	C	1,9
Pyralidae					
Dioryctria abietella Den. & Schiff.	PIN	Olig	Y	BM	4
D. mutatella Fuchs	Pin	Mono	Y	BM	1,4
D. schuetzella Fuchs	Pic,Abi	Olig	Y	C	1,4

* The Picea-Pinus-race that might be a species (two other races exhibit other host plant preferences)

[1] Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

[2] Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

[3] Y = young tissue (buds and current-year needles) and O = old tissue (1-year-old or older needles).

[4] C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Escherich (1931), 3) Spuler (1913), 4) Schwenke (1978), 5) Schnaider (1976), 6) Trägårdh (1915), 7) Hannemann (1977), 8) Hannemann (1961), 9) Hannemann (1964), 10) Browne (1968), 11) Martin (1959), 12) Patocka (1960), 13) Führer (1967), and 14) Pointing (1963).

APPENDIX B

Host-plant utilization, host range, utilized tissue-age, and feeding mode of macrolepidoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Elmqvist et al. (1977); reference not provided.

Family Species	Host plants^1	Host range^2	Tissue age^3	Feeding mode^4	References
Geometridae					
Biston betularia L.	Lar,Pic,D,H	Poly	?	C	1,2
Bupalus piniarius L.	PIN	Olig	Y+O	C	1,3,4
Deileptenia ribeata Cl.	PIN,D	Poly	?	C	1,3
Ectropis bistortata Goeze	PIN,D,H	Poly	Y?	C	1,3
Entephria caesiata Den. & Schiff.	Pin,D,H	Poly	?	C	1,2
Eupithecia conterminata Zell.	Pic	Mono	O?	C	2,5
E. indigata Hb.	PIN	Olig	Y	C	1,3
E. intricata Zett.	Jun	Mono	?	C	1,2,5
E. lanceata Hb.	PIN	Olig	Y	C	2,3
E. laricata Fr.	Lar,Jun	MonoJ	Y?	C	1,2,3
E. nanata Hb.	PIN,H	Poly	?	C	1,2,6
E. pusillata Den. & Schiff.	PIN	Olig	Y+O	C	2,3,7
Gymnoscelis rufifasciata Haw.	Pic,Pin,D,H	Poly	?	C	1,2
Hydriomena furcata Thnbg.	Pic,Pin,D,H	Poly	?	C	1,3
Hylaea fasciaria L.	Pin,(Pic),D	Poly	O	C	1,3,8
Odontopera bidentata Cl.	Pin,Abi,H	Poly	O	C	1,2,3
Operophtera brumata L.	Pic,D	Poly	Y	C	1,2,3
O. fagata Scharf.	Pic,D	Poly	Y	C	1,2,3
Peribatodes secundaria Esp.	Pic,Pin	Olig	(Y)O	C	1,3,7
Perizoma didymata L.	Pic,Pin,H	Poly	?	C	1,2
Semiothisa liturata Cl.	PIN,Jun	OligJ	O	C	1,9,10
S. signaria Hb.	PIN	Olig	O	C	1,3
Thera cognata Thnbg.	Jun	Mono	?	C	1,2
T. firmata Hb.	Pin,Jun	MonoJ	O	C	1,3,11
T. juniperata L.	Pic,Jun	MonoJ	?	C	1,3
T. obeliscata Hb.	PIN,Jun	OligJ	?	C	1,3
T. variata Den. & Schiff.	PIN,Jun	OligJ	Y+O	C	2,3,8
Lymantriidae					
Lymantria dispar L.	Lar,Pin,D,H	Pol*	Y	C	1,3,12
L. monacha L.	PIN,D	Poly	Y+O**	C	1,3,12
Orgyia antiqua L.	PIN,D,H	Poly	Y(O)	C	1,2,3
Noctuidae					
Acronicta rumicis L.	Pic,D,H	Poly	?	C	1,2,13

APPENDIX B continued

Family Species	Host plants[1]	Host range[2]	Tissue age[3]	Feeding mode[4]	References
Blepharita adusta Esp.	Pic,Pin,H	Poly	O	C	1,13
Ceramica pisi L.	Lar,Pic,D,H	Poly	?	C	1,3,13
Panolis flammea Den. & Schiff.	PIN,(Jun),D	Poly	Y+O	C	1,3,14
Panthea coenobita Esp.	PIN	Olig	O	C	2,3,7
Lasiocampidae					
Dendrolimus pini L.	PIN	Olig	Y+O	C	3,15
Lasiocampa quercus L.	PIN,D,H	Pol*	?	C	1,3
Macrothylacia rubi L.	Pic,D,H	Poly	?	C	1,2
Selenephera lunigera Esp.	PIN	Olig	?	C	2,3
Sphingidae					
Hyloicus pinastri L.	PIN	Olig	?	C	1,3,16

* Possibly ecological races with respect to host plant choice
** If on spruce, feeds as young larvae on young tissue and later as old larvae on old tissue; if on pine, vice versa

[1] Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

[2] Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

[3] Y = young tissue (buds and current-year needles) and O = old tissue (one-year-old or older needles).

[4] C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Nordström et al. (1941), 3) Schwenke (1978), 4) Engel (1939), 5) Hoffmeyer (1966), 6) Browne (1968), 7) Patocka (1960), 8) Escherich (1931), 9) Schwenke (1953), 10) Hofmann (1941), 11) Larsson and Tenow (1980), 12) Trägårdh (1939), 13) Forster and Wohlfahrt (1971), 14) Schwerdtfeger (1970), 15) Grönberg (1903), and 16) Nunberg (1939).

APPENDIX C

Host-plant utilization, host range, utilized tissue-age, and feeding mode of Hymenoptera, Symphyta feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Hedqvist (pers. comm.).

Family Species	Host plants[1]	Host range[2]	Tissue age[3]	Feeding mode[4]	References
Pamphiliidae					
Acantholyda erythrocephala L.	Pin	Mono	(Y)O	C	1,2
A. flaviceps Retz.	Pin	Mono	Y+O	C	2
A. posticalis Mats.	Pin	Mono	Y+O*	C	1,2
Cephalcia abietis L.	Pic	Mono	(Y)O	C	2
C. arvensis Panzer	Pic	Mono	Y→O	C	2
C. erythrogastra Htg.	Pic	Mono	Y+O	C	3
C. falleni Dalm.	Pic	Mono	Y+O	C	2
Diprionidae					
Diprion butovitschi Hedqv.	Pin	Mono	Y+O	C	2,3
D. pini L.	Pin	Mono	Y→O	C	1,2,4
D. simile Htg.	Pin	Mono	Y+O	C	1,2,5
Gilpinia frutetorum F.	Pin	Mono	Y+O	C	1,2,4
G. hercyniae Htg.	Pic	Mono	(Y)O	C	1,2
G. pallida Klug	Pin	Mono	Y+O	C	1,2
G. verticalis Guss.	Pin	Mono	Y+O	C	2,6
G. virens Klug	Pin	Mono	Y+O	C	1,2
Microdiprion pallipes Fall.	Pin	Mono	Y+O	C	1,2,7
Monoctenus juniperi L.	Jun	Mono	Y+O	C	1,2
M. obscuratus Htg.	Jun	Mono	Y+O	C	2
M. subconstrictus Thoms.	Jun	Mono	Y+O	C	2
Neodiprion sertifer	Pin	Mono	O	C	1,2,4
Tenthredinidae					
Pachynematus montanus Zadd.	Pic	Mono	Y→O	C	1,2
P. scutellatus Htg.	Pic	Mono	Y→O	C	1,2
Pristiphora abietina Christ.	Pic	Mono	Y+O	C	1,2
P. ambigua Fall.	Pic	Mono	Y+O	C	1,2
P. amphibola Först.	Pic	Mono	Y+O	C	1,2
P. compressa Htg.	Pic	Mono	Y→O	C	1,2
P. saxesenii Htg.	Pic	Mono	Y→O	C	1,2
P. subarctica Forssl.	Pic	Mono	Y+O	C	1,2

* Two forms, one feeding on young tissue and the other on old tissue

[1] Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

[2] Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

[3] Y = young tissue (buds and current-year needles) and O = old tissue (one-year-old or older needles).

[4] C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Schwenke (1982), 3) Hedqvist (pers. comm.), 4) Escherich (1931, 1942) 5) Monro (1935), 6) Hedqvist (1972), and 7) Eidmann and Klingström (1976).

APPENDIX D

Host-plant utilization, host range, utilized tissue-age, and feeding mode of Coleoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Ehnström (pers. comm.).

Family Species	Host plants[1]	Host range[2]	Tissue age[3]	Feeding mode[4]	References
SPECIES IN WHICH LARVAE FEED ON NEEDLES AND/OR BUDS					
Anobiidae					
Dryophilus pusillus Gyll.	PIN	Olig	Y	C	1,2
Curculionidae					
Anthonomus phyllocola Hrbst.	Pin,(Pic)	Olig	Y?	C	1,2
A. pinivorax Silfverb.	Pic,Pin	Olig	Y	C	1,2
Brachonyx pineti Payk.	Pin	Mono	?	C	1,2
SPECIES IN WHICH IMAGINES FEED ON NEEDLES AND/OR BUDS					
Scarabaeidae					
Amphimallom solstitiale L.	Pin,D	Poly	?	C	2
Cerambycidae					
Monochamus galloprovoncialis Ol.	Pin,(Pic)	Olig	?	C	1,2,3
M. sutor L.	Pic,Pin	Olig	?	C	1,2
Chrysomelidae					
Calomicrus pinicola Duft.	Pin,(PIN)	Olig	O	C	1,2
Cryptocephalus pini L.	PIN,(Jun)	OligJ	Y?	C	1,2
C. quadripustulatus Gyll.	PIN	Olig	?	C	1,2
Syneta betulae F.	Pic,D	Poly	Y	C	1,2
Curculionidae					
Anthonomus phyllocola Hrbst.	Pin,(Pic)	Olig	?	C	1,2
A. pinivorax Silfverb.	Pic,Pin	Olig	Y?	C	1,2
Brachonyx pineti Payk.	Pin	Mono	?	C	1,2
Brachyderes incanus L.	Pin	Mono	?	C	1,2
Otiorrhyncus leoidopterus F.	PIN	Olig	?	C	1,2
O. nodosus Mull.	Pin	Mon?	?	C	1
O. scaber L.	PIN	Olig	?	C	2
O. singularis L.	PIN,D,H	Poly	Y(O?)	C	2,4
Philopedon plagiatum Schall.	Pin,Pic,D,H	Poly	?	C	1
Strophosoma capitatum de G.	Pin,Pic,D,H	Poly	?	C	1
S. melanogrammum Forst.	Pin,Pic,D,H	Poly	?	C	1

[1] Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

[2] Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

[3] Y = young tissue (buds and current-year needles) and O = old tissue (one-year-old or older needles).

[4] C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Ehnström (pers. comm.), 2) Schwenke (1974), 3) Hellrigl (1971), and 4) Browne (1968).

SAWFLIES AND PONDEROSA PINE: HYPOTHETICAL RESPONSE SURFACES FOR PINE GENOTYPE, ONTOGENIC STAGE, AND STRESS LEVEL

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INTRODUCTION

Patterns that occur in nature are the result of a complex set of current and historical factors that interact with one another and the adaptive plasticity of plants. Scientists are forced to assess such processes on the basis of series of "snapshots" over a relatively short time that represent only part of the grand pattern. In the case of insects interacting with forest trees, there are dozens of environmental and host plant factors that could be the key factor responsible for the patterns we observe. Because of the high experimental standards of research and the many potentially important factors, scientists tend to construct models by which to test specific hypotheses about key factors. This methodology produces a body of knowledge about a particular factor (e.g. moisture stress) that does not necessarily integrate well with the body of knowledge about a second factor (e.g. genetic resistance). These disjoint sets of data encourage scientists to think in terms of components, and that leads them to draw conclusions about single factors, in isolation from many other important factors. Such conclusions can be misleading.

Given the single-factor focus of the scientific community, it is not surprising that inconsistencies and apparent contradictions are abundant. For example, despite considerable research effort, no clear pattern has emerged to determine the role of environmental stress in creating insect outbreaks (Larsson 1989). Drought or poor site conditions have been correlated with outbreaks of forest insects (Mattson and Haack 1987a, 1987b). In the specific case of sawflies (Hymenoptera: Diprionidae), many outbreaks have been correlated with drought conditions (Kapler and Benjamin 1960, McLeod 1970, Averill and Fowler 1973, Knerer and Atwood 1973, Larsson and Tenow 1984). One hypothesis explaining this phenomenon is that environmental stress changes the host plants and thereby increases herbivore performance in some way. Tests of this hypothesis for sawflies have not been consistently supportive (McCullough and Wagner 1987, Craig et al. 1991, Wagner and Frantz 1990). Meyers (1988) and Larsson (1989) have suggested that the general hypothesis that host plant stress causes outbreaks is "still very much open to debate." Careful reviews of the literature which stratify the evidence by insect feeding guilds clarify the question for some guilds such as bark beetles, but not for others such as defoliators (Larsson and Tenow 1984, Larsson 1989). The recent studies cited above might lead us to conclude that there is no relationship between stress and insect outbreaks, but what about all the previous correlative evidence and the anecdotal evidence that stress is related to insect outbreaks? It seems reasonable to hypothesize that stress is important under some circumstances and not others. The critical point is that several factors interact to create the particular insect/tree pattern we observe

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BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

at any given moment. When we consider multiple factors simultaneously, we can better define those instances in which a factor will or will not be influential.

In this paper I discuss the general evidence from the literature and my preliminary experimental evidence that at least three variables (genotype, ontogeny, and stress) influence the population parameters of *Neodiprion* spp. (Hymenoptera: Diprionidae), which feed on ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. I also present some hypothetical response functions for these single factors. Then I generate some three-dimensional figures that illustrate how two individual variables could interact to create a response surface. Finally, I illustrate how it is possible to generate from very realistic univariate response functions complex response surfaces which could explain otherwise apparently contradictory results.

ROLE OF GENOTYPE IN SAWFLY-PONDEROSA PINE INTERACTION

For most plants there is a range of natural suitability for insects that appears to be genetically controlled. Significant genotype variation in forest trees to insects has been identified for bark beetles (Stark 1965, Callaham 1966, Berryman 1972, Smith 1972, Smith 1975), scales and aphids (Hoff and McDonald 1977, Mattson et al. 1988), pitch midge (Hoff 1988), pine weevils (Hall 1959, King 1971, Wilkinson 1979, Harris et al. 1983, Brooks et al. 1987), shoot moths (Hertel and Benjamin 1975, Charles et al. 1982), cone insects (Askew et al. 1985), defoliators (Tigner and Mason 1973, Genys and Harman 1976, McDonald 1979, 1982, Fogal et al. 1982), and pine sawflies (Arend et al. 1961, Wilson 1966, Wright et al. 1967, Henson et al. 1970). Interestingly, Mattson et al. (1988) argue that there is relatively little evidence for genetic resistance to free-feeding defoliators. Part of their data is based on examination of the susceptibility of trees in range-wide provenance plantations. It may be that the procedures used for creating the provenances trials resulted in inadvertent selection of only susceptible genotypes. For example, it may be that the provenance collection sites were areas with relatively low defoliator pressure and hence a low selection for insect resistance. At any rate, the evidence suggests that there is some genotypic variation in insect susceptibility for most tree species.

For the past 3 years I have been attempting to identify individual trees that exhibit phenotypic resistance to pine sawflies. My basic procedure has been to identify unattacked trees within sawfly outbreak areas. These phenotypically resistant trees have then been paired with nearby phenotypically susceptible trees. To date 10 pairs of trees have been identified. I have bioassayed the trees by caging sawflies on them and measuring stage-specific survival. Following Hanover (1975), seed has been collected from 14 of the 20 trees and half-sib families have been established. The performance of sawflies on the maternal trees of the 14 half-sib families is presented in Fig. 1. Whether the traits that influence susceptibility to sawflies in the maternal trees are inherited by the progeny (half-sibs) has yet to be determined, but it is clear that there is considerable variation in sawfly resistance in the maternal phenotype (2 to 65 percent sawfly survival), and this is an indication of genetic resistance (Bingham 1966, McDonald 1979).

On the basis of the previously cited literature and my preliminary findings, I believe that there is substantive genetic variation in ponderosa pine resistance to herbivores. In other words, when all other factors are held constant, there can be considerable variation in insect performance based on plant genotype alone. For example, I observed a thirtyfold variation in sawfly survival among different ponderosa pine individuals (Fig. 1). As yet it cannot be established that all of this variation is the result of genetic factors, but it is highly probable that some of the variation is due to genetic factors. Greater knowledge about the genetic variation of ponderosa pine could greatly clarify our understanding of how host plants and herbivores interact.

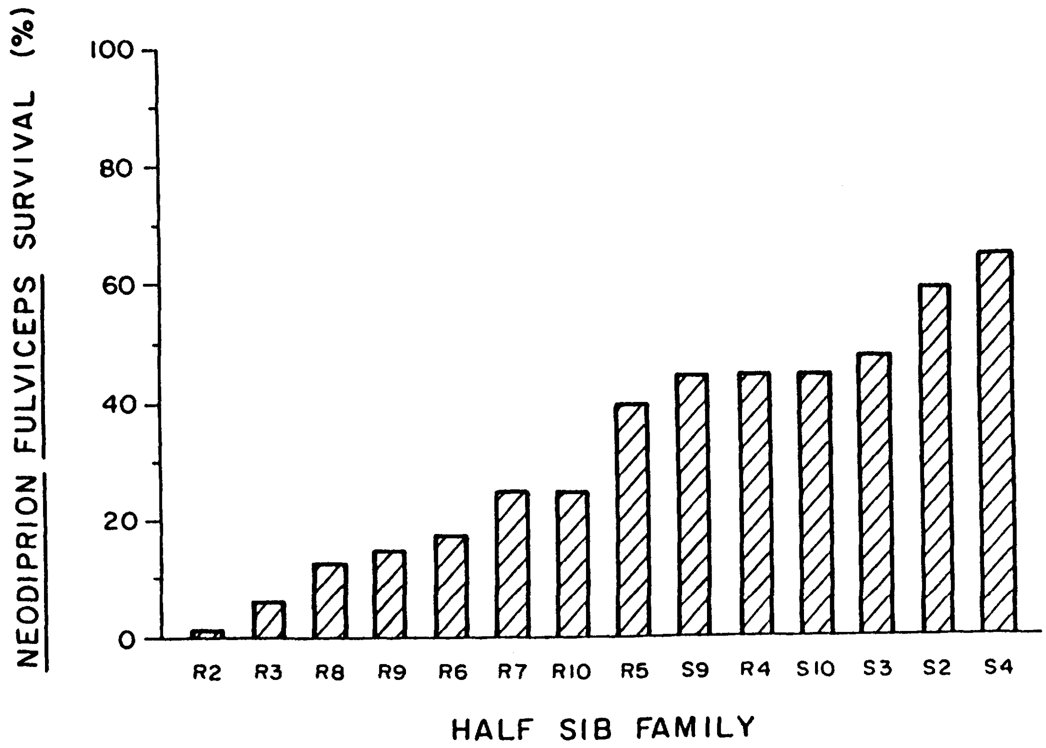

Figure 1. Total generational survival of *Neodiprion fulviceps* on maternal ponderosa pine trees from which 14 half-sib families have been established.

ROLE OF ONTOGENY IN SAWFLY-PONDEROSA PINE INTERACTIONS

Many plants show age-related changes in susceptibility to attack by specific insects. Some insect species attack juvenile trees, such as sawflies on willows (Craig et al. 1986), cynipid wasps on oaks (Washburn and Cornell 1981, Frankie and Morgan 1984), and a chrysomelid beetle on cottonwood (Kearsley and Whitham 1989). Other insects attack primarily mature trees: budworms (Blais 1958), spruce beetles (Schmidt and Frye 1977, Hard 1985), and *Pemphigus* aphids (Kearsley and Whitham 1989). Pine sawflies commonly show age-related preferences on their pine hosts (Knight and Heikkenen 1980, Coulson and Witter 1984, Wagner et al. 1986) and generally prefer pole-sized or smaller trees.

In 1987 we conducted some preliminary tests of the age-related suitability of ponderosa pine to *Neodiprion fulviceps* (Cresson). Branches were collected from five trees (similar vigor) of six different ages (1, 2, 5, 10, 15, and 20 years). One-year-old foliage was bioassayed under laboratory conditions. We observed patterns of oviposition (Fig. 2) and survival (Fig. 3) that suggested an effect of tree age. *Neodiprion fulviceps* had highest survival on 15-year-old trees which is within the usual range of tree ages where this sawfly species occurs. It is interesting to note that the optimal age for oviposition (< 10 years) was not the same as for survival. Because the trees used in this study were of unknown genotype and because the sample size was small, these data are tentative.

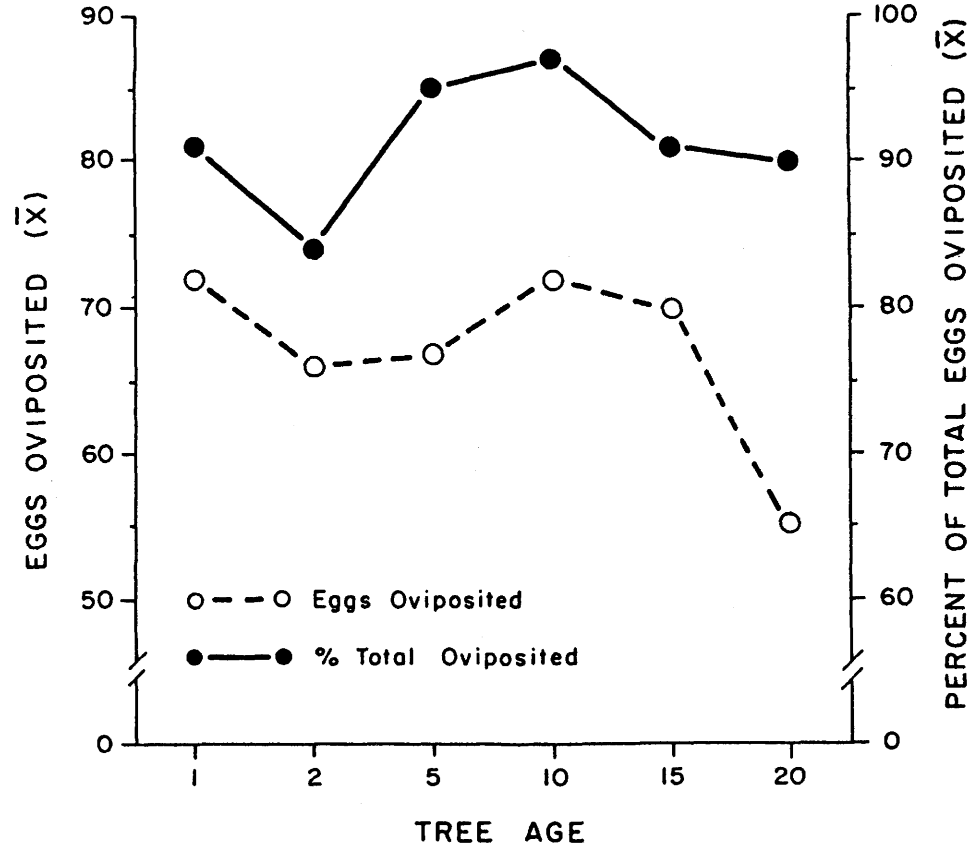

Figure 2. Influence of tree age on the number of eggs laid and the percent of total female fecundity oviposited for *Neodiprion fulviceps* on 1-year-old foliage of six different ages of ponderosa pine.

On the basis of the literature and the preliminary evidence collected, I hypothesize that for any given sawfly species there is a tree age at which sawfly survival would be optimal. The preferred tree age could vary among sawfly species on the same host. This could indicate a method by which sawfly species with similar life cycles partition their food resources to avoid competition. A hypothetical response function for the relationship between sawfly survival and tree age is presented for three ponderosa pine-feeding sawflies (Fig. 4). In this case *Neodiprion gillettei* (Rohwer), which occurs in nature on seedlings, would probably have optimal survival on young trees. In contrast, *Neodiprion fulviceps*, which occurs on much older trees in nature, would probably have optimal survival on older trees. I assume that both species' survival response to tree age approximates a normal curve.

The critical point here is that sawfly survival probably depends on tree age independent of other factors. It is possible that an experimental bioassay of a highly resistant and highly susceptible ponderosa pine genotype, above or below the acceptable age range for a particular sawfly species might indicate that there was no genetic effect, whereas the identical bioassay at the optimal age would indicate a clear difference in performance between genotypes. Any insect-plant interaction experiments conducted with plant material of an inappropriate age might produce very misleading results.

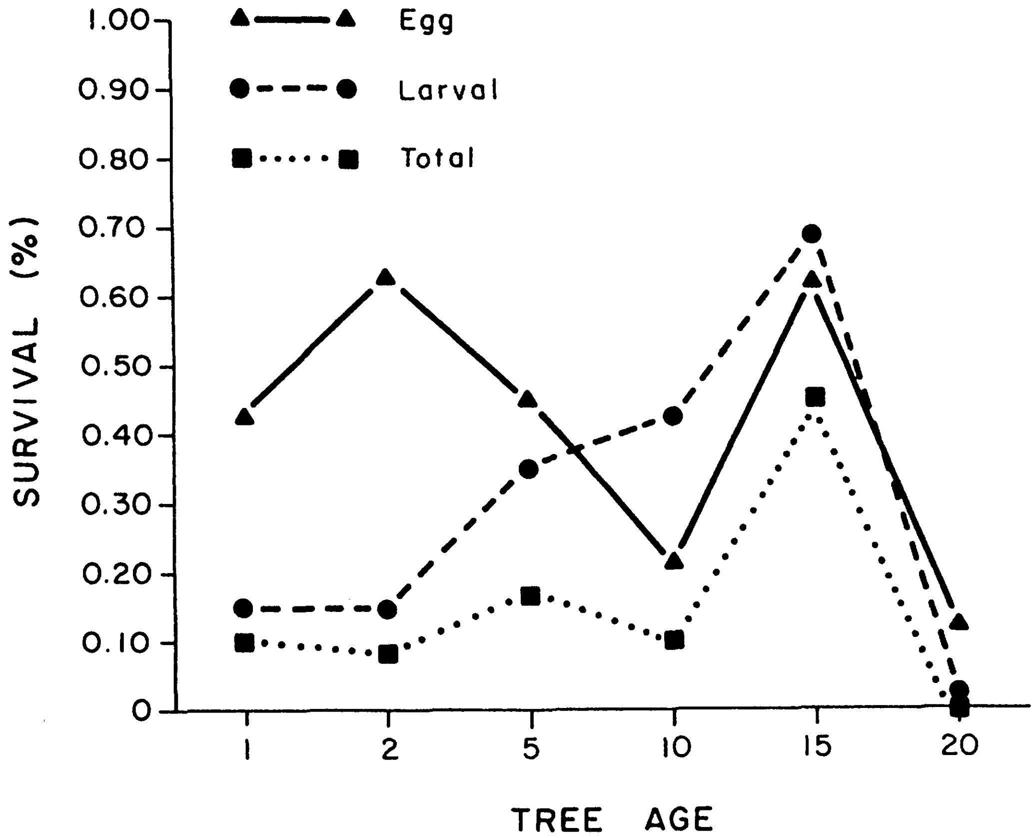

Figure 3. Influence of tree age on egg, larval, and total survival of *Neodiprion fulviceps*.

ROLE OF STRESS IN PINE SAWFLY-PONDEROSA PINE INTERACTIONS

There is yet no clear consensus on the role of environmental stress in provoking insect outbreaks even for a single-model system. After 5 years of experimentally stressing ponderosa pine under field conditions, we still have not established a clear pattern of stress effect (McCullough and Wagner 1987, Wagner and Frantz 1990, Craig et al. 1991). Larvae performed more poorly on stressed trees than on controls for most years. However, we have observed that increasing stress caused increased, then decreased sawfly performance at some period during the 5-year study. This suggests that there is some stress level for the plant at which insect performance is optimal and above or below which performance declines. Because our studies are on wild populations of unknown genotype and because the environmental conditions are not uniform between years, our data are inconclusive. Only rigorous, highly controlled experimental testing will reveal the true nature of the response function for sawfly survival as a result of ponderosa pine stress. In one of the most rigorous studies of water-stress effects on herbivores, English-Loeb (1989) measured a nonlinear population response by the

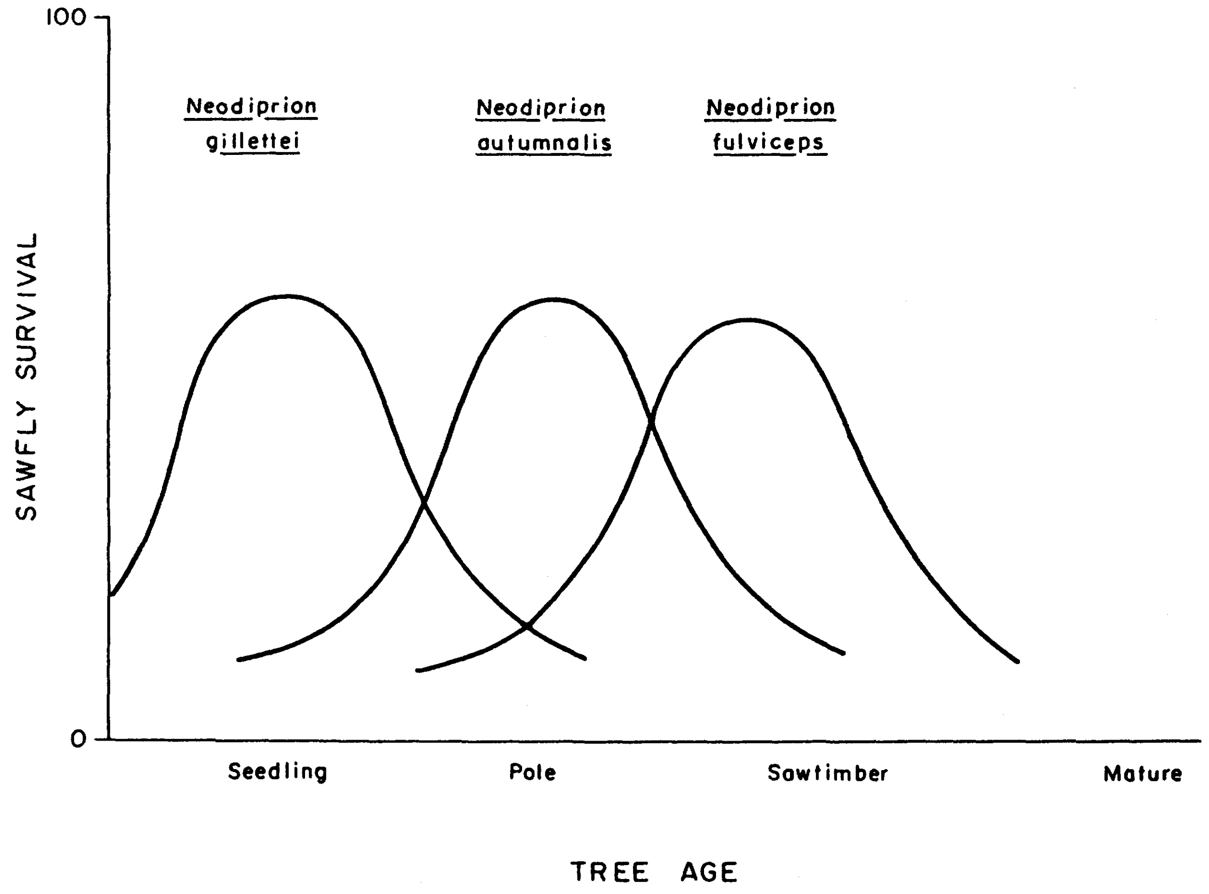

Figure 4. Hypothetical response functions for the effect of tree age on the survival of three species of pine sawflies that feed on ponderosa pine.

two-spotted spider mite, *Tetranychus urticae* Koch, to a range of water-stress levels of its host plant. The response was a modified cosine function in which, as stress increased, mite performance first declined, then increased to an optimum, and then declined again.

Considerably more data are required before a complete response function can be presented for the effect of ponderosa pine stress on pine sawfly performance. However, it is possible to suggest some shapes that response functions may take (Fig. 5). The three hypothetical response functions presented in Fig. 5 represent a range of relationships, any one of which might be the real one. The shape of that function can have profound effects on the interpretation of experimental results, as I will show in the next section.

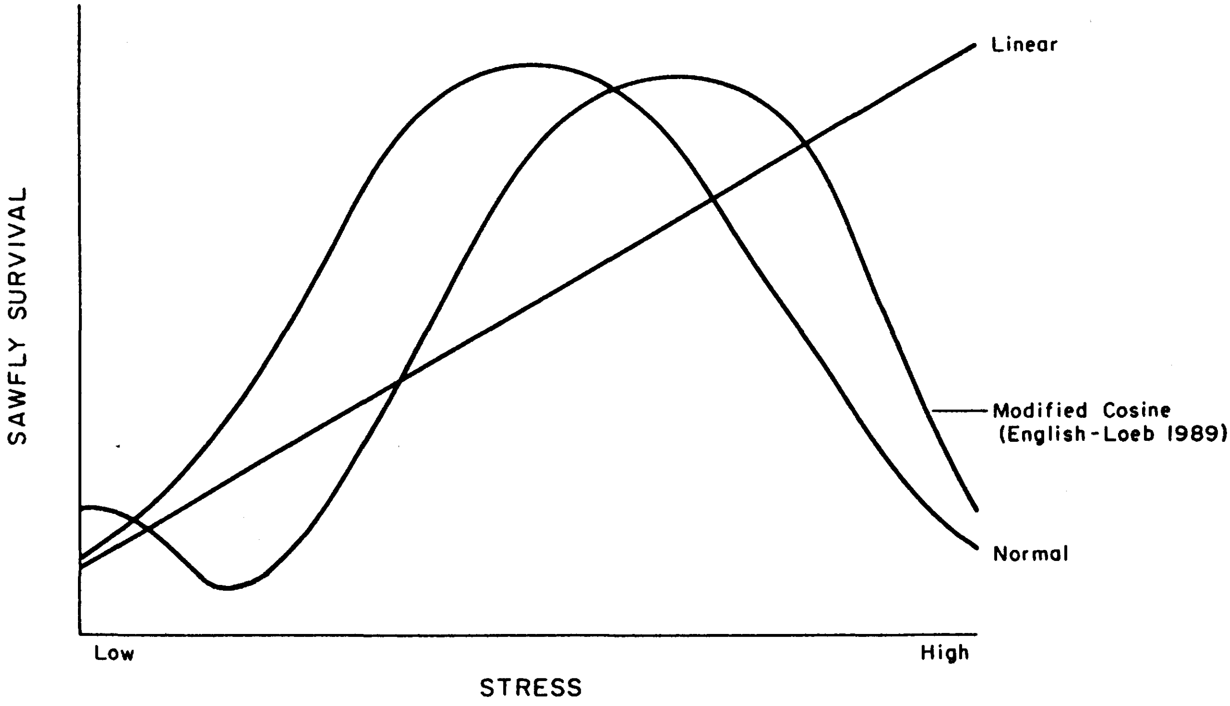

Figure 5. Three hypothetical response functions for the relationship between sawfly survival and the stress level of ponderosa pine.

RESPONSE SURFACES FOR HYPOTHETICAL RESPONSE FUNCTIONS

Up to this point, I have attempted to identify reasonable single-factor response functions for the effects of genotype, ontogeny, and drought stress on pine sawfly performance. In this section I present some reasonable response surfaces of two factors in combination and illustrate how they might influence sawfly survival.

Six hypothetical response surfaces are presented in Fig. 6. In each of the six cases, I have assumed that resistance is a linear function of genotype as approximated by the slope created by the bars in Fig. 1. While holding the genetic resistance factor constant, I have plotted the effect of tree age based on the hypothetical response functions presented in Fig. 4 (Fig. 6a, b, c) and the effect of stress based on the hypothetical response functions presented in Fig. 5 (Fig. 6d, e, f).

In examining the effect of tree age across a range of genotypes, one finds several interesting patterns emerging. First, sawfly survival can vary dramatically for a given tree age and sawfly species depending on the host genotype. The optimal age of ponderosa pine for *N. gillettei* on a resistant genotype would result in less than 50 percent survival, for example, whereas on a susceptible genotype, survival would be 100 percent (Fig. 6a). Likewise for a given genotype and sawfly species, sawfly survival can vary dramatically as a function of tree age. In the case of *N. autumnalis* Smith (Fig. 6b), survival on a susceptible genotype at the preferred age would be 100 percent, but survival on the same susceptible genotype at the least preferred age would be only about 50 percent. If an experimental system does not have control over both of these variables, it is possible to generate experimental data that demonstrate an infinite array of responses for sawfly performance as a function of tree age.

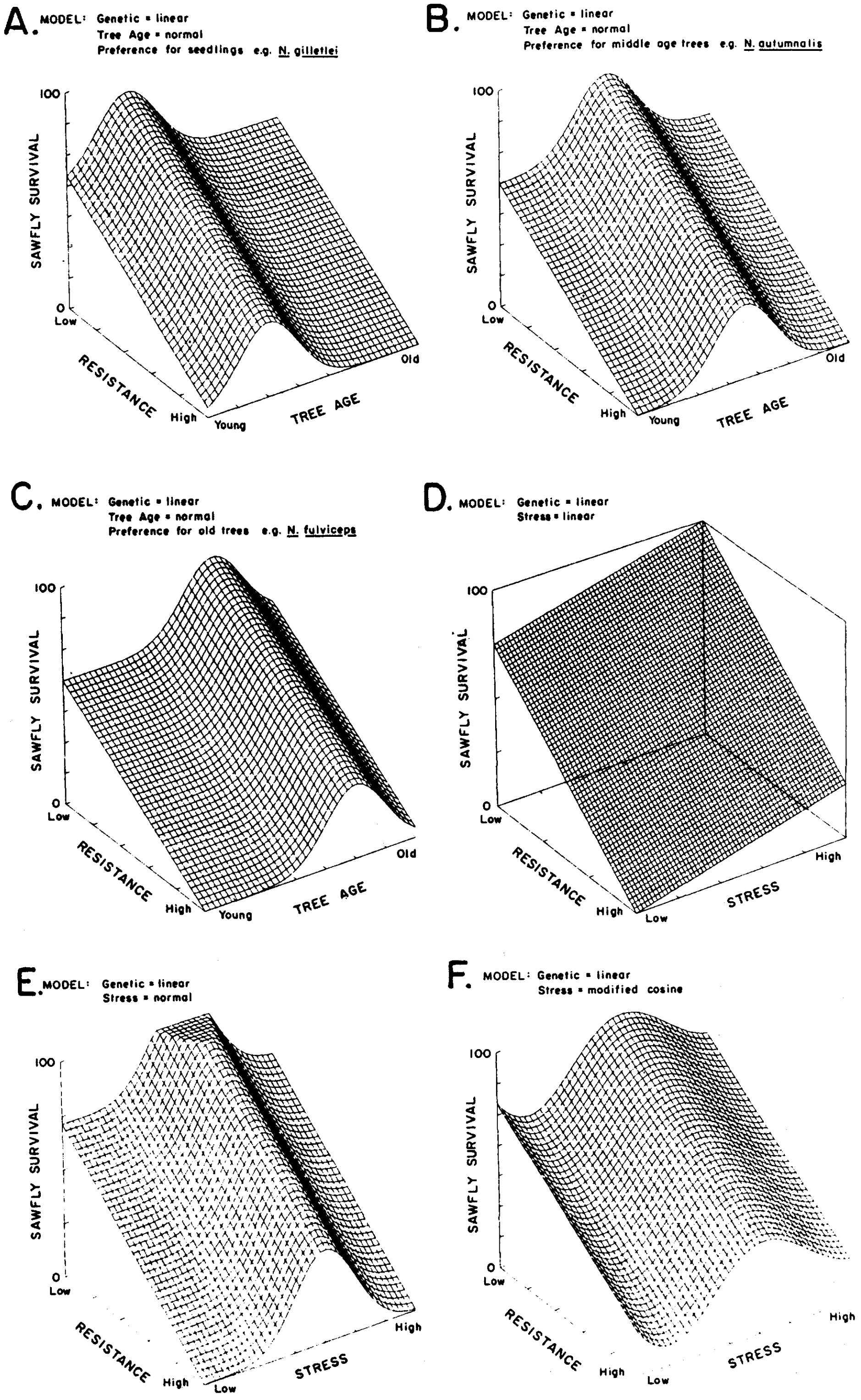

Figure 6. Hypothetical response surfaces for the effects of ponderosa pine genotype, tree age, and stress on the survival of pine sawflies. Response surfaces assume that the effects of tree age and stress are independent of genotype.

Similarly, tree stress can result in widely different effects depending on the tree genotype. Even in the simplest case, when the effects of stress and genotype are linear (Fig. 6d), it is still possible to obtain highly variable responses if either genotype or stress is not carefully controlled. In the most complicated case, when resistance is linear and stress is a modified cosine function (Fig. 6f), it is possible to observe an increase or decrease in sawfly survival with increasing stress depending on the initial level of stress. Finally, it is important to recognize that a wide variety of genotype, age, and stress levels could produce the same sawfly survival. A resistant genotype that was highly stressed could produce the same degree of sawfly survival as a susceptible genotype that was not stressed. Thus examination of response surfaces can greatly facilitate our understanding of these relationships.

RESPONSE SURFACES AS AN EXPLANATION OF CONTRADICTORY RESULTS

One of the assumptions I made in generalizing the hypothetical response surfaces in Fig. 6 was that the effects of tree age and stress were the same across all genotypes. In other words, I assumed that a resistant genotype would have the same response curve to tree age and stress as would a susceptible genotype. In fact there is no reason to assume that is so. For example, sawfly survival may not increase on a resistant genotype until that genotype is very heavily stressed. Conversely, sawfly survival might increase quickly with low-level stress on a susceptible genotype, but drop drastically at moderate to high levels of stress.

I have illustrated the potential effects of variable response functions across genotypes in Fig. 7. In this case I create slightly different response functions for susceptible and resistant genotypes. It is possible to observe (Fig. 7, large stress arrow) quite variable effects of an increase in stress at different specified stress levels. For genotype A, an increase in stress results in a decrease in sawfly survival, whereas for genotype B, an increase in stress results in an increase in survival. Likewise for a specific genotype (Fig. 7, large genotype arrow), sawfly survival will decrease with an increase in stress at stress level A and increase with an increase in stress at stress level B. It becomes obvious with examination of Fig. 7 that all of the hypothetical response functions presented for the effect of stress in Fig. 5 could be contained in a single complex response surface. The contradictory results reported in the literature and emerging from our own experimental data could be explained by a complex model such as that presented in Fig. 7.

UTILITY OF EXAMINING RESPONSE SURFACES

The purpose of the previous discussion on response surfaces was to demonstrate how reasonable, individual variable response functions could be combined to create very complex response surfaces. I have discussed only cases involving two factors interacting to influence sawfly survival. We know that in nature many more factors interact. I am led to conclude that much more carefully controlled experimental work is required before true response surfaces are likely to emerge for any insect-plant system and for any two sets of variables. Without a very disciplined approach to the analysis of individual factors and combinations of factors, we will probably wander for years generating points on a response surface without ever fully recognizing the shape of the overall surface.

To improve the probability of our discovering the true response surface of host plant variables influencing insect survival, I propose the following protocols. 1) Research should focus on single insect/host models. Only long-term attention to key host plant traits can identify true response surfaces. 2) Strongly experimental approaches are required which attempt to hold as many factors constant as possible while testing for the factor of interest. Common garden/field, greenhouse, or laboratory studies are more productive than natural field studies in which many variables are not controlled. 3) Experiments on single factors such as stress must test across the full range of that factor. As Figs. 6 and 7 demonstrate, an increase in stress could lead to quite variable effects on survival depending on the initial stress level. 4) Multifactor experiments are useful only when the

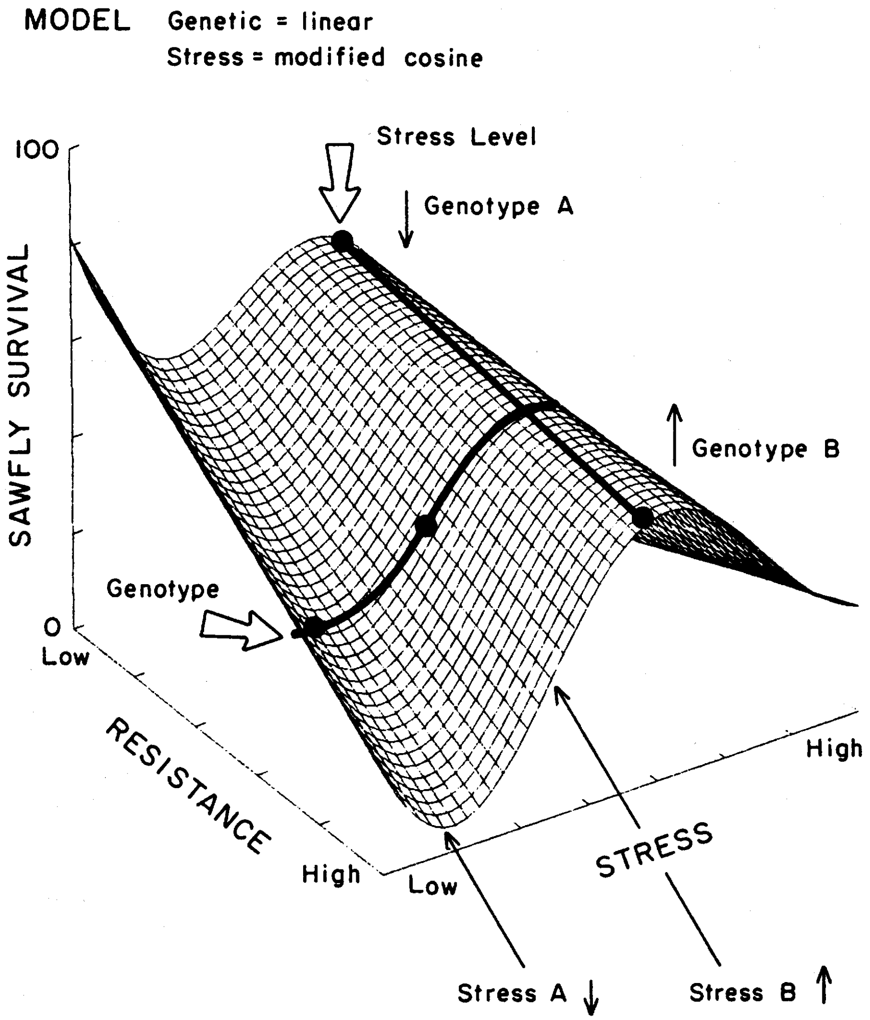

Figure 7. Hypothetical response function for the effects of genotype and stress on sawfly survival. Model assumes the stress response function is dependent on genotype.

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individual factors are thoroughly understood. 5) Insect response variables need to be chosen carefully. The response variable chosen (e.g. total survival) should be one that can have a significant effect on insect population dynamics. Field data and population dynamics models can be helpful in identifying which population parameters are most important for a given insect/plant system. 6) We should be very careful about generalizing across insect and plant systems. What may be a key factor in one system may be unimportant in another. Observation of natural patterns will suggest which factors are most likely to be important for a given system and these should be explored first. 7) Finally, response surfaces must be carefully defined. As this paper has attempted to demonstrate, relatively simple single-factor response functions, when combined, can produce complicated response surfaces which must be understood before definitive conclusions can be drawn.

SUMMARY

In this paper I have reviewed the general literature and examined preliminary data that implicate genotype, ontogeny, and stress as host factors that influence survival of pine sawflies on ponderosa pine. Data and the literature have been used to generate hypothetical single-factor response functions. These response functions have been combined to create response surfaces illustrating the potentially complex nature of response surfaces derived from relatively simple response functions. Finally I propose some research protocols to ensure efficient methods of generating response surfaces in order to establish clear relationships between host plants and their insect herbivores.

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DOES REPRODUCTION COMPROMISE DEFENSE IN WOODY PLANTS?

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PRINCIPLES OF RESOURCE ALLOCATION

A general principle of adaptive allocation was proposed by Cody (1966) who hypothesized that 1) all living organisms have finite resources to partition among growth and competing physiological processes such as reproduction and defense; and 2) natural selection results in the evolution of unique resource allocation patterns that maximize fitness in different environments. Today, it is well established that plants have limited resources to allocate among these processes (Bazzaz et al. 1987), and theories of life-history strategy rests on the assumption that there are fitness trade-offs associated with varying patterns of resource allocation (Stearns 1976, 1989, Reznick 1985, Bazzaz et al. 1987, Lovett Doust 1989). Trade-offs occur when an increase in resources allocated to one fitness component, such as growth, reduces the allocation to another, such as reproduction. Natural selection (acting within phylogenetic, physiological, and ecological constraints) should shape patterns of resource allocation, balancing the costs and benefits associated with these trade-offs, resulting in the evolution of life-history strategies maximizing fitness. There are direct and indirect costs associated with allocation to "nongrowth" processes such as reproduction. Direct costs are energy and assimilates invested in reproductive structures. Indirect costs are unrealized growth and future reproduction as a result of this investment (Bazzaz and Reekie 1985, Bloom et al. 1985, Bazzaz et al. 1987, Reekie and Bazzaz 1987c, Ronsheim 1988, Lovett Doust 1989).

The physiological cost of reproduction in the form of reduced vegetative growth has been documented in a number of cases (Gross 1972, Harper and White 1974, Gifford and Evans 1981, Willson 1983, Luken 1987, Clark and Clark 1988, Snow and Whigham 1989, Dick et al. 1990). However, this cost may not be universal (Tuomi et al. 1982, Reekie and Bazzaz 1987c, Reznick 1985). Genetic, ecological, and physiological trade-offs between growth and defensive secondary chemistry are also well documented (Bryant et al. 1983, Krischik and Denno 1983, Coley et al. 1985, Loehle 1988, Bazzaz et al. 1987, Pimentel 1988). Resource allocation patterns are the expression of source-sink

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interactions within the plant and their control on assimilate partitioning. Complex physiological changes in patterns of assimilate partitioning are required to bring about the maturation of inflorescences, fruits, and seeds. Very likely, these changes will affect traits conferring plants with resistance to herbivores. Few studies, however, have examined the potential interactions between reproduction and defense.

In this paper we explore two hypotheses suggesting how plant reproduction may directly and indirectly affect herbivory and review the limited experimental evidence supporting each:
1) reproductive structures as carbon sinks reduce the allocation of resources to defense; 2) reproductive structures as nutrient sinks increase the carbon/nutrient ratio in nearby vegetative tissues, resulting in their increased secondary metabolism and consequent increased resistance to herbivores.

TRADE-OFFS BETWEEN REPRODUCTION AND DEFENSE

Plants have limited resources to support their physiological processes, hence all requirements can not be met simultaneously, and trade-offs occur among growth, maintenance, storage, reproduction, and defense processes. Consequently, there is sequential growth and maturation of tissues within organs and organs within plants and/or strong inverse relationships between the allocation of resources to growth and nongrowth processes, including reproduction and defense (Mooney 1972, Mooney and Chu 1974, Gifford et al. 1984, Bloom et al. 1985, Willson 1983, Krischik and Denno 1983, Coley et al. 1985, Alpert et al. 1985, Loehle 1988, McLaughlin and McConathy 1979, Bazzaz et al. 1987, Patrick 1988).

Though rarely documented, reproductive effort may come at the expense of defense, if resources are diverted from resistance mechanisms to reproductive structures. This may occur commonly in the case of nitrogen-based secondary metabolites such as alkaloids and cyanogens, the concentrations of which often decline in foliage as growth shifts from vegetative to reproductive processes (Mattson 1980, Krischik and Denno 1983, Harborne 1990).

Resistance of conifers to bark beetles is generally correlated with their growth efficiency, i.e. stemwood production per unit foliage (Waring et al. 1980, Waring 1983, Mitchell et al. 1983, Larsson et al. 1983, Waring and Pitman 1985). Susceptible individuals with low growth efficiencies are characterized by depleted levels of the stored energy necessary to support defensive reactions (Waring and Schlesinger 1986, Christiansen et al. 1987). Because heavy pollen and cone production can reduce growth efficiency, episodes of reproduction may increase susceptibility to bark beetles. For example, cone production has been shown to depress stem-wood growth and leaf area in several species of conifers (Eis et al. 1965, Owens 1969, Tappeiner 1969, Dick et al. 1990). Carbon allocated to reproduction at the expense of energy and substrate required for resin synthesis and wound-induced hypersensitive responses may contribute to increased bark beetle and pathogen susceptibility. Reproductive effort may interact with environmental stress to suppress conifer resistance to bark beetles and contribute synergistically to outbreaks.

Birch Reproduction and Resistance to Bronze Birch Borer

The pistillate catkins of *Betula* are known to be strong photosynthetic sinks, competing with and reducing resource allocation to vegetative growth (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Frequently trees producing especially heavy seed crops subsequently exhibit severe dieback symptoms (Gross 1972, Houston 1987).

Our studies into the physiology of birch resistance to bronze birch borer suggest there may be a direct trade-off between female reproductive effort and resistance to the bronze birch borer (*Agrilus anxius*). Bronze birch borer larvae feed under the bark on the xylem-cambium-phloem interface and are restricted to feeding upon living tissue. Feeding girdles the tree, disrupting the downward transport of photoassimilates. Dieback of roots occur as they are isolated from their energy source, thereby limiting nutrient and water uptake. As attack intensifies, dieback initiates and spreads within the canopy. Heavily infested trees are invariably killed (Anderson 1944, Barter 1957, Carlson and Knight 1969).

From 1986 to 1989, we conducted a controlled, factorial, field experiment investigating the effects of soil moisture, soil fertility, and defoliation on the expression of birch resistance to bronze birch borer. We found soil moisture to be the most important environmental variable affecting resistance. Water deficit reduced rates of photosynthesis, growth, and wound-callus formation, as well as resistance to bronze birch borer (Herms and Mattson, unpubl. data). We found that paper birch resistance to bronze birch may be based largely on generalized trunk responses to wounding, especially rapid wound-callus formation. Furthermore, we found that the strength of this response is dependent on an adequate supply of available current photosynthate (Herms and Mattson, unpubl. data). Feeding-wounds stimulate callus formation, which if rapid enough, may entirely encapsulate small larvae within suberized tissue containing high concentrations of secondary chemicals and low concentrations of nutrients. Normally xylem tissue is a poor source of nutrition (Haack and Slansky 1987); callus tissue may be even worse, preventing larvae from completing development. Larvae may also be physically crushed as they are overgrown by callus. In effect, larvae may be in a developmental race against the tree. Larvae move through the tree in essentially two-dimensional space as they feed, their rate of progress correlated with their rate of consumption. Lesion development characteristic of a hypersensitive response occurs in phloem and xylem tissue surrounding the wound. A rapid rate of callus formation, coupled with reduced rates of larval movement through the wood, may result in larval encapsulation. Implicit in this hypothesis is the prediction that the rate of callus formation necessary for resistance should be presented by a threshold value approximately equal to the maximum rate of larval movement through the plant. Our data suggest that birch trees with rates of callus formation falling below about 0.02 mm/day are highly susceptible to bronze birch borer.

Paper birch (*Betula papyrifera*) is monoecious, with pistillate (female) and staminate (male) catkins produced as separate structures. Male catkins are produced at the end of indeterminate long-shoots in mid- to late-summer following the termination of shoot elongation. They overwinter, elongating and releasing pollen as vegetative buds open in spring. Female inflorescences emerge from overwintering-buds on short shoots as buds break in spring. Female catkin maturation commences upon pollination, and continues throughout the growing season. Seeds mature in late summer and drop throughout the fall and winter.

The results of our experiments confirm previous reports showing a trade-off between vegetative growth and female catkin production (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Plants capable of altering the balance of resources allocated between male and female organs generally allocate proportionally more resources to female functions in high resource environments (Freeman et al. 1980). This occurs, presumably, because successful female reproduction requires, in general, a greater commitment of resources than does male reproduction. In our experiment, however, increased female reproductive output in 1 year was associated with resource-limited growth during the previous year. Slow growth may stimulate the initiation of female flowers. Female reproduction itself then further reduces vegetative growth through resource competition. A positive feedback loop may result. Female reproductive effort stimulated by slow growth further reduces growth, which further stimulates female reproduction. Because of reduced rates of callus formation associated with increased female reproductive effort, this positive feedback loop may result in ever-increasing susceptibility to bronze birch borer and eventual tree death. In fact, stress-triggered seed production may be an adaptation which maximizes the life-time reproduction of suppressed trees that are competitively doomed and are likely to be soon killed by bronze birch borer.

Another Look at Birch Dieback: Bronze Birch Borer is Central

Some students of forest decline in North America have been reluctant to assign the bronze birch borer a central role in the occurrence of widespread birch dieback (Anderson 1944, Hawboldt 1947, Carlson and Knight 1969, Houston 1987). At best, the bronze birch borer has been credited with a minor effect on over-all patterns of tree mortality, primarily killing trees already predisposed to death by other factors, such as disease. We argue that patterns of bronze birch borer outbreaks are in some ways analogous to those of the mountain pine beetle, *Dendroctonus ponderosae*, and are sufficient in themselves to contribute significantly to historical patterns of birch dieback in North America:
1) outbreaks of the bronze birch borer, like those of the mountain pine beetle, can be classified as "eruptive" (Berryman and Stark 1985), or more specifically "pulse eruptive" (Berryman 1987); 2) much like the mountain pine beetle (Raffa and Berryman 1983, 1987, Berryman and Stark 1985), we argue that bronze birch borer populations are usually regulated largely by the availability of host plants suitable for larval development and survival (e.g. Carlson and Knight 1969). Outbreaks occur at irregular intervals when biotic and/or abiotic stress factors increase the availability of suitable host trees. 3) Once populations reach epidemic proportions, the outbreak spreads to adjacent stands as large numbers of larvae are able to overwhelm the defenses of vigorous, normally resistant trees.

Paper birch frequently forms even-aged, monospecific stands throughout the boreal forest of North America. Under conditions favoring rapid tree growth, populations of bronze birch borer are constrained to endemic levels by lack of susceptible host material. In this situation, birch borer reproduction is primarily restricted to suppressed trees succumbing to density-dependent competition during the thinning phase of stand establishment. Intolerant of shade, suppressed trees are characterized by low net assimilation rates and lack the resources necessary to support a strong wound response.

Episodes of birch dieback, and associated out-breaks of bronze birch borer, have corresponded with periods of above-average temperatures and below-average precipitation (Hawboldt and Skolko 1948, Redmond 1955, Clark and Barter 1958). Combinations of severe stresses such as drought and defoliation may simultaneously weaken trees over wide geographic areas, resulting in rapid and substantial increases in host material suitable for the bronze birch borer, thereby releasing them from this constraint on population growth (Carlson and Knight 1969).

Female reproduction in birch may play a key role in sustaining bronze birch borer outbreaks. If stress-induced reductions in growth stimulates female reproduction, and female reproductive effort further compromises resistance to bronze birch borer, the result may be a positive feedback loop which rapidly increases the number of susceptible hosts, intensifying and sustaining an outbreak.

Under conditions of extremely high attack density, the defense mechanisms of otherwise resistant trees may be overwhelmed by simultaneous colonization by many larvae. Under these circumstances, larval-feeding behavior may act to subvert host defense mechanisms, facilitating the success of their own colonization as well as colonization by other larvae. When feeding in vigorous hosts, larvae display a zig-zag pattern of gallery formation as they continually double-back against the grain of the wood (Carlson and Knight 1969). This pattern of feeding may partially girdle the tree, causing localized reductions in the strength of wound-induced resistance mechanisms. On the other hand, in severely stressed host trees, galleries show no consistent pattern, as larvae apparently feed on the freshest phloem they encounter (Carlson and Knight 1969).

As borers kill susceptible trees, thereby removing them from the pool of suitable hosts, and as environmental conditions change favoring increased tree growth and stronger wound responses, the epidemic subsides. The borer population declines to an endemic level as the supply of suitable hosts dwindles.

Birch trees experiencing traumatic trunk and canopy death frequently maintain sufficient stored reserves to resprout from the roots. Substantial resprouting often follows above-ground mortality resulting from fire or snowshoe hare browsing. Higher levels of terpenoid surface resins of the bark of juvenile growth originating from root-sprouts are toxic to snowshoe hares and may contribute to the decline of hare population outbreaks (Bryant 1981, Fox and Bryant 1984). Trees killed by bronze birch borer can resprout, as well, and sprouts may be too small to permit bronze birch borer colonization for several years. Sprouting following trunk death is obviously an adaptation to catastrophic disturbances such as fire and herbivore outbreaks, contributing to the continued dominance by birch of seral sites.

Sexual Variation in Resistance and the Carbon/Nutrient Balance

Dioecious plants frequently exhibit sexual dimorphism in resources allocated to reproductive effort, with female effort generally greatest because of resources required for seed and fruit maturation (Lloyd and Webb 1977, Wallace and Rundel 1979, Hoffmann and Alliende 1984, Bullock 1984, Clark and Clark 1988, Snow and Whigham 1989, Allen and Antos 1988). Several studies have documented intraspecific sexual variation in the degree of herbivory experienced by dioecious plants (Dannell et al. 1985, Lovett Doust and Lovett Doust 1985, Ågren 1987, Elmqvist et al. 1988, Alliende 1989, Boecklen et al. 1990). The resource-competition hypothesis predicts increased herbivory on female plants because their typically greater reproductive effort competes for resources with defense mechanisms. However, data from the few existing studies suggest that the opposite is true. Male plants generally experience greater herbivory (Bawa and Opler 1978, Dannell et al. 1985, Ågren 1987, Alliende 1989, Boecklen et al. 1990).

Male and female plants may often segregate along environmental gradients (Putwain and Harper 1972, Freeman et al. 1976, Bawa 1980, Cox 1981, Bierzychudek and Eckart 1988). Differential levels of herbivory, possibly resulting in skewed sex-ratios, may arise from 1) differential frequency of herbivore encounters in their respective environments, or 2) differential defensive allocations among male and female plants.

The nutrient capital required for the growth, maintenance, and maturation of flowers, fruits, and seeds can be substantial and is obtained in full from the rest of the plant (Bazzaz et al. 1979, Thompson and Stewart 1981). Limiting nutrients may be mobilized in relatively high proportions from vegetative tissue to reproductive sinks, thereby contributing to the reductions in vegetative growth associated with reproduction (Mooney 1972, Sinclair and de Wit 1975, 1976, Thompson and Stewart 1981, Bloom et al. 1985, Alpert et al. 1985). The high quantities of nutrients required for fruit and seed maturation may contribute to nutrient deficiencies and ensuing growth reductions in female relative to male plants (Bullock 1984, Allen and Antos 1988).

The reproductive structures of many species are photosynthetic, contributing in varying degrees to their own economy of energy and biomass (Dickmann and Kozlowski 1970, Bazzaz et al. 1979, Reekie and Bazzaz 1987a). Furthermore, enhanced sink strength associated with rapidly developing reproductive structures may stimulate increased photosynthesis in nearby source leaves, through feedback mediated effects (Neales and Incoll 1968, Watson and Casper 1984, Foyer 1988, Dick et al. 1990). As a result, the diversion of carbon from vegetative to reproductive structures may be proportionally less than that of nutrients, especially in female plants (Sinclair and de Wit 1975, 1976, van Andel and Vera 1977, Lovett Doust 1980, Williams and Bell 1981, Abrahamson and Caswell 1982, Mooney and Gulmon 1982, Bullock 1984, Allen and Antos 1988, Reekie and Bazzaz 1987b, Esler et al. 1989). Biomass alone may not always be a suitable measure of reproductive effort (Thompson and Stewart 1981, Abrahamson and Caswell 1982, Bazzaz and Reekie 1985, Reekie and Bazzaz 1987b).

Rapidly growing tissues are invariably strong photosynthetic sinks (Wareing and Patrick 1975, Patrick 1988). However, nutrient limitation slows their growth (Ågren 1988, Patrick 1988).

Photosynthesis, however, can be maintained in existing cells, at nutrient concentrations below those limiting to growth (Chapin 1980, Dietz 1989). Under sink-limiting conditions the carbon/nutrient ratio of the plant increases. Photosynthate assimilated in excess of growth requirements is frequently allocated to secondary metabolism, frequently increasing the plant's resistance to herbivores (Mattson 1980, Bryant et al. 1983, 1987a, 1987b, Mihaliak et al. 1985, 1987). Since "excess" photosynthates could be stored and contribute to future growth rather than be used in defense, enhanced secondary metabolism in response to sink limitation may represent a selected, adaptive use of resources minimizing herbivory (micro and macro) when the plant has limited ability to compensate (via growth) for it.

A nutrient deficiency in vegetative parts female plants relative to male plants resulting from a disproportionate allocation of nutrients from vegetative sources to reproductive sinks may limit vegetative growth (Allen and Antos 1988). Photosynthetic stimulation of source leaves by feedback control exerted by strong reproductive sinks, coupled with direct photosynthetic activity of reproductive tissues, may contribute to a favorable carbon economy within the plant. Together, these factors may interact to increase carbon/nutrient ratio in the foliage of female plants relative to males.

Female plants, because of reduced growth due to their greater reproductive effort, may have limited ability to compensate for herbivory relative to male plants (Ågren 1987, Elmqvist et al. 1987, 1988). Limited compensatory ability coupled with the need by female plants to protect their reproductive investment, may result in females being under stronger selection than males for powerful defense (Putwain and Harper 1972, Ågren 1987, Boecklen et al. 1990). Consequently, patterns of defense observed in female relative to male individuals of a species may mirror the phenotypic patterns of defense predicted by Bryant et al. (1983) in nutrient-deficient relative to nutrient-rich plants. Female plants, like nutrient-deficient plants, should display reduced growth, increased carbon/nutrient balance in vegetative structures, and higher concentrations of secondary metabolites. Very limited evidence supports this pattern. Male plants do seem to receive higher levels of herbivory (Putwain and Harper 1972, Dannell et al. 1985, Ågren 1987, Elmqvist et al. 1988, Alliende 1989, Boecklen et al. 1990, Krischik and Denno 1990, Jing and Coley 1990) and contain lower concentrations of secondary metabolites or have less tough foliage (Palo 1984, Boecklen et al. 1990).

Reproductive Effort in Monoecious Plants May Enhance Their Resistance to Folivores

The principles discussed above should also apply to monoecious plants if they translocate proportionally more nutrients than carbon from vegetative sources to reproductive sinks. This hypothesis predicts that the carbon/nutrient ratio of vegetative tissues will increase with increasing reproductive effort, resulting in increased concentrations of carbon-based secondary metabolites, and possibly enhanced resistance to folivores.

SUMMARY

The process of plant reproduction has pervasive effects on virtually all aspects of plant physiology and should have important effects on plant resistance to herbivores. We hypothesize that increased susceptibility to stem-invading herbivores could result as a consequence of the substantial cost of reproductive effort as resources are diverted from defensive structures and reactions to reproduction. On the other hand, we hypothesize that reproduction can increase plant resistance to folivores. Reproductive effort may result in an increased carbon/nutrient ratio in foliage, as nutrients are translocated to developing flowers, fruits, and seeds. Associated with this increased carbon/nutrient balance may be enhanced allocation to secondary metabolic pathways and increased resistance to some herbivores. Few data are available with which to test these hypotheses. The potential interactions between plant reproduction and herbivory are ripe for investigation.

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PLANT REPRODUCTIVE ORGANS AND THE ORIGIN OF TERRESTRIAL INSECTS

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INTRODUCTION

It is widely believed that plants facilitated the evolution of terrestrial insects (Southwood 1973). However, the mechanisms by which this evolution occurred are not yet fully understood. I therefore propose a hypothesis about one possible mode of formation of terrestrial insects and fauna. The soil, warm shallow lagoons, tidal zones, and accumulations of detritus are assumed by many authors to be the "bridges" for the transition of aquatic organisms to terrestrial existence.

The linkage of insects to plants has been offered as an explanation for the evolution of complete metamorphosis and the ability to fly. It has been suggested that holometabolism occurred in narrow cavities of the substrate, which might be represented by the cavities and ducts in the plant reproductive organs. It is assumed that wings and the ability to fly evolved owing to its advantages in finding food and escaping from enemies.

The Transit to Land

The aquatic fauna is known to be extremely diverse; ancestors of the present arthropods were highly differentiated in the aquatic environment. In the transient water-land zones, the proto-insect's migration onto the land seemed inevitable, although this transit took a long time. Thus it could not have been simultaneous for various insect groups, although some groups evolved concurrently. Each group probably had its own bridge. Let us imagine those conditions which contributed to an obligatory and inevitable transition of aquatic organisms to land. The earth at that time (the Lower Silurian-Upper Devonian) was represented mostly by rocky, dry desert with scanty vegetation, oxygen deficiency, and unlimited amounts of severe ultraviolet radiation.

Organisms living in water were shielded from UVR and from drying and over-heating. They could easily move in a water environment which provided them with necessary support. Those organisms which moved onto land faced formidable ecological difficulties, the most serious being the lower viscosity and density of the air as compared to those of the water. Their bodies actually lost support and their free movement became impaired. For such groups of ancestral arthropods, soil might have been the bridge to terrestrial life. The land was almost devoid of organic life, having drastic changes of temperature, humidity, and illumination. The chance to survive and have progeny was probably very small. The vegetation (the plant protocommunities) had not yet contributed to the process apart from accumulations of detritus and remnants of aquatic plants which served as screens.

Another, later evolutionary branch of aquatic arthropods was associated with the transition of plants to terrestrial existence. This happened as a result of differentiation of the plant life cycle into

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sexual (gametophyte) and asexual (sporophyte) generations which was accompanied by the formation of a special reproductive organ "strobilus," which may be regarded as an analogue of modern cones.

Primary-terrestrial plant protocommunities were prostrate creeping plants partly yet connected with water, and served as optimal habitat for Arthropoda ancestors to be temporarily found outside the water. The reproductive organs rose above the water surface. If we take into account the fact that plants in a water environment could have been used as food and shelter by insects, then endophyte mode of life could be optimal. Plant fibers on land contained moisture and oxygen, and perhaps the reproductive structures provided for the best isolation from external hostile conditions. Moreover, they were food substrates rich in nutrients.

Within this hypothesis it is impossible to imagine other more ecologically optimal habitats for the insect's ancestors. Thus we can postulate the existence of two likely "bridges" for the transition onto the land of aquatic ancestors; they moved via the soil and via plant reproductive structures. This by no means excludes other ways and means. We should emphasize that these two bridges established the two further directions of evolution of terrestrial Arthropoda. The soil bridge Arthropoda actually "stopped" their evolution, e.g. the modern Apterygota, Myriapodes, and Arachinoides. Their environments excluded both the possibility and the necessity of complete metamorphosis and flying ability. The second group has undergone substantial evolution and has transformed into the modern Holometabola. We should postulate on the basis of the above that the aquatic ancestors of modern insects have not experienced any metamorphosis; this conclusion is recognized by many authors.

The Origin of Flight

We can suggest that flight and metamorphosis are inherent features of higher insects and have a common origin. They appeared because the association with plants predisposed their evolution. Peculiar features of plant reproductive organs, as habitats for endophytes, are their ephemeral, patchy existence in comparison with the constant character of the plant proper. They formed on the ends of the branches, being unevenly and irregularly distributed depending on dynamic weather and soil conditions. In other words, the habitats and food resources of this branch of terrestrial insects originally appeared to be discrete in space. Evolution in insects could have proceeded in the following way: a certain group of terrestrial insects under certain favorable conditions could make locally a morphological and physiological "jump" which can be regarded as aeromorphosis.

Living conditions in strobilus (or other reproductive organs) were such that an insect as a rule could not complete its ontogenesis in one strobilus, it had to move to another one situated nearby, on a neighboring branch, or a neighboring plant, the time for migration being extremely limited. Similar migrations were performed by adult insects to lay eggs and to provide the food for its progeny. Crawling would not have been optimal. A jump would be more advantageous, but jumping makes it necessary to overcome gravity and to move large distances. Insects with elongated bodies would be favored. The necessity for organs to appear, which would make the insects able to fly first in a passive mode and then in an active mode, would be accompanied by re-structuring of muscles and formation of a wing.

Let us now examine a hypothetical fate of an insect grown in the primary plant reproductive organ. Its life time was determined by the fulfillment of its own reproduction and was quite short, though this does not mean that the whole period of plant reproduction was so short: strobila (or other organs) could exist in the tree crowns quite long, new strobilae substituting for old ones. Those insects which could deposit their eggs faster had a higher probability to survive and have progeny, laying their eggs in the neighboring reproductive organs or in those which died later. Larvae hatched from these eggs, that is embryonization of post-embryonal development occurred as postulated by Iezhikov-Berleze theory. Under such conditions larvae had to live through unfavorable nutrition and development periods (cooling periods, droughts, absence of food and habitats). The development under these unfavorable conditions became retarded, but it should have been compensated for by faster rates of physiological metabolism (hystolis, histogenesis) in the period of transition from a wingless, sexless larva to the winged and sexually mature "imago."

The development within the living plant tissues did not require the development of morphological and physiological adaptation. Exactly the same advantages are available to primary wingless insects which occur (and still occur) in strongly moisturized soil cavities. (See Gilyarov 1970.) However, the temporal discreteness of plant organs and tissues forced the insect to exist outside plants during a certain period of their ontogenesis, which resulted in the forming of new adaptations. The development of an isolated pupa (where these processes take place), not affected by the environment, appeared to be an optimal evolutionary trend. In a number of cases the developed ability of retarding or stopping the development without morphological reconstructions was fixed, i.e. diapause.

On the other hand, those insects who primarily or secondarily were related to non-discrete plant organs (leaves, branches) and have created not only the chewing feeding mode but also a sucking one as well (Orthoptera, Heteroptera, Homoptera) did not develop the pupal stage, they are known as Hemimetabola.

The above presents the main concepts of a theory which is by no means complete. It should be considered as a preliminary assumption for a future hypothesis.

PREFERENCE OF DENDROPHAGOUS INSECTS FOR FOREST BORDERS

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INTRODUCTION

Numerous investigations have shown that forest insect outbreaks usually occur in specific habitats. Frequently these outbreaks do not generally extend to other territories occupied by these same host trees. Moreover, in every stand subjected to an outbreak, both slightly undamaged plots and heavily damaged plots are found. Perhaps some plots are initially more resistant to insect attack, and insect distribution within forest ecosystems may have a mosaic pattern. Therefore investigation of the relation between dendrophagous insect distributions and initial heterogeneity of ecosystems may help us to understand the nature of forest stand resistance. This question lends interest to the peculiarities of dendrophagous insect distribution in relation to forest borders because borders and different glades are important factors in forest ecosystem heterogeneity.

INSECT DISTRIBUTION WITHIN STANDS

There is no large body of information on this question in the literature. I have used the available information on different species from several natural zones and considered the distribution of 180 species belonging to 33 families of six insect orders. Insect distribution was analyzed only at the main feeding stages.

Table 1 shows the majority (73.3 percent) of the species considered to prefer the forest border and its analogues (single growing trees or low-density stands).

Distribution of insects within a forest stand may depend on two main factors: 1) the presence of available food; and 2) microclimatic conditions. It is known that availability of food is more important for xylophagous insects than for phyllophagous ones. On the other hand, microclimatic conditions are more important for phyllophagous free-living species than for xylophagous ones. Thus it is necessary to analyze the distribution of both these insect groups separately. My analysis showed the forest border and its analogues to be preferable for the majority of species from both groups: 59 percent of xylophages and 66 percent of phyllophages. Thus these stations may satisfy different requirements (food and climate, among others) of the majority of dendrophages.

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Table 1. Preferred distribution of 180 phytophagous insect species over different forest parts

Habitats	Number of species	
	Total	%
Forest borders and their analogues		
Isolated trees (A)	3	1.7
A + B	5	2.8
Forest borders (B)	18	10.0
B + C	46	25.6
Open, low-density stands (C)	49	27.2
A + B + C	11	6.1
Forest thickets and their analogues		
Closed, high-density stands (D)	29	16.1
C + D	7	3.9
Uncertain distribution		
A + B + C + D	4	2.2
B + C + D	1	0.5
Uncertain	7	

Climatic conditions are different in every natural zone, however, and the insect species areas may occur over several bioclimatic zones. Therefore dendrophage distribution in relation to forest borders may be different. Dispersal from one natural zone to another provide ample evidence that insect species exchange one kind of habitat for another. We should take this principle into account in our strategies for controlling insect species epidemics, but for our present purposes it is more interesting to consider dendrophage distribution within different zones, such as forest and steppe regions.

My data analysis again showed the majority of species to prefer the forest border and its analogues: 84 percent the forest zone and 71 percent the steppe. So these "border" habitats are assumed to have an advantage over forest thickets and their analogue for insects.

There is data indicating some abundant species use the forest borders as a refuge between outbreaks. Moreover, the initial outbreak areas often coincide with these refugia. At the same time, my analysis showed both outbreak and nonoutbreak insect species (81 percent and 79 percent respectively) to prefer forest borders. We may say, then, forest borders not only function as refuges for abundant species, but are preferred habitats for the majority of nonoutbreak species as well. The question is why?

EXPLAINING HIGH BORDER PREFERENCE

Let us consider some possible reasons why forest insects prefer forest borders. Forest border habitats are characterized by a great variety of 1) microsites and 2) tree and shrub species. For these reasons, rich insect species communities occur in these habitats. The existence of species variety is impossible within narrow local microclimatic conditions. However, since the forest borders are characterized by maximal amplitudes of microclimatic parameter fluctuations, they allow for the coexistence of insect species with different microclimatic requirements.

It might be thought that all these factors relate only to phyllophages because xylophages depend on microclimatic conditions to a lesser degree and for them the availability of food is more important. Only the tree borders are subjected to strong winds and other unfavorable influences, however, and that circumstance makes for constant renewal of the food base by xylophagous insects.

It is necessary, finally, to account for the preference of forest borders by cone and seed insects. Unlike the trees in forest thickets, border trees such as conifers may produce cones between "yield years." As a rule, only border and single-growing trees produce cones every year. Consequently, border habitats become refugia for cone and seed insects. This may also be a factor in the preference for forest borders by dendrophages.

Thus we may conclude that: 1) forest borders and their analogues are preferable habitats for a great number of dendrophagous insects; 2) forest borders and their analogues are strategic sites for control of abundant forest insect species; and 3) forest borders may be used expressly for the analysis of fauna of dendrophagous species in certain forest ecosystems.

WOODY PLANT GRAZING SYSTEMS: NORTH AMERICAN OUTBREAK FOLIVORES AND THEIR HOST PLANTS

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INTRODUCTION

In North America, about 85 species of free feeding and leafmining folivorous insects in the orders Lepidoptera and Hymenoptera periodically cause serious and widespread defoliation of forest trees (Appendix 1). We call these insects expansive outbreak folivores based on the following criteria: 1) population eruptions occur two or more times per 100 years, 2) severe host defoliation (> 50 percent) occurs for 2 or more years per eruption, and 3) the area of each individual outbreak exceeds 1,000 contiguous ha. There are about 20 other insects whose populations meet criteria one and two, but not criterion three. These we term local outbreak folivores and do not deal with them in this paper because they may operate on an entirely different scale than the expansive species.

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CHARACTERISTICS OF EXPANSIVE FOLIVORE OUTBREAKS

Continent-Wide Infestation Area and Frequency

Between 1957 and 1987 in the United States, at least 60 species caused outbreaks exceeding 1,000 ha (USDA, Forest Service). The largest outbreak area (summed over many different geographic regions) caused by a single insect species (*Malacosoma disstria*) in a single year was 13.5 million ha (Appendix 2). At least 14 species had single-year infestation areas that covered 0.5 million ha. The four insects showing the most consistent outbreak frequency (> 25 yrs) as well as largest mean annual infestation areas (> 0.5 million ha) were the eastern and western spruce budworms, *Choristoneura fumiferana* and *C. occidentalis*, respectively, the forest tent caterpillar, *M. disstria*, and the gypsy moth, *Lymantria dispar* (Table 1). These insects are largely in a league by themselves because most other species had less frequent and less expansive outbreak areas. Although we did not examine similar data from Canada, the pattern is likely to be much the same but with a bias toward folivores of *Populus*, *Betula*, and boreal conifers. For example, in 1975 *C. fumiferana* was at a century-high defoliation peak on more than 55 million ha in eastern Canada (Kettella 1983). On the average, at least 7.6 million ha were under severe defoliation each year by all species combined between 1957 and 1987 in the United States (Appendix 2). These are conservative estimates because of the difficulty of exactly delimiting the beginning, ending, and area of each outbreak. Generally, only the most severe cases are observed.

Six Correlates of Defoliation Severity

The impact of outbreak defoliations on forest stands differs with the insect species and the characteristics of the forest. Nevertheless, some generalities seem to hold regardless of the particulars of individual cases: 1) defoliation severity increases directly with homogeneity of the forest composition, 2) defoliation severity increases with the average amount of exposure of the individual tree crowns, 3) defoliation severity increases, though not necessarily linearly, with tree age, 4) defoliation severity increases with warm, dry weather during the growing season, 5) defoliation severity increases with the folivore's predilection for polyphagy, and 6) the effects of defoliation on tree vigor are cumulative and not linear. These six factors may contribute to outbreaks for the following reasons: increasing the amount of available food per unit area (1,5) increases the insect's chances for survival and ultimate population growth; warmer, drier environments appear to favor folivorous insects (2,4) (Mattson and Haack 1987a, 1987b); and finally, as trees age, their crowns enlarge and they begin to flower, which can have both positive and negative effects on folivorous herbivores (see Herms and Mattson this volume). At the same time the trees become less suitable for sapfeeders (Schowalter 1989), which may have several important beneficial effects on free folivores (Mattson et al. 1989).

In North America, most cases of substantial tree mortality caused by outbreak folivores have occurred primarily in aging, "overmature" forests (Kinghorn 1954, Carroll 1956, McLeod 1970, Struble 1972, Turnock 1972, Drooz 1980, Lynch and Witter 1984). However, site quality and tree vigor status interact significantly with tree age--low vigor trees growing on poor sites are much more vulnerable to death after outbreak folivory than are vigorous trees on rich sites (Mason and Tigner 1972, Turnock 1972, Witter et al. 1975, Schultz and Allen 1977, Lynch and Witter 1984, Hix et al. 1987, Archambault et al. 1990). However, qualification is necessary here. Moderately poor sites may actually sustain less mortality per unit of defoliation than rich sites because the former tend to be under less intense plant-plant competition and have trees with higher relative root and storage investments that allow them to tolerate both abiotic and biotic stresses. Rich sites induce more severe competition for space and light which favors individuals that invest proportionally more in canopy (Clark 1990). Accordingly, they have intrinsically higher rates of natural mortality owing to larger numbers of trees that are under severe competition and that invariably succumb during defoliation episodes (Clark 1990, Crow and Hicks 1990).

Table 1. Numbers of folivore species in different outbreak frequency classes, and mean annual area size classes between 1957 and 1987 in the United States.

Outbreak frequency class (yrs)	Mean annual outbreak area class: (1000 ha)			
	1-5	6-50	51-500	501-5000
< 5	8	16	9	4
< 10	0	9	4	2
< 15	1	5	3	1
< 20	0	0	3	0
> 20	0	1	0	4

Data derived from Appendix 2.

High Grazing Tolerance: Woody Plant Grazing Systems

We hypothesize that many natural plant systems that regularly support expansive outbreak folivores have only nominal regulatory (damage inducible) defenses against those folivores. The same is probably not true for other folivore guilds that are more truly parasitic, such as phloem and xylem sappers (Mattson et al. 1988b). And, it is certainly not the case for the inner-bark feeding guilds (see Mattson et al. 1988a). In fact, the outbreak patterns observed for expansive folivores are an inevitable consequence of the plant's regulatory capacity. These plants have evolved only very weak capacities for regulating canopy herbivores because outbreak folivores generally have minimal impact on plant fitness. Note that this does not mean they have negligible impact on plant growth and reproduction. It means that when such impact occurs, it is nearly equally felt by all plants. For these reasons, we label them grazing systems as did McNaughton (1984, 1986) for certain grassland systems that are highly tolerant of and may be dependent on grazing by generalist mammalian herbivores.

We do not imply that forest and grassland systems are identical, only that they are similar because folivory may be a fundamental part of the overall adaptive syndrome of both. Both systems, by virtue of their large areal sizes of relatively uniform plant form, are predisposed to chronic and substantial folivores--albeit of different types. Both also support folivores that exhibit substantial mobility and little host plant specificity (i.e. grazers, sensu McNaughton 1984, Thompson 1988). Their level of adaptation to and interaction with host plants is more at the scale of the landscape and biome rather than the individual plant. The physiological constraints and the ecological consequences that accompany a perennial, woody plant life history strategy cause the two kinds of systems to differ on the basis of their time scales. Woody plant grazing systems are defined by 1) their expansive, dense, and usually mono-oligodominant community structure that predisposes them to severe canopy herbivory, 2) their capacity to physiologically tolerate consecutive seasons of high levels of grazing, 3) their capacity to ecologically tolerate grazing (maintain their competitive positions), 4) their generally low defenses against canopy herbivores, and 5) their commensalistic (indifference) or mutualistic dependence on folivory in fulfilling their life history strategy. That is, folivores have either a minor role or a very positive role in the plants' life history (Mattson and Addy 1975).

CONDITIONS SHAPING THE EVOLUTION OF PLANT DEFENSES

Physiological Capacity to Recover From Folivory

After experiencing herbivory, a plant must recover both physiologically and ecologically (Mattson et al. 1988b). Both recovery processes influence the eventual evolution of plant defenses. In physiological recovery, herbivore removal of tissues or fluids, for which the plant has little or no capacity to replace or compensate for should elicit strong selection pressure for the evolution of powerful and fast acting defenses (McKey 1979, Rhoades 1979). For example, herbivore consumption of phloem/sapwood tissue is far more serious than equivalent biomass removal from the leaf canopy because the plant's capacity to compensate for the former is negligible compared to the latter. Moreover, damage to vascular tissues has strong, immediate negative repercussions to all other plant organs (canopy, roots, etc.), whereas damage to the canopy has less effect. Accordingly, the defensive systems of trees against inner-bark feeders are among the most powerful known in woody plants (see Mattson et al. 1988a).

On the other hand, leaves are one of the tissues that plants are most capable of replacing. However, the total physiological cost of losing and replacing leaves differs substantially with the size, resources, and adaptive strategy of the plant (Givnish 1988). Plants may compensate for low to moderate (< 30 percent) levels of folivory by increased rates of photosynthesis in the other intact leaves due to 1) more light reaching lower and previously shaded leaves, 2) more water and nutrients available to the intact leaves, and 3) long-term acceleration of nutrient cycling (Mattson and Addy 1975, Ericsson et al. 1980a, 1980b, McNaughton 1984, Verkaar 1988, Maschinski and Whitham 1989, Prins et al. 1989, Williamson et al. 1989).

However, if folivory chronically exceeds a plant's capacity for tolerance, mortality can result directly from exhaustion of tree energy reserves or indirectly from secondary agents such as wood borers, bark beetles, and pathogens (Kinghorn 1954, Barbosa and Wagner 1989).

Ecological Capacity to Recover: Plant-Plant Competition

Although there is substantial evidence that severe defoliation can reduce tree growth and reproduction, and increase tree mortality, there is little substantive information about its impact on tree-tree competition. However, the important effects of folivory on non-woody plant competition and succession are much more widely appreciated (Cottam 1985, Cottam et al. 1986, Milchunas et al. 1988, Brown and Gange 1989, Crawley 1989a, 1989b, Jarosz et al. 1989, Polley and Detling 1989, Louda et al. 1990, Prins and Nell 1990a, 1990b). Competition is pervasive in all plant communities; it is one of the principal ecological variables affecting the evolution of carbon allocation patterns. Thus, an understanding of the effects of herbivory on competition is crucial to interpreting its effects on the evolution of woody plant defenses (Taylor et al. 1990, Tilman 1990, Herms and Mattson 1991).

CONDITIONS FAVORING PLANT GROWTH INSTEAD OF DEFENSE

In many systems prone to outbreaks, certain biological and ecological conditions interact to prevent the evolution of strong plant defenses against canopy folivory. For example, herbivory that occurs in overmature trees has little impact on fitness (except through effects on parent-progeny interactions) because such trees have already largely spent their reproductive capacity.

Oligospecies Plant Communities: Pioneer, Growth-Adapted Species

Folivory occurring in vast, monodominant communities of rapidly growing species (such as those typically created when pioneering tree species invade en masse following extensive disturbances) has little chance of selecting for the evolution of powerful, regulatory plant defenses. First of all, the suite of plant traits that are conducive to successful competition in such environments is not physiologically compatible with high defensive investments (Huston and Smith 1987, Loehle 1988, Taylor et al. 1990, Tilman 1990). Fast growth is of paramount importance for competitive success, and defense will come at its expense (Harper 1989, Herms and Mattson 1991). This requires that plants maintain large foliar surface areas having high levels of leaf nutrients and water, and low levels of secondary metabolites (Gower and Richards 1990, Hilbert 1990). Such species have high capacity to outgrow others but low capacity to tolerate resource depletion (Tilman 1990), because competition for light is largely asymmetric (Wiener 1990).

Second, in monodominated communities there is little evidence of consistent, long-term, differential herbivory among plants (although see Batzer 1969, Clancy this volume, Wagner this volume). Most outbreak folivores seem to exhibit little fine-tuned selectivity for individual host plants (Price et al. 1990). This is particularly true for macrolepidoptera on conifers, which seem to have broad host plant feeding capabilities (Holloway and Hebert 1979). Most often insect egg densities per tree increase directly with tree size or "target" area (Witter et al. 1975, Mattson et al. 1988c, Batzer et al. 1991) as would be expected if trees differ little in quality from the insect's perspective. Furthermore, larvae of these species exhibit little fidelity to their "mother" plant. In fact, in the case of *Malacosoma disstria*, the opposite is true: most larvae abandon their mother plant at about the third instar regardless of its current defoliation level (pers. observ.). For many other species, larvae regularly disperse by ballooning when very small or by dropping and crawling when large (Coulson and Witter 1984, Barbosa et al. 1989)--dispersal mechanisms with very high risk of mortality and low probability of finely tuned host selection.

Few studies have shown that inter-tree variation in folivory has a genetic basis (Mattson et al. 1988b, Ayres et al. this volume), except where differences in tree phenology are the explanation (Witter and Waisanen 1978, Du Merle 1988). The scant existing evidence suggests that all members of the host population within a forest are nearly equally susceptible to defoliation, although this does not imply that all the trees are equally suitable for insect performance (Harris et al. 1982, Mattson et al. 1988b, Schmid and Bennett 1988, Batzer et al. 1991). For example, during forest tent caterpillar outbreaks in trembling aspen forests (*Populus tremuloides*), virtually every member of the canopy community will be severely defoliated several times, including "nonhosts" that are never attacked when growing in isolation or in other communities. Defoliation also extends to most members of the small tree/shrub stratum, even into neighboring forest communities (Hodson 1941, Witter et al. 1975, pers. observ.).

Uniform Folivory Favors Evolution of Tolerance

Given that all members of the community receive equal levels of folivory during epidemics, can herbivory significantly alter the existing competition-derived fitness ranking of the member plants? We think not. Recovery is closely linked to size and growth capacity. Invariably, the suppressed, subdominant host trees quickly die, but they would probably not have survived thinning anyway. Severe defoliation shifts the competitive edge in favor of the larger and faster growing plants, selecting for tolerance traits, the capacity to quickly and strongly recover. We argue that tolerance capacity is the most likely evolutionary response by the plant population to folivory. Nonbiotic defoliation from hail, wind, and ice and snow storms may be more frequent (though not serially cumulative) than outbreak folivory and even more severe in some forests (Grier 1988), and it thus reinforces the evolution of general compensatory responses.

Physiological Cost of Leaves Increases with Plant Height

If the physiological cost of leaves (sensu Givnish 1988) to such plants is low enough, they may be able to cope forever with severe herbivory through compensatory mechanisms, as some grasses do (McNaughton 1984, 1986). However, this is unlikely for taller, woody plants because the physiological cost of a leaf increases directly with its height above ground due to the added construction costs of stem and roots for support and nutrient transport (Givnish 1988). Hence, we speculate that there is a vertical size threshold, above which plants need to use some kind of low cost defenses for curtailing the long-term, severe herbivory that seems inevitable in vast monodominant communities. We and others hypothesize that these should build with canopy injury, i.e. delayed inducible resistance (DIR, sensu Haukioja and Neuvonen 1987, Bryant et al. 1988, Haukioja 1991) and should interfere minimally with plant growth and other recovery processes, but at the same time erode the herbivore's continued capacity to grow and multiply (Haukioja 1991). One extreme solution might be to produce no leaves for one generation of the folivore, thereby forcing its starvation. Although effective for strictly univoltine insects, it is not viable because the cost is too high, and bivoltinism and extended diapause are easy counteradaptions. A less extreme but nevertheless efficacious variation of this tactic, is to produce less nutritious leaves for the next several growing seasons that directly debilitate the herbivore and concomitantly cause it to be more susceptible to natural enemies (Myers 1988b, Edelstein-Keshet and Rausher 1989, Haukioja 1991). This is apparently the case for *Betula resinifera* and *Populus tremuloides* in Alaska (Werner 1979, 1981). Most DIR traits appear to be amplifications of existing constitutive secondary metabolite pathways (Tuomi et al. 1988a, 1988b, 1990), coupled to diminished nutrient levels.

Can Natural Enemies Substitute for Delayed Inducible Resistance?

The evolution of DIR will be favored to the extent that it contributes to outbreak decline before folivory precipitates widespread mortality due to exhaustion of plant reserves (and concomitant attack by wood borers) or competitive exclusion by some other nonhost species. At this point, cost of defense is no longer important because death is the alternative. However, if there are abundant, efficacious natural enemies (pathogens, parasitoids, predators) that are consistently capable of numerical responses to mounting folivore populations, then they may obviate the plant's need for DIR. Instead, the plants may need only to evolve strong recovery capacity and perhaps traits that enhance their natural enemies: nectar secretions, domatia (leaf structures which shelter predaceous mites), etc. (Mattson et al. 1989, Herms and Mattson 1991).

Localized Rapid Inducible Resistance Complements Tolerance

In resource-rich, oligo-dominant communities, highly sensitive, systemic, rapid inducible resistance (RIR), and/or high levels of constitutive defenses are not viable tactics against free feeding folivores. Perpetual, whole-plant induction would chronically diminish the high growth rates that are fundamental to the basic life history strategy of such plants (Herms and Mattson 1991). However, very localized RIR may be a viable tactic if it serves only to disperse folivores among modules so as to reduce the average impact of folivory per plant (see Bogacheva this volume). In other words, RIR in this case functions primarily as a complement to physiologically based tolerance. However, RIR in these communities is not sufficient to prevent periodic, severe defoliation by "adapted" folivores because its proximate effects on behavior can be overwhelmed by starvation. Even biochemically very different, "nonhost" plants in and near the outbreak communities are stripped of their canopies.

We propose, therefore, that selection pressure by herbivores favors primarily 1) high levels of tolerance to injury, coupled to 2) some form of low cost, highly localized RIR, and finally 3) density-dependent DIR that increases the probability of folivore mortality from natural enemies that build in response to herbivore populations.

Grow and Then Reproduce: an Evolutionarily Stable Strategy?

Is it possible that herbivory in these communities could favor high levels of constitutive defenses, and/or a more powerful, regulatory defensive strategy? We think not. The underlying life history strategy of growth-dominated, shade-intolerant, pioneering plants provides strong physiological and ecological constraints to other evolutionary solutions (Huston and Smith 1987, van der Meijden et al. 1988, Taylor et al. 1990). Competition for light by juvenile plants is so intense that rapid growth coupled to minimal defense systems will always be favored. For example, Makela (1985) concluded that the maximum fitness strategy in a dense, monodominant system will result from first growing as fast as possible and then switching to reproduction when the cost of further height growth is more than the cost of subsequent shading from neighbors. Because all individual plants often establish simultaneously and play by the same fundamental physiological rules, they end up highly synchronized throughout life and even in death (Mueller-Dombois 1987). Their simultaneous, wave-like or cohort-like decline may be a consequence of the entire adaptive syndrome.

CONDITIONS FAVORING THE EVOLUTION OF STRONG DEFENSES

Oligospecies Plant Communities: Stress Adapted Species

Many of the preceding arguments apply also to oligospecies communities in low resource environments. However, the physiological capacity for tolerating and recovering from defoliation may now be substantially less than in high resource environments. This means that the physiological cost of leaf loss and replacement is much higher (sensu Givnish 1988). Hence, the adaptive strategy of stress-adapted plants requires a different mix of traits than those of growth-adapted plants (Huston and Smith 1987, Taylor et al. 1990). High rates of growth and leaf replacement are generally not sustainable due to shortages of critical resources (nutrients, water, etc). Therefore, plant emphasis is on the acquisition and efficient use of nutrients, low leaf turnover, and survival during critical drought and stress periods, etc.

Thus, environmentally induced slow growth and longer leaf longevity (in evergreen species) create a high risk of injury from herbivores. At the same time, however, they significantly reduce the opportunity costs of defensive investments (Herms and Mattson 1991). Therefore, it should be adaptive that such plants should protect well their foliage, at least in direct proportion to each foliage cohort's contribution to plant vitality (McKey 1979, Rhoades 1979, Mattson et al. 1988b). There is essentially a dichotomy between stress-adapted deciduous and evergreen species because of the different suites of adaptations that entail each kind of strategy (Bryant et al. 1988, Dickson 1989, 1991, Gower and Richards 1990). For example, the former tend to have higher rates of photosynthesis over a short photosynthetically active period and rely exclusively on storage for fueling each season's early growth. The latter have much lower rates of photosynthesis over a longer period and rely more on current photosynthates and leaf-stored nutrients to support early growth (Dickson 1989, 1991, Sprugel 1989). Foliage loss is more damaging to evergreen species because generally they do not refoliate in response to defoliation, and thus the losses must be integrated over the multi-year life span of such leaves.

Uniform Herbivory Favors Tolerance

A uniform plant community predisposes the plants to expansive outbreak herbivores and so does the wider tree spacing that often occurs on stressful sites. Under these circumstances, herbivore selection pressure still favors the evolution of tolerance to the degree that it is possible (in inverse relationship to the stress adaptation required). However, we hypothesize (Herms and Mattson 1991) that its complement, localized RIR, is not as adaptive in low as in high resource environments because of fundamental physiological and ecological constraints on its efficacious expression (especially in evergreen conifers). Furthermore, unlike the high resource case, folivory will favor additional, purely defensive traits that 1) reduce both the mean background level of herbivory and the likelihood of herbivore population buildup, and 2) more swiftly stop herbivory once it has exceeded tolerance levels, i.e. a more powerful DIR. In the case of the first, higher levels of constitutive defenses and lower foliar nutritional quality will simultaneously reduce the overall herbivore species loading per plant (see Niemelä et al. 1982, Tahvanainen and Niemelä 1987) and lower the intrinsic rate of population increase of the many fewer adapted herbivore species. As for the second, there is good evidence in at least two deciduous tree-herbivore systems: *Larix decidua/Zeiraphera dineana*, and *Betula pubescens tortuosa/Epirrita autumnata* (Haukioja 1991). Likewise, the *B. resinifera/Rheumaptera hastata* and *P. tremuloides/Choristoneura conflictana* systems in Alaska may qualify (Haukioja and Neuvonen 1987.) However, there is yet little substantive evidence for significant DIR in evergreen conifers (see Neuvonen and Niemelä in this volume). If DIR does occur, it is most likely to be manifested in currently produced foliage, which is probably the only leaf tissue physiologically capable of DIR (Leather et al. 1987, Wagner 1988, Buratti et al. 1990, Geri et al. 1990) and in fast growing seedlings and saplings (Karban 1990a, 1990b).

Small Size and Slow Growth Preclude Tolerance Responses

Being very small predisposes young woody plants to the high probability of catastrophic, i.e. fatal, injury from herbivores merely because a small amount of herbivory is capable of devastating small plants. Normally, the risk of such injury would be small because it is spread widely among the vast number of individual seedlings that regenerate in cohort-like waves. However, slow growth compounds this risk significantly in direct relation to the time it takes to outgrow the risk of most such injury. Therefore small, slow growing, woody plants may die unless they use potent, deterrent constitutive defenses.

Polyspecies Plant Communities: Pioneer, Growth-Adapted Species

Selection pressure by herbivores for plant defenses is likely to be much more intense in polyspecies than in monospecies, pioneering communities. Consistent, differential herbivory among individual plants is more probable when the community is comprised of many species of plants. Each species, because of its inherent anatomical/morphological and biochemical uniqueness, tends to have its own suite of herbivores. Even polyphagous insects such as the gypsy moth show obvious host preferences. As a result, the preferred species are defoliated first and usually sustain the highest cumulative defoliation, and consequently, the highest mortality rates over an infestation episode (Crow and Hicks 1990).

In brief, then, the selective pressure from folivores in a polyspecies, pioneering community is likely to be higher and different than in an oligospecies community. This should be expected because interspecies plant competition for light and nutrients will generally lead to different evolutionary adaptations than will primarily intraspecies competition (Aarssen 1989, Keddy and Shipley 1989, Barnes et al. 1990, Connolly et al. 1990).

However, the high growth strategy of such plants entails a suite of correlated physiological and ecological traits that may constrain costly defensive investments. Therefore, we hypothesize that different, but ecologically equivalent, defensive tactics will evolve as a result of plants balancing investments in defenses against growth (including reproduction). The diversity of evolutionary solutions will depend on the number of competing plant species. One solution might be high growth and low constitutive defenses with concomitantly higher species loading per plant, while another might be medium growth with higher standing defense and lower herbivory per plant, and so on. For example, Prins and Nells (1990a, 1990b) and Prins et al. (1989) have elegantly shown that two competing herbaceous plant species can experience vastly different levels of herbivory, and can coexist because of different leaf tissue chemistries and specific elements of their life history strategies.

Defenses Vary in Relation to Intensity of Plant Competition

The strength of the DIR defensive response will vary with the time scale of plant-plant competition. Where interspecific competition is intense (e.g. rich sites) and debilitation over successive growing seasons can cause a serious loss in competitive status, we predict powerful, fast acting defenses that will impact the next generation of the herbivore. At the other end of the continuum, where competition is less intense and debilitation over two growing seasons does not seriously jeopardize an individual's competitive status, then "slower" defenses (within two to three growing seasons) are adequate.

Because competition is not constant over the course of plant ontogeny, constitutive and inducible defenses may also vary with the plant ontogeny in direct relation to competition. For example, per capita mortality rate curves for trees often are believed to be U-shaped, i.e. high mortality due to density independent factors and competition (other trees, shrubs, herbaceous matter, etc.) during the early period of establishment, followed by lower and relatively stable tree-tree competition-induced mortality up to old age, when mortality rates may rise again due to senescence (Harcombe 1987, Clark 1990). Hence, herbivore injury may be more critical in early life when plants are also more susceptible to competitive displacement. At this time, therefore, defenses would be desirable to prevent the compounding negative effects of herbivory. However, they should not come at the expense of competitive capacity (i.e. growth). One solution is escape as implied by Janzen (1970), who predicted that the success of such understory propagules will increase with their distance from parents or like conspecifics. Apparently, this is being borne out in tropical forests (Clark 1986). Other solutions would be low cost defenses such as bioassociations, or low concentrations of highly toxic, deterrent secondary chemicals (Herms and Mattson 1991).

Polyspecies Community: Shade-Tolerant Species

Shade tolerant species in polyspecies communities clearly require stronger defenses. Their strategy, at least in their early years, is often one of competition tolerance, the capacity to endure, to subsist on the meager amounts of light that reach the dimly lit forest understory (Givnish 1988, Taylor et al. 1990). One would expect, based on their unique suite of physiological and ecological traits, that they should also differ markedly from pioneering species in their evolutionary responses to herbivory (Loehle 1988, Taylor et al. 1990). Long periods of slow growth in low light (light stress) require strong defenses to survive prolonged exposure to mammalian and micro-herbivores. Because plant recovery capacity will be very limited, strong, highly effective constitutive defenses that drastically lower the herbivore loading per plant should be highly adaptive.

The capacity of such plants to tolerate herbivory may be so limited that neither localized RIR nor general DIR is a viable evolutionary option for understory plants, at least not until those plants are released from shade stress and growing substantially above their whole-plant, physiological compensation point (Givnish 1988). In fact, when occupying full light (e.g. full canopy position), they may exhibit some of the characteristics of pioneering species. In other words, some plants may have two suites of adaptive syndromes: one when subjected to very low light and the other when subjected to medium-full light and capable of faster growth. Such is apparently the case for sugar maple, *Acer saccharum*, a very shade tolerant tree species in eastern North America (Canham 1989).

Polyspecies Plant Communities: Conversion To Monodominance

Some polyspecies communities can eventually become oligospecies, monodominated communities (if left undisturbed) because of steadily increasing recruitment by species that have the least demand for light. This commonly happens in the Great Lakes Region where sugar maple and balsam fir often assume complete dominance in their respective mixed species forests (in the absence of fire) because of their superior shade tolerance and highly aggressive recruitment under their own canopies (Bourdo

1969, Tubbs 1969). This is also a well-established phenomenon in the world's tropical forests (Hart et al. 1989). Such single-species dominated, late successional forests can eventually become extensive over time. Hence, like the oligospecies, pioneer tree species forests, they may be highly prone to outbreak folivores. However, unlike the pioneer species, the late successional species have evolved in an environmental matrix consisting of polyspecies competition and shade tolerance. Some of the physiological traits needed for success there will likely carry over into those environments where the forest acquires monospecific dominance: stronger constitutive defenses, weaker DIR, lower tolerance capacity. On the other hand, such a plant species may be phenotypically plastic so that it acquires some of the traits of a pioneering tree species when growing monodominantly in full sunlight.

CHARACTERISTICS OF OUTBREAK FOREST SYSTEMS

Oligospecies Forests: Extremes of Shade Tolerance

There are about 85 species of expansive outbreak folivores in North America, but the number of plant systems supporting these insects is substantially smaller, between 30 and 40. Thus, some plant systems support more than one outbreak species: e.g. *A. balsamea/Picea* spp.: 4, *A. saccharum/Fagus grandifolia*: 5, *Pinus contorta*: 7, *P. tremuloides*: 8, *Pseudostuga menziesii*: 8, etc. (Appendix 3).

Likewise, some insect species have several races that can reach outbreak proportions in more than one system: e.g. *Malacosoma disstria* in *A. saccharum*, *N. sylvatica*, *P. tremuloides*, and *Quercus* spp. forests.

Almost all these outbreak systems are oligospecies communities dominated by just one or two plant species (e.g. *P. tremuloides*, *Betula papyrifera*, *A. saccharum/F. grandifolia*, *Pinus banksiana*, *Pinus ponderosa*, *A. balsamea*, etc.). These species tend to fall largely into either one of two shade tolerance classifications: 1) highly light demanding, i.e. shade intolerant, or 2) highly shade tolerant, and capable of developing into monodominant communities (Appendix 3). This classification may also apply to outbreak forest systems in the tropics (Bruenig and Huang 1989). Some oak species exhibit medium shade tolerance and thus may be an exception.

Predictions of Insect Loading, Outbreak Frequency, Duration

The following predictions can be derived from the preceding discussions of plant life history strategies:

1) folivores species loading, and mean level of herbivory should rank as follows: pioneering, growth-adapted species (PGAS) > pioneering, stress-adapted, deciduous species (PSASd) > pioneering, stress-adapted, evergreen species (PSASe) > competition- and shade-tolerance adapted species (CSTS);

2) the frequency of outbreaks per unit life span should rank as follows: PGAS > PSASd > PSASe > CSTS;

3) the duration of outbreaks should rank as follows: PSASe > PGAS > PSASd > CSAS.

This ranking reflects the limited capacity of some stress-adapted plants, especially evergreen conifers, to exhibit substantive, efficacious inducible defenses of any kind (RIR, DIR) (Bryant et al. 1988, Neuvonen and Niemelä this volume, Herms and Mattson 1991). For example, severe defoliation of evergreen conifers can lead to an increase in adventitious sprouting and a general increase in foliar nitrogen (Batzer 1969, Goyer et al. 1990, Långström et al. 1990, Piene and Little 1990). The net result may ameliorate rather than deteriorate foliage quality for herbivores (Haukioja 1991, Haukioja et al. 1990) at least until substantial rootlet mortality causes nutrient impoverishment to be more severe than plant carbon limitations.

Outbreak Patterns by Plant Growth and Shade Tolerance Classes

Outbreak Frequency

There is very little information regarding the number of outbreaks that occur during the life span of a given tree species under given site conditions. Instead, most information concerns insect dynamics over broad geographic regions (Myers 1988a). Thus, it is difficult to generate sound generalizations about differences in outbreak patterns among tree species. For most short-lived species (< 125 yrs), the data suggest that at least two outbreak episodes occur, invariably during the second half of the life span of these species. For some longer lived species, such as *P. menzeisii*, several outbreak episodes are likely during the second half of their life span (Swetnam and Lynch 1989). For other species, however, there is not enough information to make any conclusions.

In a few cases, obvious, regular patterns have been recognized in middle-aged to older trees: the apparent 5-year and 10- to 15-year-cycles of *M. disstria* on *Nyssa aquatica* (Goyer et al. 1990), and *P. tremuloides*, respectively (Hodson 1941, pers. observ.), the 10- to 15-year-cycles of *Acleris variana* (Miller 1966), the 35-40 year cycles of *C. fumiferana* on *A. balsamea* (Royama 1984), and the apparent 10-year-cycles of *Orgyia pseudostugata* and 28-year-cycles of *C. occidentalis* on *P. menzeisii* in British Colombia (Myers 1988a, Shepherd et al. 1988).

Outbreak Duration

Only slightly more information is available about the average duration of outbreaks (Table 2). To look for trends in duration of defoliation by plant life history strategies, we classified insects on the basis of the shade tolerance and the growth rates of their primary host trees (Table 3). Few obvious patterns emerged. This is not altogether surprising, given the vagueness of the available data. Typically, most outbreaks lasted 2 to 3 years, regardless of the host plant's growth/shade classification (Tables 2, 3). However, some unusually chronic cases are associated with conifers and/or leaf miners: *Coleotechnites* spp. on *Pinus contorta* (> 10 yrs), *Pristiphora erichsonii* on *Larix laricina* (> 6 yrs), *Choristoneura* spp. on *Abies* spp. and *P. menzeisii* (> 6 yrs), *Archips argyrospila* on *Taxodium distichum* (> 5 yrs), and the maple leaf cutter, *Paraclemensia acerifoliella*, on *Acer saccharum* (> 4 yrs) (Ross 1962, Struble 1972, Turnock 1972, Swetnam and Lynch 1989, Goyer et al. 1990, see also Neuvonen and Niemelä in this volume).

Effects of Natural Enemies on Outbreak Patterns

Because host effects on folivore population dynamics are naturally confounded with natural enemy effects, it is difficult to tease apart the two (McNamee et al. 1981, Hanski 1987, Goyer et al. 1990). For example, it seems that most outbreak folivores are prone to bacterial, fungal, and viral epizootics that may limit their population outbreaks to about 3 years (Myers 1988a, Shepherd et al. 1988). If it is generally the case that natural enemies limit the duration of outbreaks, then one may have to seek enemy-free conditions to test the true host effects on folivore dynamics. For example, Shepherd et al. (1988) reported that where virus was not evident in *O. pseudotsugata* outbreaks, they either ended quickly by killing the host plants or they lasted for as long as 9-12 years on isolated *Picea* spp. Goyer et al. (1990) concluded that in permanently flooded *T. distichum* and *N. aquatica* wetlands where parasites and predators of folivores are scarce, *A. argyrospila* and *M. disstria* populations cycle continuously in response to foliage depletion. Other authors have also concluded that natural enemy-impoverished habitats are prone to more frequent and severe outbreaks of folivores (Turnock 1972, Hanski 1987, Mason 1987).

Table 2. Average duration (years) of outbreaks by different insects in North America.

Species	Years	Species	Years
Acleris gloverana	2-3	*Heterocampa manteo*	2
Acleris variana	2	*Lambdina fiscellaria lugubrosa*	3
Archips argyrospila	5	*Malacosoma americanum*	2-3
Archips semiferanus	2	*Malacosoma disstria*[1]	3
Bucculatrix candensisella	2-3	*Malacosoma californicum*	3-5
Choristoneura conflictana	2-3	*Melanolophia imitata*	2
Choristoneura fumiferana	5-8	*Neodiprion pratti banksianae*	2-3
Choristoneura occidentalis	3-6	*Neodiprion swainei*	3-4
Choristoneura pinus	2-4	*Nymphalis californicum*	1-2
Coleotechnites milleri	10-20	*Orgyia pseudotsugata*	1-3
Coleotechnites starki	10-20	*Paraclemensia acerifoliella*	3-6
Coloradia pandora	6-8	*Parorgyia grisefacta*	3
Datana integerrima	2	*Pristiphora erichsonii*	3-20
Dryocampa rubicunda	2	*Rheumaptera hastata*	2
Hetercampa guttivita	1-3		

Table 3. Comparing the duration of insect outbreaks by tree growth rates and shade tolerance classifications. Each number in the table represents an average outbreak period in years for an insect species that occurs on a host having that growth and shade classification.

Growth rate[2]	Low shade tolerance[2]	Medium shade tolerance	High shade tolerance
Low	2,3,7,15,15	2,5	2,2,2,4
Medium	2,3,3	2	3,3,3
High	2,2,2,3,3,3,3,3,4,6	n.a.	2,6
Very high	3,3,3	n.a.	n.a.

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[1] *M. disstria* in aspen forests.

[2] Data about tree classes derived from Appendix 3.

CLASSIFYING GRAZING SYSTEMS IN NORTH AMERICA

Although there may be only 85 species of outbreak folivores in North America, they annually chew their way though about 7.6 million ha of tree leaves across the United States (USDA, Forest Service). Most of the forests impacted by outbreaks support more than one species of outbreak folivore and sustain at least two severe defoliation episodes. Yet the forests survive, even though in some unique cases most overstory individuals die as a result of the defoliations (e.g. *Choristoneura* spp. on *Abies* spp.). Most vigorous trees, in fact, have the capacity to physiologically tolerate 2 successive years of near complete defoliation of current-year foliage. Moreover, those trees that grow in vast monodominant stands are not subject to the usual interspecies competitive encroachment that occurs during such outbreaks. The following is a partial description of three different types of grazing systems: chronic, coup-de-grâce, and limited systems.

Chronic Grazing Systems: Short-lived, Growth-Adapted Pioneers

In the case of most folivores that do not usually cause tree mortality, we argue that folivory is not so much a mutualistic as it is a commensalistic consequence of the plant's "life-style." Outbreak folivores are inevitable where plants grow in vast, monodominant, largely even-aged, pioneer communities. We label those as "chronic grazing systems," which by virtue of their short lifespan, high growth strategy, and low competition tolerance, cannot make substantive investments in defense. Chronic herbivory can be physiologically tolerated with little or no consequence to the competitive status of individuals--barring compounding stresses such as severe moisture deficits or excesses, and pollution. Such systems would be those dominated by *P. tremuloides*, *B. papyrifera*, *N. aquatica*, and perhaps some intolerant, fast-growing conifers such as *P. banksiana*, interior *P. menzeisii*, and *L. laricina*.

Coup-de-Grâce Grazing Systems: Short-lived, Shade-Tolerant Species--*Abies* spp.

True firs and tortricids appear to be a special case, i.e. a "coup-de-grâce grazing system." For example, the interaction between *C. fumiferana* and *A. balsamea/Picea* spp. forests in eastern North America may be highly coevolved because it apparently dates back at least 8,000-10,000 years (Anderson et al. 1986). Clearly, *A. balsamea* is not threatened by its association with *C. fumiferana* even though substantial mortality invariably results when outbreaks occur in mature stands (MacLean 1980). Such mortality increases nonlinearly with the age of the stand, the percentage basal area in balsam and spruce, and the severity of moisture stress (Batzer 1969, MacLean 1980, Hardy et al. 1983, Lynch and Witter 1984, Archambault et al. 1990). In fact, it is likely that the insect enhances balsam's ability to compete with other trees. Being shorter lived, faster growing, and more shade tolerant than its common associates (*P. glauca*, *P. rubens*, *P. mariana*), balsam competes by more rapidly turning over its populations, aided by wind, root, and stem herbivores, and *C. fumiferana* (Sprugel and Bormann 1981, Harcombe 1987, Loehle 1988). The spruces, on the other hand, are much less subject to windthrow and defoliation-induced mortality (Archambault et al. 1990, MacLean 1980) and compete through their greater persistence (Gordon 1985). However, attaining larger size and older age is not always adaptive where the growing season is cold limited and where soils are shallow and nutrient poor. Givnish (1988) argued that because foliage costs increase substantially with tree height, the whole plant ecological compensation point dictates a smaller stature in resource limited environments.

Limited Grazing Systems: Long-lived, Shade- and Stress-tolerant Species

Shade-adapted species such as *A. saccharum/F. grandifolia*, and *Tsuga* spp., as well as the long-lived, stress-adapted species such as some *Quercus* spp., and *Pinus* spp. (e.g. *P. ponderosa*) may have very limited physiological capacity to tolerate severe, prolonged defoliation, especially as they reach maturity. Hence, we classify systems dominated by these as "limited grazing systems." They are subject to extinction unless defoliation is in some sense limited, either quantitatively or qualitatively.

For example, the evergreen conifers may be able to cope much longer, if new growth is spared and folivory is strictly confined to older age classes of needles as is the case for sawflies (Diprionidae) and some lepidopterans such as the pandora moth, *Coloradia pandora.*

SUMMARY

High growth-adapted, short-lived plant species that form mono- and oligo-dominated systems are most susceptible to and most capable of tolerating chronic defoliation (Table 4). These plants tend to be shade intolerant and invest a very large fraction of their resources into enlargement of their canopies which have high nutrient and low allelochemical levels, i.e. high specific leaf areas.

High stress-adapted species that form mono- and oligo-dominant systems are also very susceptible to but not highly tolerant of chronic, severe defoliation (Table 4). Consequently they ought to have evolved defensive mechanisms to limit the frequency, duration, and the nature of folivory. They will have high levels of foliar allelochemicals, low levels of nutrients, and perhaps a significant delayed inducible defense--at least for deciduous species.

Table 4. Defensive responses[3] evolved against folivores by plants that have different life history strategies.

	Monodominant-adapted life history		Polydominant-adapted life history	
	Deciduous	Evergreen	Deciduous	Evergreen
High growth adapted	Tol. high Con. low RIR weak DIR weak	Tol. med.[4] Con. med. RIR weak DIR weak	Tol. med. Con. med. RIR strong DIR strong	Tol. low Con. high RIR med. DIR med.
High stress adapted	Tol. low Con. high RIR weak DIR med.	Tol. low Con. v. high RIR none DIR none	Tol. v. low Con. v. high RIR weak DIR med.	Tol. v. low Con. v. high RIR none DIR none

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[3] Tol. = tolerance capacity, Con. = constitutive defense level, RIR and DIR = rapid inducible and delayed inducible resistance, respectively.

[4] Med. = medium

Growth-adapted, short-lived, shade tolerant plant species that form polydominant plant systems when young, but monodominant when older, may have the phenotypic plasticity to exhibit a blend of strategies for coping with outbreak folivores. When slow growing in heavy light competition with other species, they may be highly defended against folivores. On the other hand, when older and growing monodominantly they may rely more on tolerance and defenses similar to those of the shade intolerant group.

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APPENDIX 1

Outbreak folivores in North America and their primary host plants.

Genus	Species	Family	Primary host plant
Acleris	*gloverana*	Tortricidae	*Tsuga heterophylla*
	variana	Tortricidae	*Abies balsamea*
Alsophila	*pometaria*	Geometridae	*Quercus* spp.
Anacamptodes	*ephyraria*	Geometridae	*Taxodium distichum*
Anisota	*senatoria*	Saturniidae	*Quercus* spp.
Archips	*argyrospilus*	Tortricidae	*Quercus* spp.
	argyrospilus		*Taxodium distichum*
	semiferanus		*Quercus ellipsoidalis*
Argyresthia	*thuiella*	Argyresthiidae	*Thuja occidentalis*
Argyrotaenia	*tubulana*	Tortricidae	*Pinus contorta*
Bucculatrix	*canadensisella*	Lyonetiidae	*Betula papyrifera*
Caliroa	spp.	Tenthredinidae	*Quercus* spp.
Choristoneura	*biennis*	Tortricidae	*Abies lasiocarpa*
	conflictana		*Populus tremuloides*
	fumiferana		*Abies balsamea*
	lambertiana		*Pinus contorta*
	occidentalis		*Pseudotsuga menziesii*
	orae		*Abies amabalis*
	pinus		*Pinus banksiana*
	retiniana		*Abies concolor*
	viridis		*Abies concolor*
Coleophora	*laricella*	Coleophoridae	*Larix laricina*
	serratella		*Betula papyrifera*
Coleotechnites	*milleri*	Gelechiidae	*Pinus contorta*
	starki		*Pinus contorta*
Coloradia	*pandora*	Sphingidae	*Pinus contorta*
	pandora		*Pinus jeffreyii*
	pandora		*Pinus ponderosa*
Dasychira	*pinicola*	Lymantriidae	*Pinus banksiana*
Datana	*integerrima*	Notodontidae	*Carya illinoensis*
Diapheromera	*femorata*	Phasmatidae	*Quercus rubra*
Diprion	*similis*	Diprionidae	*Pinus strobus*
Dryocampa	*rubicunda*	Saturniidae	*Acer* spp.
Ectropis	*crepuscularia*	Geometridae	*Tsuga heterophylla*
Ennomos	*subsignarius*	Geometridae	*Carya* spp.
Epinotia	*meritana*	Olethreutidae	*Abies concolor*
	solandriana		*Betula papyrifera*
	tsugana		*Tsuga heterophylla*
Epirrita	*autumnata omissa*	Geometridae	*Tsuga heterophylla*
Erannis	*tiliaria*	Geometridae	*Acer saccharum*
Fenusa	*pusilla*	Tenthredinidae	*Betula papyrifera*
Galenaria	*consimilis*	Geometridae	*Pseudotsuga menziesii*
Halisidota	*argentata*	Arctiidae	*Tsuga heterophylla*

APPENDIX 1 continued

Genus	Species	Family	Primary host plant
	argentata subalpina		*Juniperus scopulorum*
Heterocampa	*guttivita*	Notodontidae	*Fagus grandifolia*
	manteo		*Quercus alba*
Hydria	*prunivorata*	Geometridae	*Prunus serotina*
		Gracillariidae	*Populus tremuloides*
Lithocolettis	*ontario*		
Lambdina	*fiscellaria fiscellari*	Geometridae	
	fiscellaria lugubrosa		*Tsuga heterophylla*
	fiscellaria somniaria		*Quercus garryana*
	punctata		*Quercus gambelii*
Lymantria	*dispar*	Lymantriidae	*Quercus* spp.
Malacosoma	*americanum*	Lasiocampidae	*Prunus serotina*
	californicum fragile	Lasiocampidae	*Populus tremuloides*
	constrictum		*Quercus douglasii*
	disstria		*Acer saccharum*
	disstria		*Nyssa aquatica*
	disstria		*Populus tremuloides*
	disstria		*Quercus* spp.
Melanolophia	*imitata*	Geometridae	*Pseudotsuga menziesii*
Neodiprion	*abietis*	Diprionidae	*Abies balsamea*
	abietis		*Abies concolor*
	burkei		*Pinus contorta*
	educolis		*Pinus edulis*
	excitans		*Pinus taedae*
	gillettei		*Pinus ponderosa*
	lecontei		*Pinus resinosa*
	nanulus contortae		*Pinus contorta*
	pratti banksianae		*Pinus banksiana*
	pratti pratti		*Pinus virginiana*
	swainei		*Pinus banksiana*
	taedae linearis		*Pinus taedae*
	tsugae		*Tsuga heterophylla*
Neophasia	*menapia*	Pieridae	*Pinus ponderosa*
Nepytia	*freemani*	Geometridae	*Pseudotsuga menziesii*
	phantasmaria		*Pseudotsuga menziesii*
Odontota	*dorsalis*	Chrysomelidae	*Robinia pseudoacacia*
Operophtera	*bruceata*	Geometridae	*Acer saccharum*
	bruceata		*Populus tremuloides*
Orgyia	*pseudotsugata*	Lymantriidae	*Abies grandis*
	pseudotsugata		*Pseudotsuga menziesii*
Paraclemensia	*acerifoliella*	Incurvariidae	*Acer saccharum*
Parorgyia	*grisefacta*	Lymantriidae	*Pinus ponderosa*
Phaeoura	*mexicanaria*	Geometridae	*Pinus ponderosa*
Phryganidia	*californica*	Dioptidae	*Quercus lobata*
Phyllocnistis	*populiella*	Gracillariidae	*Populus tremuloides*

APPENDIX 1 continued

Genus	Species	Family	Primary host plant
Pristiphora	*erichsonii*	Tenthredinidae	*Larix laricina*
Rheumaptera	*hastata*	Geometridae	*Betula papyrifera*
Sciaphila	*simplex*	Olethreutidae	*Populus tremuloides*
Semiothisa	*sexmaculata*	Geometridae	*Larix laricina*
Symmerista	*albifrons*	Notodontidae	*Acer saccharum*
	canicosta		*Quercus alba*
Xylomgyges	*simplex*	Noctuidae	*Pseudotsuga menziesii*
Zeiraphera	*hesperiana*	Olethreutidae	*Pseudotsuga menziesii*
	improbana		*Larix occidentalis*
Zelleria	*haimbachi*	Yponomeutidae	*Pinus ponderosa*

Data derived from Furniss and Carolin 1977, Drooz 1985, and others.

APPENDIX 2

Size (ha) and frequency of outbreak areas by different folivore species in the United States during a 28-year period between 1957 and 1987. Derived from Annual Pest Reports by USDA, Forest Service.

Outbreak insect species	Average[5] area/episode	Maximum area	Frequency (yrs)	Average[6] area/year
Acanthodyla circumcinta	36,437	36,437	1	1,301
Acleris gloverana	3,980	27,530	12	1,706
Acleris variana	39,472	115,789	5	7,049
Alsophila pometaria	82,195	450,607	16	46,969
Anacamptodes vellivolata	20,243	20,243	1	723
Anisota senatoria	1,113	2,105	2	80
Archips argyrospila	19,555	47,773	10	6,984
Archips semiferanus	420,520	1,417,004	6	90,111
Argyresthia thuiella	52,632	52,632	1	1,880
Bucculatrix candensisella	6,073	8,097	2	434
Argyrotaenia gogana	41,970	80,972	3	4,497
Caliroa spp.	735,830	1,336,032	2	52,559
Choristoneura carnana	39,541	52,632	3	4,237
Choristoneura conflictana	362,295	2,631,579	19	245,843
Choristoneura fumiferana	1,384,858	3,103,644	26	1,285,940
Choristoneura lambertiana	26,846	109,717	8	7,670
Choristoneura occidentalis	2,290,445	5,353,610	28	2,290,445
Choristoneura orae	1,923	2,713	2	137
Choristoneura pinus	99,154	379,352	16	56,659
Choristoneura retiniana	152,591	224,049	4	21,799
Choristoneura viridis	43,015	143,320	5	7,681
Coleophora laricella	1,183,240	12,064,777	12	507,103
Coleotechnites milleri	105,457	242,915	13	48,962
Coloradia pandora	6,904	18,016	13	3,205
Croesia albicomana	140,663	323,887	4	20,095
Daschyra pinicola	7,535	25,709	9	2,422
Diaphemorata femorata	19,703	54,656	6	4,222
Diprion similis	974,176	1,943,320	2	69,584
Dryocampa rubicunda	12,551	24,291	2	896
Ennomos subsignarius	300,174	620,243	7	75,043
Epinotia meritana	8,967	47,368	11	3,523
Epinotia solandriana	14,650	59,166	6	3,139
Erannis tiliaria	1,754	4,049	3	188
Galenaria consimilis	1,518	2,429	2	108

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[5] Infestation areas summed over the entire United States and divided by frequency (yrs).

[6] Average area x frequency ÷ 28.

APPENDIX 2 continued

Outbreak insect species	Average area/episode	Maximum area	Frequency (yrs)	Average area/year
Halisodota argentata alpina	2,699	4,049	3	289
Heterocampa guttivita	125,586	465,587	14	62,793
Heterocampa manteo	544,356	2,226,721	6	116,648
Hydria prunivorata	85,425	163,968	6	18,305
Ichthyura inclusa	6,680	6,680	1	239
Lambdina anthasaria	17,304	17,304	1	618
Lambdina fiscellaria fiscellar	207	405	2	15
Lambdina fiscellaria somniaria	826	842	2	59
Lambdina fiscellaria lugubrosa	8,085	28,340	8	2,310
Lithocolletis ontario	109,603	209,085	2	7,829
Lithophane antennata	42,510	80,972	2	3,036
Lymantria dispar	774,275	5,263,158	26	718,970
Malacosoma disstria	934,676	13,461,538	28	934,676
Malcosoma californicum fragile	30,476	121,943	16	17,415
Nacophora mexicanara	3,684	6,073	2	263
Neodiprion pratti paradoxicus	422,348	422,348	1	15,084
Neodiprion abietis	7,547	16,194	3	809
Neodiprion educolis	101,215	101,215	3	10,844
Neodiprion excitans	22,901	121,457	6	4,907
Neodiprion gillettii	810	810	1	29
Neodiprion lecontei	908	2,632	6	195
Neodiprion nanulus contortae	2,834	3,239	2	202
Neodiprion pratti banksianae	24,291	36,437	2	1,735
Neodiprion pratti pratti	633,907	1,113,360	4	90,558
Neodiprion taeda linearis	45,443	275,992	9	14,607
Neodiprion tsugae	11,985	28,664	8	3,424
Neophasia menapia	9,075	30,769	8	2,593
Neptyia freemani	904	1,417	3	97
Opheropthera bruceata	60,134	152,227	5	10,738
Orgyia pseudotsugata	36,433	323,887	21	27,325
Paleacrita vernata	5,465,775	10,931,174	2	390,413
Paraclemensia acerifoliella	9,399	24,291	3	1,007
Phyllocnistis populiella	202,429	202,429	3	21,689
Pristiphora erichsonii	85,701	202,429	11	33,668
Rheumaptera hastata	485,946	2,359,919	9	156,197
Sciphila duplex	37,454	68,826	4	5,351
Semiothisa sexmaculata	101,822	202,429	2	7,273
Stilpnotia salicis	3,644	3,644	1	130
Symmerista albicosta	13,360	18,219	2	954
Symmerista canicosta	220,951	526,316	4	31,564
Xylomyges simplex	3,239	3,239	1	116
Zeiraphera griseana	81,344	209,717	6	17,431
Zeiraphera hesperiana	45,142	49,798	2	3,224

APPENDIX 2 continued

Outbreak insect species	Average area/episode	Maximum area	Frequency (yrs)	Average area/year
Zeiraphera improbana	17,465	61,134	4	2,495
Zeiraphera ratzeburgiana	34,818	34,818	1	1,243
Zelleria haimbachi	15,083	69,636	11	5,926
Grand total area/year				7,618,488

APPENDIX 3

Outbreak host plant systems and their outbreak folivores in North America defined by the dominant plant species. Shade tolerance and growth rate classifications,[7] typical age of mortality from Loehle (1988), and percent host domination of system from various sources, primarily Folwells (1965).

	Host plant parameters				
Species	Shade tolerance	Growth rate	Average age at death	Percent system domination	Outbreak folivore species
Abies amabalis	4	3	400	50	*Choristoneura orae*
Abies balsamea	5	4	125	50	*Acleris variana* *Choristoneura fumiferana* *Lambdina fiscellaria fiscella* *Neodiprion abietis*
Abies concolor	5	3	10	50	*Choristoneura retiniana* *Choristoneura viridis* *Epinotia meritana* *Neodiprion abietis*
Abies grandis	4	3	200	60	*Orgyia pseudotsugata*
Abies lasiocarpa	5	3	150	65	*Choristoneura biennis*
Acer saccharum	5	2	300	50	*Erannis tiliaria* *Malacosoma disstria* *Operophtera bruceata* *Paraclemensia acerifoliella* *Symmerista albifrons*
Acer rubrum	5	2	150	50	*Dryocampa rubicunda*
Betula papyrifera	2	4	100	75	*Bucculatrix canadensisella* *Coleophora serratella* *Epinotia solandriana* *Fenusa pusilla* *Rheumaptera hastata*
Carya illinoensis	2	3	300	50	*Datana integerrima*
Carya spp.	2	2	200	n.a.	*Ennomos subsignarius*

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[7] Classes range from 1 to 5, low to high, respectively.

APPENDIX 3 continued

Species	Host plant parameters Shade tolerance	Growth rate	Average age at death	Percent system domination	Outbreak folivore species
Fagus grandifolia	5	2	300	50	*Heterocampa guttivita*
Juniperus scopulorum	1	2	250	70	*Halisidota argentata subalpina*
Larix laricina	1	3	150	80	*Coleophora laricella* *Pristiphora erichsonii* *Semiothisa sexmaculata*
Larix occidentalis	1	2	700	70	*Zeiraphera improbana*
Nyssa aquatica	2	4	80	90	*Malacosoma disstria*
Pinus banksiana	1	4	80	80	*Choristoneura pinus* *Dasychira pinicola* *Neodiprion pratti banksianae* *Neodiprion swainei*
Pinus contorta	2	2	120	80	*Argyrotaenia tubulana* *Choristoneura lambertiana* *Coleotechnites milleri* *Coleotechnites starki* *Coloradia pandora* *Neodiprion burkei* *Neodiprion nanulus contortae*
Pinus edulis	1	1	350	50	*Neodiprion educolis*
Pinus jeffreyii	2	3	400	80	*Coloradia pandora*
Pinus ponderosa	2	3	600	70	*Coloradia pandora* *Neodiprion gillettei* *Neophasia menapia* *Parorgyia grisefacta* *Phaeoura mexicanaria* *Zelleria haimbachi*
Pinus resinosa	1	4	200	90	*Neodiprion lecontei*
Pinus strobus	2	2	200	50	*Diprion similis*

APPENDIX 3 continued

Species	Host plant parameters Shade tolerance	Growth rate	Average age at death	Percent system domination	Outbreak folivore species
Pinus taedae	2	4	100	70	*Neodiprion excitans* *Neodiprion taedae linearis*
Pinus virginiana	2	3	100	80	*Neodiprion pratti pratti*
Populus tremuloides	1	5	70	80	*Choristoneura conflictana* *Malacosoma californicum fragile* *Malacosoma disstria* *Operophtera bruceata* *Phyllocnistis populiella* *Lithocolletis ontario* *Sciaphila simplex*
Prunus serotina	2	4	100	50	*Hydria prunivorata* *Malacosoma americanum*
Pseudotsuga menziesii	2	4	750	50	*Choristoneura occidentalis* *Galenaria consimilis* *Nepytia freemani* *Nepytia phantasmaria* *Orgyia pseudotsugata* *Xylomgyges simplex* *Zeiraphera hesperiana* *Melanolophia imitata*
Quercus alba	2	3	300	50	*Heterocampa manteo* *Symmerista canicosta*
Quercus douglasii	2	2	100	70	*Malacosoma constrictum*
Quercus ellipsoidalis	2	2	80	50	*Archips semiferanus*
Quercus gambelii	2	2	90	n.a.	*Lambdina punctata*
Quercus garryana	2	2	300	n.a.	*Lambdina fiscellaria somniaria*
Quercus lobata	2	4	200	70	*Phryganidia californica*
Quercus rubra	3	4	200	50	*Diapheromera femorata*

APPENDIX 3 continued

Species	Host plant parameters: Shade tolerance	Host plant parameters: Growth rate	Host plant parameters: Average age at death	Host plant parameters: Percent system domination	Outbreak folivore species
Quercus spp.	3	3	150	50	*Malacosoma disstria* *Alsophila pometaria* *Anisota senatoria* *Archips argyrospilus* *Caliroa* spp. *Lymantria dispar*
Robinia pseudoacacia	2	4	60	70	*Odontota dorsalis*
Taxodium distichum	3	2	600	50	*Anacamptodes ephyraria* *Archips argyrospilus*
Thuja occidentalis	4	2	300	50	*Argyresthia thuiella*
Tsuga heterophylla	5	3	400	50	*Acleris gloverana* *Ectropis crepuscularia* *Epinotia tsugana* *Epirrita autumnata omissa* *Halisidota argentata* *Lambdina fiscellaria lugubrosa* *Neodiprion tsugae*

VARIATION IN THE NUTRITIONAL PHYSIOLOGY OF TREE-FEEDING SWALLOWTAIL CATERPILLARS

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INTRODUCTION

A key problem in addressing patterns of interaction between forest insects and their host trees is determining the level at which important ecological and evolutionary interactions occur. We commonly view plant-herbivore relations as herbivore species interacting with plant species, tacitly assuming that variation among members of either species is small and one can represent their interaction by the average characteristics of the insect and the tree species (Ehrlich and Raven 1964, Feeny 1976, Rhoades and Cates 1976, Scriber and Feeny 1979). This simplistic view is violated if insects within a species differ markedly in their ability to grow on a particular host, or if trees within a species differ substantially in quality as perceived by the insect. If variation within both insect and host species is large and pervasive, then insect-plant interactions may be best studied at the level of genotypes and populations (Edmunds and Alstad 1978, Fox and Morrow 1981, Thompson 1988a, Ng 1988, Karban 1989). Clearly intraspecific variation exists. For example, potato beetles, checkerspot butterflies, tortoise beetles, autumnal moths, and tiger swallowtails are each comprised of populations that differ in their ability to use key hosts (Hsiao 1978, Rausher 1982, 1984, Haukioja and Hanhimaki 1985, Scriber 1986a, Hare and Kennedy 1986). Likewise mountain birch, cottonwood, honeylocust, and a variety of other trees are comprised of populations that differ in their suitability for specific herbivores (Hanover 1980, Haukioja and Hanhimaki 1985, Pakash and Heather 1986, Herms et al. 1987). Even within populations, individual trees may be highly variable (Edmunds and Alstad 1978, Whitham and Slobodchikoff 1981, Smiley et al. 1985, Ayres et al. 1987, Whitham 1989). The emerging problem is to quantify variation within and between populations relative to variation at other levels.

Our studies have addressed variation in the nutritional physiology of tree-feeding swallowtail caterpillars (Papilionidae: Lepidoptera). A central objective has been to determine the level at which ecological and evolutionary divergence has occurred. For example, physiological adaptation of caterpillars to their host plants may occur at the level of genotypes and populations, at the level of species and species groups, or both. Genetic variation within and between populations implies a potential for adaptation to local conditions. Alternatively, substantial variation between closely related species, with little intraspecific variation, implies that adaptive shifts occur via reproductive isolation and are often associated with speciation events (Mayr 1963). In this case, it is appropriate to emphasize species attributes.

Our research has concentrated on traits of likely ecological importance, and especially on traits subject to geographically variable selective pressures. In addition to nutritional physiology and detoxification, these include mate choice and reproductive allocation (Burns 1966, Svard and Wiklund 1986, Lederhouse et al. 1989), cold hardiness and diapause biology (Shimado 1988, Hagen and Scriber

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BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

1989, Kukal et al. in prep.), host choice and oviposition behavior (Grossmueller and Lederhouse 1985, 1987, Thompson 1988b, 1988c, Bossart and Scriber in prep.), and larval temperature responses (Scriber and Lederhouse 1983, Ritland and Scriber 1985). Our ability to draw inferences about the evolutionary history of these attributes is strengthened by the existence of a large number of *Papilio* taxa with differing degrees of relatedness (Hagen and Scriber 1990). Here we describe recently completed experiments testing the nature and extent of variation within two closely related species of *Papilio*, *P. glaucus*, and *P. canadensis*.

BACKGROUND

Nearctic Tree-feeding Swallowtails

Most of the common tree-feeding papilionids in North America belong to two sister clades within the genus *Papilio*: the *P. glaucus* and *P. troilus* species groups. Host use patterns in the *P. troilus* group are typical of the Papilionidae in that all its members (*P. troilus* L., *P. palamedes* Drury, and *P. pilumnus* Boisduval) are restricted to hosts from a single plant family (Lauraceae). In contrast, all six members of the *P. glaucus* group (*P. glaucus* L., *P. alexiares* Hoppfer, *P. canadensis* R & J, *P. eurymedon* Lucas, *P. rutulus* Lucas, and *P. multicaudatus* Kirby) feed on more than one family of hosts (Scriber 1973, 1984). Polyphagy appears to be a derived trait (synapomorphy) within the *P. glaucus* group (Scriber et al. 1991). Unlike the *P. troilus* group, neonate larvae of the *P. glaucus* group typically initiate feeding on virtually any foliage they encounter, toxic or not (Scriber et al. 1991). This behavioral difference may have been a critical precondition for the evolution of polyphagy in *P. glaucus* and its relatives because selection cannot screen for suitable physiologies unless the larvae feed (Feeny 1991). All members of the *P. glaucus* group share the ability to feed on black cherry (*Prunus serotina*, Rosaceae) and chokecherry (*Prunus virginiana*), but *P. glaucus* species differ in their growth performance on most host taxa other than *Prunus* (Scriber et al. 1991). *P. eurymedon* appears to be uniquely capable of developing on *Rhamnus* (Rhamnaceae). *P. canadensis*, *P. eurymedon*, and *P. rutulus* generally grow well on plants of the Salicaceae, yet few *P. glaucus* or *P. alexiares* survive beyond the first instar. Magnoliaceae are typically lethal to all *P. glaucus* taxa except *P. glaucus* and *P. alexiares*.

Papilio glaucus and *Papilio canadensis*

Best known among the tree-feeding swallowtails are two taxa formerly regarded as subspecies, but now believed to be separate species (Hagen et al. in prep.). The transition zone between *P. glaucus* (= "*glaucus*") and *P. canadensis* (= "*canadensis*," formerly *P. g. canadensis*) coincides with a complex ecotone that runs through central Wisconsin and Michigan and extends eastward through northern Pennsylvania, central New York, and southern New England (Scriber 1988). The ecotone has long been recognized as the transition between boreal coniferous forests and diverse deciduous southern forests (Curtis 1959, Braun 1974). This zone marks a climatic boundary between regions influenced by cool, dry air masses to the north and warmer, wetter air masses to the south; it approximates the 1,400 degree day isotherm (10° C base), which is the lower limit for bivoltine potential in *glaucus* (Scriber 1988). The ecotone also corresponds to the southern edge of Pleistocene continental glaciation and thus marks a discontinuity in soil types, topography, and history of occupancy by plants and animals.

P. glaucus and *P. canadensis* are distinguishable by wing morphology, allozymes, and mitochondrial DNA restriction sites (Luebke et al. 1987, Hagen 1990 and in prep.). They also differ in several characteristics of obvious ecological significance. Diapause is induced by short photoperiods in the multivoltine *glaucus*, while *canadensis* is necessarily univoltine (Rockey et al. 1987a, 1987b). The species also differ in the expression (y-linked trait in *glaucus*) and suppression (x-linked trait in *canadensis*) of a mimetic dark morph in the females (Clarke and Sheppard 1962, Hagen and Scriber 1989). Host use differences between *glaucus* and *canadensis* are especially pronounced (Fig. 1). In laboratory trials, first instar *glaucus* larvae grew rapidly on tuliptree, *Liriodendron tulipifera*, foliage (Magnoliaceae), doubling their weight in less than a day, while comparable development in *canadensis* larvae required 3 to 4 days. *P. glaucus* larvae also grew somewhat faster on hoptree, *Ptelea* (Rutaceae). Yet on *Populus tremuloides* (quaking aspen) and *Betula papyrifera* (paper birch), *canadensis* larvae grew substantially faster than *glaucus* larvae. These patterns are consistent with those based on first instar survival, total development time, and pupal mass (Scriber 1983, Lindroth et al. 1986). The northernmost limits of tuliptree and hoptree, and the southernmost limits of aspen and birch, are coincident with the transition zone between the species. However, *glaucus* and *canadensis* range limits are not a simple consequence of these host distributions because other common hosts for each, e.g. cherries (*Prunus*) and ashes (*Fraxinus*), extend either side of the transition zone.

Laboratory handpairings of *glaucus* and *canadensis* adults produced F_1 hybrids that grew and survived on both aspen and tuliptree foliage (Scriber 1986b), suggesting the involvement of two discrete detoxification systems independently controlled by autosomal loci. The ability of *canadensis* larvae to use quaking aspen depends at least in part on the ability to detoxify phenolic glycosides (Lindroth et al. 1988, Scriber et al. 1989). Backcross studies indicated a detoxification threshold necessary for survival, beyond which performance on diets containing phenolic glycoside tremulacin increased with increasing proportions of *canadensis* genes.

Intraspecific Variation

Populations of *glaucus* and *canadensis* in different regions may encounter very different communities of host plants. This is true on a relatively fine scale (river valleys versus uplands) as well as on a coarser geographic scale (the swamp bayheads of Florida versus the Appalachian forests of southern Ohio, or the northern hardwoods of the Great Lakes region versus the boreal forests of interior Alaska). Populations inhabiting regions as distant and floristically disparate as Florida and Ohio, or Alaska and the Great Lakes, must be subject to selection favoring physiological traits that improve growth performance on local hosts. Indeed, larvae from southern Florida survived better on sweetbay, *Magnolia virginiana*, the only regionally abundant host, than larvae from other *glaucus* populations (Scriber 1986a). It has been suggested that Florida populations of *P. glaucus* represent a distinct race, *P. g. australis* Maynard, but electrophoretic comparisons indicate no barriers to gene flow, and we regard the Florida insects as southern populations of *P. glaucus*.

The remainder of this paper describes experiments designed to test the prevalence of regional specialization (Hsiao 1978, Scriber 1983, Scriber 1986a) and allow for quantitative comparisons of variation within and between populations with variation between species and species groups. One set of experiments compares *canadensis* populations from Alaska and the Great Lakes region. Other experiments compare *glaucus* populations from Florida, Georgia, and Ohio. Associated electrophoretic studies provide estimates of population divergence and substructuring independent of the growth performance studies and survey specific allozymes for linkage with host-use abilities.

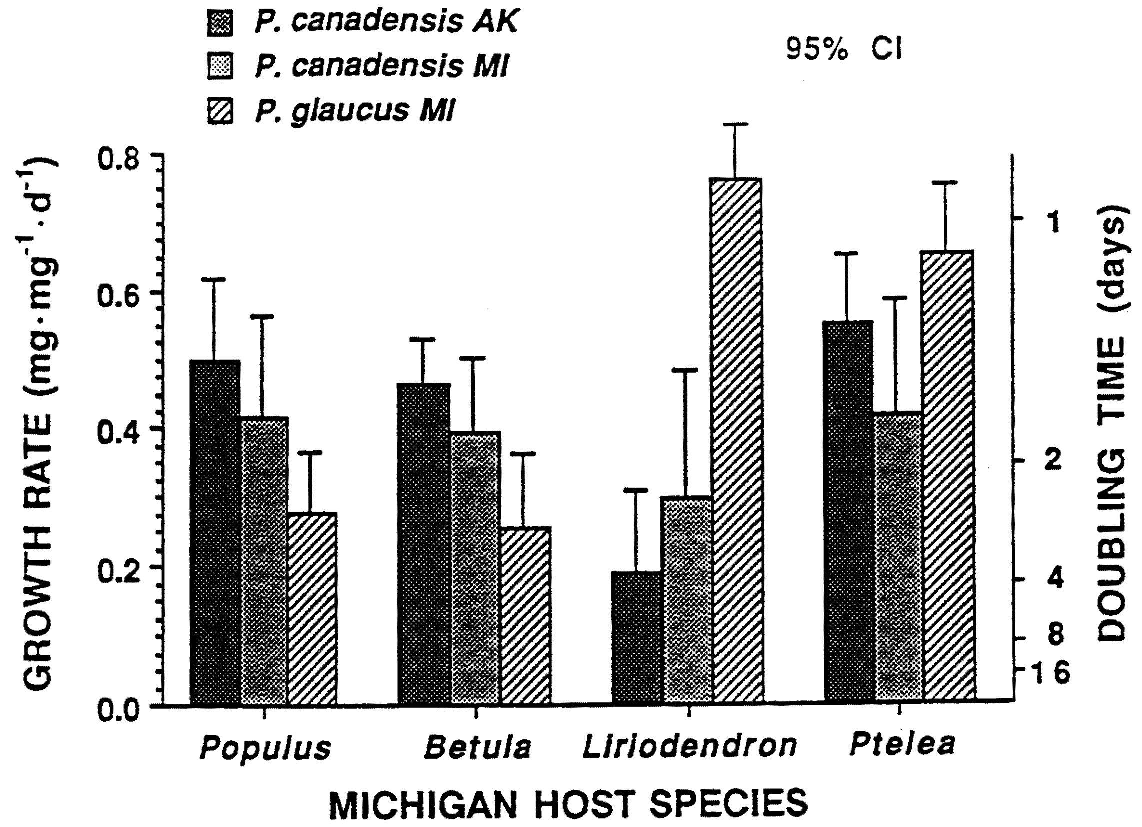

Figure 1. Relative growth rate of first instar larvae from three insect populations tested on four Michigan host species. Right hand axis shows the time required for larvae to double their weight at the corresponding growth rate. The insect populations are *P. canadensis* from Alaska, *P. canadensis* from northern Michigan, and *P. glaucus* from southern Michigan. The host species, from left to right, are *Populus tremuloides* (quaking aspen), *Betula papyrifera* (paper birch), *Liriodendron tulipifera* (tuliptree), and *Ptelea trifoliata* (hoptree). The experiment was conducted from 13 to 20 June 1988 using leaves collected from Ingham County, Michigan. Error bars indicate 95 percent confidence intervals.

METHODS

Butterfly Collection and Oviposition

Adult females were captured from populations in Florida, Georgia, Ohio, Michigan, Wisconsin, and Alaska, then transported on ice or shipped using overnight delivery to our laboratory for oviposition. Females were placed in clear plastic boxes (10 cm x 20 cm x 27 cm) with sprigs of appropriate foliage, held at 100 percent humidity under artificial illumination (4 hr dark alternating with 4 hr light), and fed a honey-water solution daily. Eggs were collected every other day, and resulting neonate larvae were used for the laboratory growth performance studies.

Electrophoresis

Butterflies were frozen at -80°C to preserve tissues for allozyme electrophoresis. Four polymorphic allozyme loci were examined using thin-layer cellulose acetate plates. Alleles were named according to their relative mobility, with the most common *P. glaucus* allele assigned the value of 100; negative numbers were assigned to cathodally migrating allozymes. Detailed techniques are described elsewhere (Hagen and Scriber 1989, Bossart in prep.)

Larval Performance of *P. canadensis*

We compared *P. canadensis* populations from interior Alaska (Fairbanks and vicinity) and the Great Lakes region (northern Wisconsin and the Upper Peninsula of Michigan), 4,000 km away. Some studies also included interspecific comparisons with *glaucus* larvae from southern Michigan and Ohio (500 to 1,000 km from the Michigan *canadensis* sites). We challenged the larvae with nine host species native to Alaska and nine host species native to the Great Lakes region. Of the Great Lakes hosts, none of the nine species and only two of the five families are sympatric with Alaska swallowtails. The Alaska tree species included the only two hosts regularly encountered by both populations (*Populus tremuloides* and *Populus balsamifera*) plus seven other species of *Salix*, *Betula*, and *Alnus*, which are encountered naturally only in Alaska. We had only limited knowledge of *canadensis* host use in Alaska, so we chose species likely to be hosts based on their distribution and taxonomy. In the first summer we documented natural use of four out of the nine species: *Populus tremuloides, Populus balsamifera, Alnus tenuifolia*, and *Salix novae-angliae* (Scriber and Ayres 1990).

Our standard measure of growth performance was first instar relative growth rate. The same protocol was used for experiments conducted in Fairbanks, Alaska, and East Lansing, Michigan. Each population was represented on each host by 17 to 20 larvae drawn from 5 to 8 full-sib families. Larvae from the two populations hatched at the same time and were tested concurrently on the same sample of leaves. Leaves were collected as the *canadensis* eggs began to hatch. Each host species was represented by leaves from five genetically distinct trees. Freshly hatched larvae were weighed, then distributed singly to clear plastic vials containing foliage from one of the experimental hosts. A moistened plaster-of-paris base in each vial provided high humidity and maintained leaf turgor throughout the trial. Nearly all larvae fed on the foliage offered them. After 2 days (24°C, photoperiod of L:D 18:6), the larvae were reweighed. A typical larva weighed 1.5 mg at hatch (T_i) and, on a good host, 6.2 mg at T_f. Final weights were reduced by 10 percent (= estimated weight of food in their gut) to make them comparable to initial weights (taken before the larvae had begun to feed). Relative growth rate was calculated as $(\ln(W_f) - \ln(W_i))/T$, where W_f equals the final weight, W_i equals the initial weight, and T equals the time in days (Gordon 1968, Ayres and MacLean 1987). Degrees of freedom for population comparisons were based on the number of families.

Larval Performance of *P. glaucus*

We compared *P. glaucus* populations from Lawrence County, Ohio, Clarke County, Georgia, and Highlands County, Florida, on three hosts: *Liriodendron tulipifera*, *Magnolia virginiana*, and *Prunus serotina*. These populations span 1,300 km, each separated from the nearest population by about 650 km. The three experimental hosts are all used naturally by *P. glaucus* and support generally high levels of growth performance. The frequency of use differs between populations. Florida *P. glaucus* are largely restricted to *Magnolia virginiana*, the only common host throughout much of peninsular Florida. In contrast, Georgia and Ohio populations rarely or never encounter *Magnolia virginiana*. A variety of host species occur in Ohio and Georgia, but the Ohio population probably encounters *Liriodendron* more frequently than other hosts and the Georgia population probably encounters *Prunus* most frequently.

In 1988 progeny from 6 Florida families, 8 Ohio families, and 14 Georgia families were reared individually in plastic petri dishes (24°C, photoperiod of L:D 18:6). Ten neonate larvae from each family were randomly allocated to each of the three hosts. *Liriodendron* and *Prunus* leaves were collected every other day from trees near East Lansing, Michigan. *Magnolia* leaves were collected from trees maintained in our greenhouses. Larvae were reared to adults. Larval duration, pupal mass, and sex were recorded. Similar experiments were conducted in 1989. Population comparisons may have been somewhat confounded by seasonal changes in the foliage because the natural phenology of the populations differed and we were unable to rear the larvae synchronously.

RESULTS AND DISCUSSION

Variation within *P. canadensis*

Relative growth rates on nine Wisconsin tree species ranged from 0.61 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ on *Betula nigra* to 0.20 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ on *Betula allegheniensis* (Fig. 2). These rates correspond to doubling times of 1.1 versus 3.5 days, respectively, indicating a broad spectrum of host quality. Overall, the Alaska and Great Lakes insect populations did not differ: least square means ± 1 SE equalled 0.425 ± 0.029 versus 0.414 ± 0.039 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ for Alaska and Wisconsin respectively ($P = 0.81$). The contrast between populations was not significant for any of the nine hosts treated separately ($P > 0.05$). These results counter predictions of the regional specialization hypothesis. A match between the physiological attributes of Wisconsin caterpillars and the nutritive characteristics of Great Lakes hosts might have arisen through the acquisition of new abilities in the Wisconsin population (e.g. a detoxification and digestive system suitable for basswood) or the loss of ancestral and unneeded abilities in the Alaska population. There is no evidence that either of these processes has occurred for any of the host taxa examined.

The reciprocal comparison between *canadensis* larvae from Alaska and Wisconsin on nine Alaska host species revealed a similar pattern (Fig. 3). There was a weak overall tendency for Alaska *canadensis* to grow faster than Wisconsin *canadensis* (least square means ± 1 SE equalled 0.525 ± 0.029 versus 0.458 ± 0.019 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ for Alaska and Wisconsin respectively, $P = 0.06$). But Alaska larvae also tended to grow slightly, though not significantly, faster on Wisconsin hosts. The contrast between *canadensis* populations was significant for only one of nine Alaska hosts (*Salix glauca*, $t = 3.44$, df = 13, $P < 0.01$). We do not interpret these modest effects as evidence of local adaptation to host characteristics. The most general test for the hypothesized pattern of local specialization to regional hosts was the ANOVA interaction between *canadensis* populations (Alaska and Wisconsin) and host community (nine Alaska host species and nine Wisconsin host species), which was insignificant ($P = 0.43$, $F = 0.64$, df = 1, 20). The test for interactions between host species and families within populations was also insignificant ($P = 0.99$, $F = 0.74$, df = 160, 357). Yet these were robust tests involving 696 larvae and 18 host species; given the observed variance, we had a high probability of detecting any ecologically meaningful differences. Far from being a mosaic of differentiated populations and variable genotypes, the host-use abilities of *P. canadensis* appear to be remarkably constant across a broad geographic range.

In contrast to the absence of variation within or between *canadensis* populations, there was a marked difference between *canadensis* and *glaucus*. First instar growth rates of *P. glaucus* from Ohio were 34 percent lower overall when tested on the same Alaska host species (Fig. 3). On all nine hosts considered separately, the mean growth rate of *glaucus* larvae was lower than both *canadensis* populations, and on six of the nine hosts, the contrast between species was significant ($P < 0.05$). Only on *Salix alaxensis*, *Salix bebbiana*, and *Betula resinifera* did *glaucus* larvae grow at rates approaching that of *canadensis* larvae. The two swallowtail species seem fundamentally different in their ability to feed on a broad array of boreal host plants.

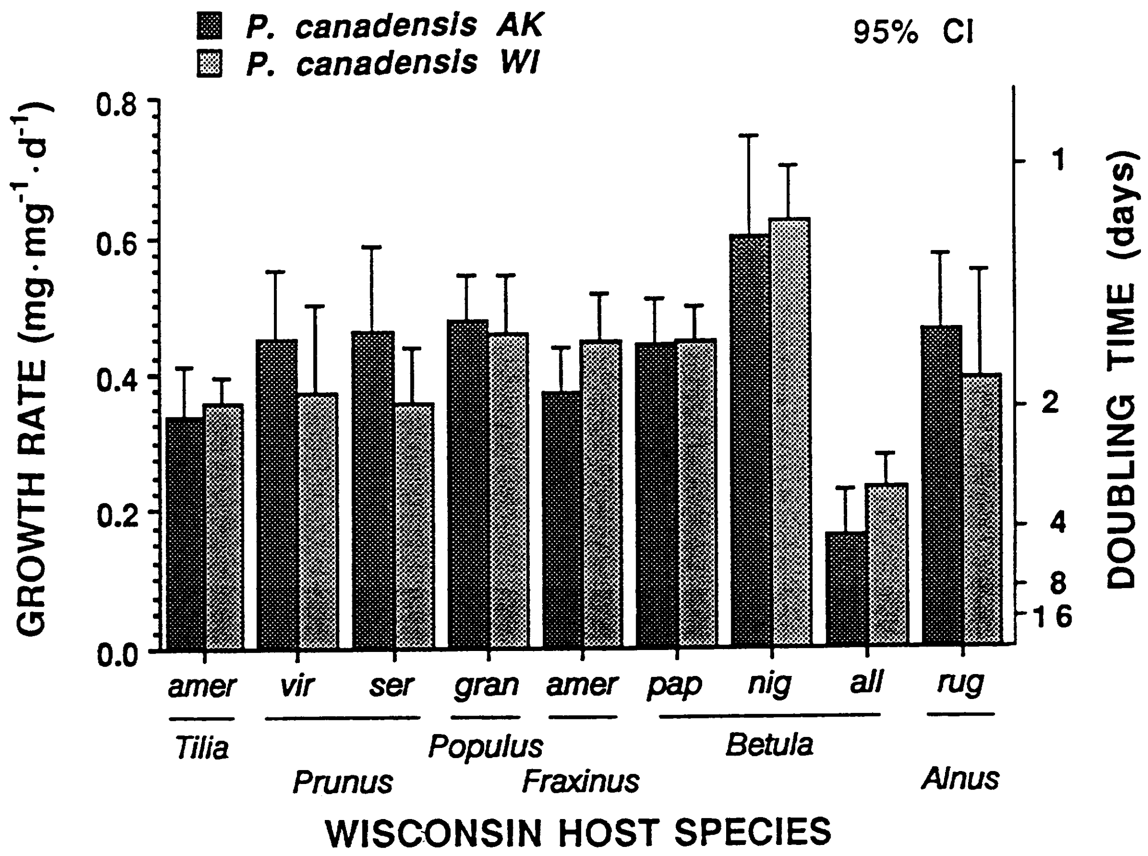

Figure 2. Relative growth rate of first instar *P. canadensis* from Alaska and Wisconsin on nine Wisconsin host species. The host species, from left to right, are *Tilia americana* (basswood), *Prunus virginiana* (chokecherry), *Prunus serotina* (black cherry), *Populus grandidentata* (bigtooth aspen), *Fraxinus americana* (white ash), *Betula papyrifera* (paper birch), *Betula nigra* (river birch), *Betula allegheniensis* (yellow birch), and *Alnus rugosa* (speckled alder). The experiment was conducted from 5 to 8 July 1989 using leaves from Dunn County, Wisconsin. Error bars indicate 95 percent confidence intervals.

First instar growth rates are just one measure of growth performance, but we have found them to be a powerful and generally reliable index. As part of a larger study (Ayres and Scriber in prep.), the 360 *canadensis* larvae initiated on Alaska hosts (Fig. 3) were reared to pupation and additional measurements collected. These data support our conclusion based on neonate performance that the populations do not differ in their nutritional physiology. Relative growth rates measured over the middle instars (day 3 to 17) did not differ between populations, nor did fifth instar growth rates, consumption rates, or conversion efficiencies. Hosts that produced high first instar growth rates tended to have higher overall survival and yield larger pupae in less time than hosts that produced low first instar growth rates. Larger pupae produce larger male and female adults that produce larger spermatophores and more eggs respectively (Lederhouse et al. in prep.).

The apparent absence of variation in detoxification systems and nutritional physiology is in contrast to other traits that do vary between the populations. Alaska females produced eggs 150 percent larger than their Great Lakes counterparts, but were able to produce only 63 percent as many

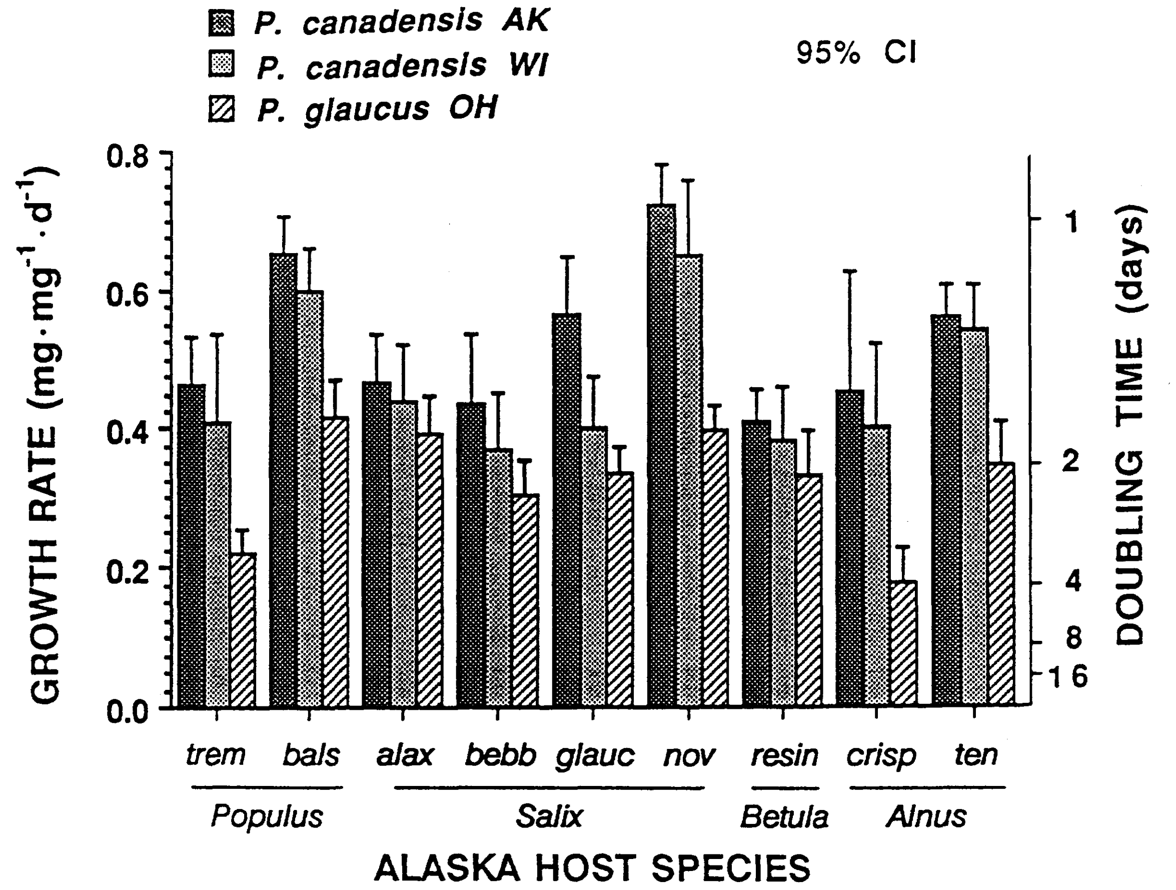

Figure 3. Relative growth rate of first instar larvae from three insect populations tested on nine Alaska host species. The insect populations are *P. canadensis* from Alaska, *P. canadensis* from Wisconsin, and *P. glaucus* from Ohio. The host species, from left to right, are *Populus tremuloides* (quaking aspen), *Populus balsamifera* (balsam poplar), *Salix alaxensis* (feltleaf willow), *Salix bebbiana* (bebb willow), *Salix glauca*, *Salix novae-angliae*, *Betula resinifera* (Alaska paper birch), *Alnus crispa* (green alder), and *Alnus tenuifolia* (thinleaf alder). The *canadensis* measurements were made from 26 to 29 June 1988 and the *glaucus* measurements from 19 to 22 August 1989; all leaves were collected from the same sites near Fairbanks, AK. Error bars indicate 95 percent confidence intervals.

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as Wisconsin females of equal size (Lederhouse et al. in prep.). These larger eggs conferred an important developmental advantage. At 17 days after hatch, the Alaska *canadensis* larvae were still 1.5 times larger, even after a 180-fold increase in weight (relative growth rates were virtually identical) (Ayres and Scriber in prep.). Further, Great Lakes larvae tended to grow for a longer period and consequently produced larger pupae, even though they hatched smaller and grew at the same rate. The populations further differed in their larval temperature responses. In particular, Alaska larvae were capable of more rapid growth and development at the relatively low temperatures of 12° and 18°C (Ayres in prep.).

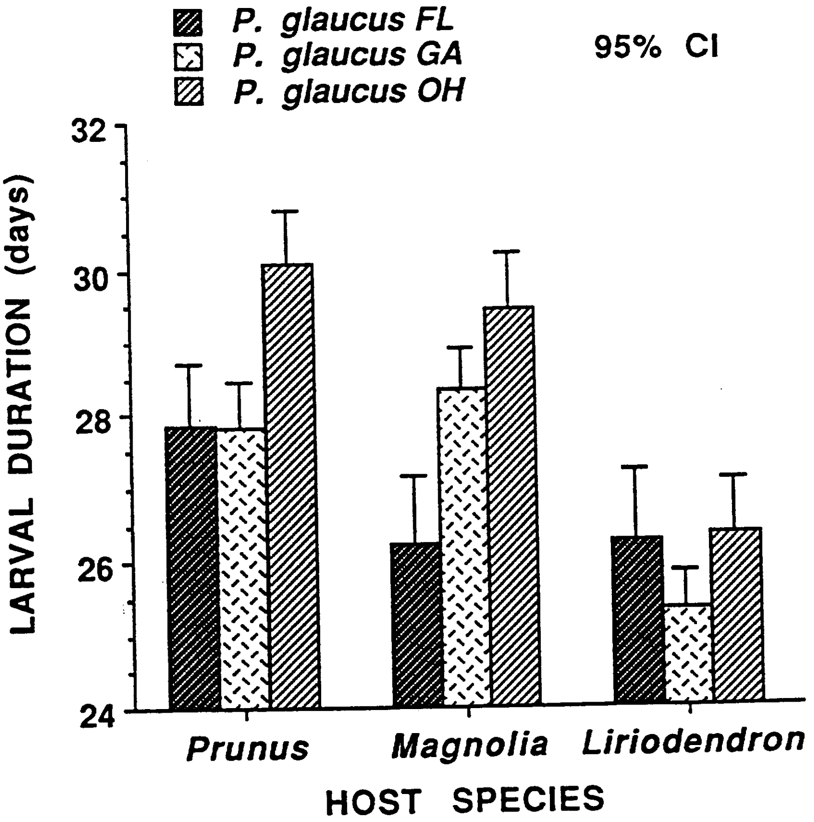

Figure 4. Larval duration of *P. glaucus* populations from Florida, Georgia, and Ohio tested on *Prunus serotina* (black cherry), *Magnolia virginiana* (sweetbay), and *Liriodendron tulipifera* (tuliptree). Measurements were made during May, August, and September 1988 for Florida, Ohio, and Georgia populations respectively. Error bars indicate 95 percent confidence intervals.

Variation within *P. glaucus*

Unlike *P. canadensis*, *P. glaucus* appears to harbor substantial genetic variation in nutritional physiology. Patterns in development time, especially significant interactions between insect populations and host species, support the hypothesis of regional specialization (Fig. 4, Table 1). Overall, the development time of Ohio *glaucus* tended to be longer than that of Florida *glaucus* (population effect, Table 1), but this difference was most pronounced on *Magnolia* (the prevalent Florida host) and nonexistent on *Liriodendron* (the prevalent Ohio host, population x host interaction, Table 1). Likewise, Georgia populations required a longer development time on *Magnolia* than Florida populations, even though development times were identical on *Prunus* (a prevalent Georgia host, Fig. 4). Significant variation among families within populations suggests an even finer level of ecological specialization, although the variation within populations was far smaller than that between populations (F = 14.95 versus 1.83 for main effects of population and family respectively, and F = 4.15 versus 1.39 for host x population interactions and host x family interactions respectively, Table 1).

Table 1. Mixed Model ANOVA (families nested within population) of larval duration for three *P. glaucus* populations tested on three host species. Data are shown in Fig. 4.

Source of variation	df	MS	Error term[a]	*F*	*P*
Population	2	134.41	Fam(Pop)	14.95	< 0.001 ***
Host	2	308.66	H x F(Pop)	45.32	< 0.001 ***
Family(Pop)	25	8.99	Error	1.83	< 0.05 *
Host x Pop	4	28.23	H x F(Pop)	4.15	< 0.01 **
Host x F(Pop)	54	6.81	Error	1.39	< 0.05 *
Error	315	4.91			

[a] Mean square used as denominator in *F* test (Ayres and Thomas 1990)

Further evidence for local adaptation lies in the relationship between larval duration (development time) and pupal mass. On *Magnolia*, Florida families with long development times tended to produce larger pupae (Fig. 5); this result is to be expected if all families grow at similar rates (are uniformly well adapted), but vary in the timing of pupation. In contrast, the negative correlation between larval duration and pupal mass of Ohio families feeding on *Magnolia* suggests differential detoxification abilities among families. For example, larvae from relatively maladapted families may partially have compensated for their low growth rates by extending the duration of growth, but the prolonged development time was inadequate to produce pupae of equal mass. On *Liriodendron*, Ohio families with relatively long development times tended to produce larger pupae, as expected for a population well adapted to *Liriodendron* (r = 0.31, P = 0.16). There was no relation between development time and pupal mass for Florida families on *Liriodendron* (r = -0.06, P = 0.86), indicating a mix of the two patterns.

Visual inspection of reaction norms further supported a physiological tradeoff (genotype-environment interaction) in the ability of full-sib families to use *Liriodendron* and *Magnolia* (Fig. 6). Within both Ohio and Florida populations, families with rapid development on *Magnolia* took relatively longer on *Liriodendron*. The tradeoff between performance on *Liriodendron* and *Magnolia* appears linked to the presence of particular glucosephosphate isomerase (GPI) alleles (Table 2). Within each population, homozygous $GPI_{100/100}$ genotypes tended to be fast growers on *Liriodendron* and heterozygous $GPI_{100/-104}$ genotypes tended to be fast growers on *Magnolia* (Bossart in prep.). Moreover, the frequency of the GPI $_{-104}$ allele tended to be higher in Florida, where *Magnolia* is the prevalent host (Table 3). We are currently unable to distinguish between genetic linkage and physiological causality as the basis for this relationship. No fixed differences in allozymes have been found between the populations, and the suggested clinal patterns were not statistically significant.

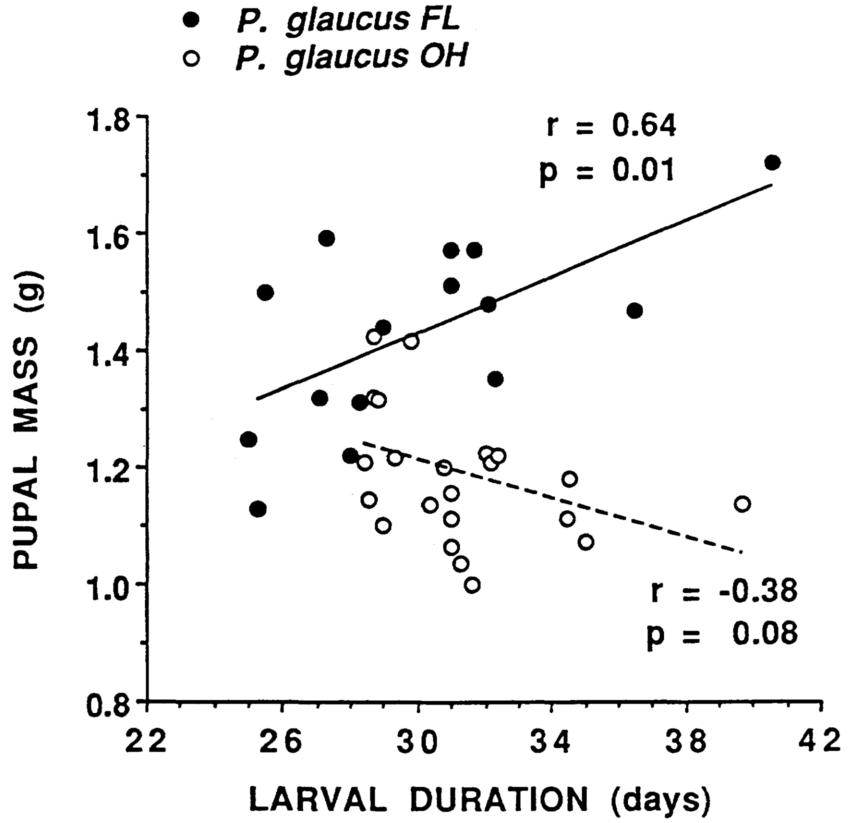

Figure 5. Relationship between larval duration and pupal mass of *P. glaucus* from Florida and Ohio reared on *Magnolia virginiana*. Each point represents the mean of 3 to 30 full-siblings. Figure includes data from 1988 and 1989.

Table 2. Larval duration of different glucosephosphate isomerase (GPI) genotypes from Florida and Ohio tested on *Magnolia virginana* and *Liriodendron tulipifera*. Values are mean ± SE (*N*). The interaction between host and genotype was significant at *P* = 0.0008 (*F* = 12.15, df = 1, 76).

	Liriodendron		*Magnolia*	
	$GPI_{100/100}$	$GPI_{100/-104}$	$GPI_{100/100}$	$GPI_{100/-104}$
Florida	22.36 ± 0.45 (11)	26.75 ± 0.75 (8)	26.06 ± 0.45 (18)	24.86 ± 0.67 (7)
Ohio	23.88 ± 0.44 (16)	27.55 ± 1.14 (11)	29.64 ± 0.95 (11)	28.50 ± 0.50 (2)

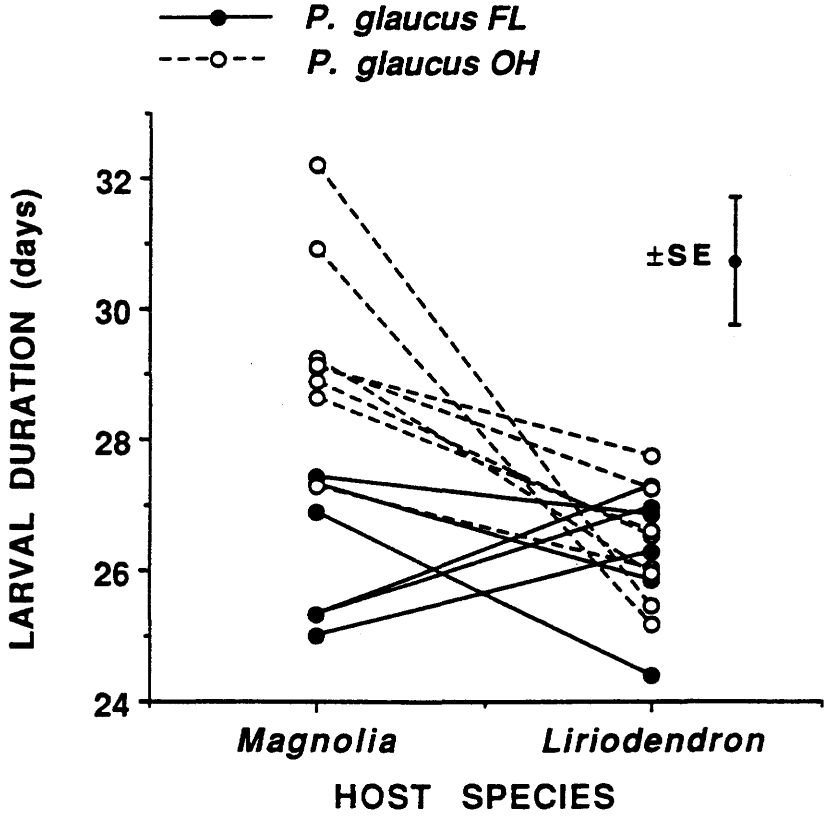

Figure 6. Larval duration of *P. glaucus* families from Florida and Ohio tested on *Liriodendron tulipifera* and *Magnolia virginiana*. Each point represents the mean of 6 to 10 full-siblings. Lines show family reaction norms. Standard error associated with family means is indicated ($SE^2 = MS_{Error}/N = 4.91/5$).

CONCLUSIONS

P. canadensis appears to be a recently evolved taxon derived from a *glaucus*-like ancestor (Scriber et al. 1991, Hagen and Scriber 1990). Our results suggest that the detoxification systems and nutritional physiology of ancestral *canadensis* became greatly modified in ways that allowed them to exploit a diversity of northern hosts. In the process, some ancestral abilities were lost (e.g. tuliptree detoxification) and others were retained (e.g. hoptree detoxification). The absence of detectable differentiation between widely separated *canadensis* populations encountering very different hosts suggests that the nutritional physiology of *canadensis* has remained largely unchanged since its divergence from a *glaucus* ancestor. The absence of detectable variation within *canadensis* populations implies that future changes in nutritional physiology will be limited by the appearance of new mutations. Its implied history of rapid evolutionary change followed by stasis is consistent with the stepwise mechanism of herbivore adaptation described by Ehrlich and Raven (1964). We note, however, that direct reciprocal evolutionary responses by the hosts are unlikely because of the low levels of damage inflicted by these herbivores. In striking contrast, *P. glaucus* appears to be a vast complex of differentially adapted genotypes and populations, which suggests that its nutritional physiology is being shaped by local selective pressures such as result from varying regional availability of hosts. The polyphagous habits of *P. glaucus* are enhanced by its variability within and between populations, which is not so for *P. canadensis*, all genotypes of which appear equally capable of using any host species within its range.

Table 3. Allele frequencies (%) at four polymorphic loci in *P. glaucus* populations from Ohio (OH), Georgia (GA), and Florida (FL). Number of alleles per sample = 48 to 84.

Locus	Allele	Population OH	 GA	 FL
PGM	91	3	1	0
	94	4	1	4
	97	12	29	16
	100	35	30	36
	103	38	27	28
	106	8	11	16
	109	0	1	0
IDH-2	100	83	92	71
	102	17	8	25
	103	0	0	4
MPI	90	3	0	0
	92	0	3	0
	94	0	11	13
	96	16	14	11
	98	22	29	20
	100	47	32	51
	102	12	11	5
GPI	-105	3	0	0
	-104	7	12	21
	100	79	78	75
	104	1	0	0
	105	7	10	4

We suggest several possible explanations for the markedly different levels of intraspecific variation within *glaucus* and *canadensis*. 1) The two species differ in population structure such that gene flow is more restricted in *glaucus* than *canadensis*. 2) *P. canadensis* originated as a very small population, perhaps as a result of Pleistocene isolation in some periglacial refugium (Scriber 1988), and low variation is a result of the associated genetic bottleneck. 3) *P. canadensis* is of such recent evolutionary origin that populations have not yet differentiated, but will in the future. 4) There is less variation in *canadensis* host use; perhaps *Populus tremuloides* is the prevalent host for all *canadensis* populations, and other host-use records are rare "oviposition mistakes" that contribute only insignificantly to selective pressures shaping the nutritional physiology of *canadensis*. 5) The boreal forest is characterized by low phytochemical diversity relative to that of temperate forests, the most ubiquitous boreal hosts being restricted to four genera in two families: *Populus*, *Salix*, *Betula*, and *Alnus*. Consequently, natural selection has favored the development of a single detoxification system that is optimal for most hosts, i.e. *canadensis* detoxification systems have been canalized such that mutations and recombination seldom lead to phenotypic variation.

Hypothesis 1 can be tested by comparing the divergence in allozyme frequencies between populations within species. If it holds true, the fixation index (F_{ST}) of *glaucus* populations should be greater than that of *canadensis* populations separated by the same geographic distance. The available data are limited, but they indicate extensive gene flow within both species (Hagen 1990); the estimated genetic distance between *P. glaucus* from Ohio and Florida was no greater than that between *P. canadensis* from Alaska and Michigan: Nei's genetic identities equalled 0.99 in both cases (Hagen and Scriber 1990). Hypotheses 2 and 3 cannot account for divergence between *canadensis* populations in traits other than nutritional physiology such as egg size, adult size, and temperature responses. Hypothesis 2 would be supported by lower levels of allozyme heterozygosity in *canadensis* than in *glaucus* (Bonnell and Selander 1974). Hypothesis 3 predicts that other recently derived swallowtail taxa (as estimated from allozyme and mtDNA sequence divergence) would be similarly invariant in their nutritional physiology. Hypothesis 4 questions our view of *P. canadensis* as a polyphagous herbivore and requires that suitable hosts go generally unused. It can be tested through quantification of oviposition patterns in the field. We presently favor hypothesis 5, which predicts that the various secondary metabolites present in boreal hosts are detoxified by *canadensis* using only one or a few biochemical systems. It further predicts that other polyphagous herbivores of the boreal forest will similarly exhibit low variation in nutritional physiology, and will be consistently less variable than related species of polyphagous herbivores from temperate and tropical forests (Mattson et al. 1988, Mattson et al. in this volume). An important correlate is that physiological preadaptation to alternative hosts will be more common in boreal forests than elsewhere. That is, boreal herbivores challenged with sympatric nonhost plant species should be more likely to successfully detoxify that foliage than temperate or tropical herbivores challenged with nonhost species from their environment.

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DO DIFFERENCES IN INDUCIBLE RESISTANCE EXPLAIN THE POPULATION DYNAMICS OF BIRCH AND PINE DEFOLIATORS?

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INTRODUCTION

Damage inflicted by insects may trigger responses in their host plants resulting either in immediate effects on herbivores either rapidly or in effects upon subsequent herbivore generations. Differentiation between rapid and delayed inducible resistance is essential since the two responses affect the population dynamics of herbivores in fundamentally different ways (Haukioja 1982). Rapid inducible resistance (RIR) tends to stabilize herbivore population dynamics. On the other hand, delayed inducible resistance (DIR) introduces a time-lag into the negative feedbacks regulating the population dynamics of insects and may generate cyclical fluctuations in density (Benz 1974, Haukioja 1980, Berryman et al. 1987).

Experiments have shown that rapid and/or delayed inducible resistance exists in some tree-herbivore systems while other systems apparently lack such responses (Haukioja and Neuvonen 1987). The variation in inducible responses may help us to understand differences in the population dynamics of defoliators on different host trees. For example, both white birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) suffer large-scale defoliation in Fennoscandia. However, the outbreaks on birches and pines show different temporal and geographic patterns. This paper compares inducible resistance mechanisms and patterns in the population dynamics of defoliating insects Scots pine and birch.

DEFOLIATING INSECTS ON SCOTS PINE AND BIRCH

Scots pines and birches are abundant and widespread in northern Europe. Thus the species richness of insects feeding on these trees is great (Larsson and Tenow 1980, Neuvonen and Niemelä 1983), though, only some of the insects cause serious damage to their host. The most important defoliators of Scots pine in Fennoscandia (*Neodiprion sertifer* and *Diprion pini*) belong to the sawflies (Symphyta: Diprionidae) (Table 1). In other areas, however, such as Central Europe and Siberia, these

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[1] Order of authorship determined by tossing a coin.

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are also lepidopteran species (*Bupalus piniarius, Panolis flammea, Dendrolimus pini*) which can become predominant defoliators of pine.

The mountain birch forests in northwestern Europe are periodically defoliated by geometrid larvae feeding mainly during the early season (Table 1). Several species (*Epirrita autumnata, Operophtera* spp., and *Erannis defoliaria*) fluctuate greatly and fairly synchronously in density (Tenow 1972, Haukioja et al. 1988). Local defoliations may also be caused by a late season sawfly, *Dineura viridiorsata* (Koponen 1981).

OUTBREAK PATTERNS

Birch-Feeding Insects

An extensive record of geometrid defoliation of Fennoscandian birch forests has been compiled over the years from 1862 to 1968. During this span of time outbreaks have occurred at 9- to 10-year intervals (Tenow 1972). The duration of these outbreaks is short, 2 to 3 years. Distribution of the outbreaks shows a number of varying patterns. Outbreaks of *Epirrita autumnata* are restricted to the mountain birch forest zone of northern Finland and the Scandinavian mountain chain. In the birch forests along the Norwegian coast, *Operophtera* spp. are the most important defoliators, and *E. autumnata* occurs mainly at higher altitudes and at inland localities with a more continental climate (Tenow 1972). Outbreaks of *Operophtera* spp. and *Erannis defoliaria* have been recorded on isolated islands in the southwest archipelago of Finland (Tenow 1972, Laasonen and Laasonen 1987). Birches are also regularly defoliated in other areas of the world, e.g. *Rheumaptera hastata* on *Betula resinifera* in Alaska (Werner 1981).

Furthermore, defoliation by *Epirrita* larvae is often topographically restricted, patches of undefoliated birch forests typically occur at the bottom of river valleys while birches at higher altitudes are usually heavily defoliated (Kallio and Lehtonen 1973, Tenow 1975).

Pine-Feeding Insects

In Fennoscandia outbreaks of diprionid sawflies are restricted chiefly to southern regions and are, with few exceptions, absent from northern areas (Christiansen 1970, Löyttyniemi et al. 1979, Juutinen and Varama 1986). Diprionid outbreaks on pine are not cyclical as are the well-known 9-year cycles of the tortricid, *Zeiraphera diniana*, on European larch (Baltensweiler et al. 1977, Hanski 1987, Geri 1988). In Sweden and Finland local outbreaks of diprionids occur every year (Larsson and Tenow 1984, Juutinen and Varama 1986). Large-scale outbreaks occur irregularly in 10- to 20-year intervals (Kangas 1963, Hanski 1987).

The duration of outbreaks in a given habitat is variable. According to Juutinen and Varama (1986), outbreaks of *N. sertifer* last 3 to 4 years in southern Finland. In the middle region of Finland the duration is 4 to 6 years. In the Saariselkä mountain chain in northern Finland, an outbreak has been chronic for the last 20 years (Juutinen 1967, Juutinen and Varama 1986).

N. sertifer outbreaks in Fennoscandia and in parts of the U.S.S.R. characteristically occur following dry summers and are restricted mainly to dry sites or dense stands (Juutinen 1967, Larsson and Tenow 1984, Sharov, this volume). Interestingly, several successive large-scale outbreaks of *N. sertifer* occurred during the warm period in the 1930s (Kangas 1963, Hanski 1987).

Defoliations by other insect pests in Fennoscandia are more sporadic than those caused by *N. sertifer*. In more southern areas of Europe, such as Germany and some parts of Britain, some populations of *Bupalus piniarius* and *Panolis flammea* show more or less regular cycles of 6 to 11 years (Schwerdtfeger 1968, Barbour 1987), while other populations are relatively stable or fluctuate irregularly, e.g. most British populations (Barbour 1988).

Table 1. Outbreak species of Scots pine (*Pinus sylvestris*) and birches (*Betula pendula* and *B. pubescens*) in Fennoscandia

Species	Family	Larval period
	Scots pine	
Neodiprion sertifer	Diprionidae	May-July
Diprion pini	Diprionidae	July-September
Gilpinia pallida	Diprionidae	June-August
Microdiprion pallipes	Diprionidae	June-August
Bupalus piniarius	Geometridae	June-August
	Birches	
Epirrita autumnata	Geometridae	May-July
Operopthera spp.	Geometridae	May-July
Erannis defoliaria	Geometridae	May-July
Dineura viridiorsata	Tenthredinidae	July-September

EXPERIMENTAL EVIDENCE OF INDUCIBLE RESISTANCE

Experiments on Birch

Rapid Inducible Resistance

Mechanically damaged birch foliage is less suitable for the growth of larvae of several lepidopteran and hymenopteran species than undamaged control foliage (Haukioja and Niemelä 1977, 1979, Hanhimäki 1989). Larvae grew for a longer time and the pupal masses were the same or lower on damaged than on control foliage (Table 2). When the total impact of RIR on the capacity of *E. autumnata* to increase were estimated by combining the effects on survival and fecundity, the reduction ranged from 0 to 22 percent (Haukioja and Neuvonen 1987). Rapid inducible resistance against *E. autumnata* seems to be equal in birch provenances from both outbreak (northern Finland) and nonoutbreak (southern Finland) areas (Haukioja and Hanhimäki 1985).

Rapid inducible resistance in birch foliage can be triggered by damaging early, but not late-season birch leaves (Haukioja and Niemelä 1979, Wratten et al. 1984). However, the responses may have such a long relaxation time that they also affect insects feeding later that season (Neuvonen et al. 1988, Hanhimäki 1989). On the other hand, not all types of damage to birch trees result in deterioration in foliage quality. Increased densities of insects have been observed on birches browsed, either artificially or by moose, during the previous winter(s) (Danell and Huss-Danell 1985), though the performance of *Epirrita* larvae was affected only slightly (Neuvonen and Danell 1987, Haukioja et al. 1990).

Table 2. The existence of rapid (RIR) and delayed induced resistance (DIR) on mature Scots pine needles and birch foliage (see Haukioja and Niemelä (1979) and Hanhimäki (1989) for more examples). 0 = no statistically significant effect, + significant increase, - significant decrease. Some statistical tests may suffer from sacrificial pseudoreplication. Damage on Scots pine needles occurred during mid or late season (for the effects of early season damage, see Neuvonen et al. 1988).

Insect species	Development/ growth rate	Pupal weight	Larval survival	References*
Scots pine needles				
RIR				
Neodiprion sertifer	+	0	+	1
Gilpinia virens	0	0	0	1
Microdiprion pallipes	0	0	-	1
Diprion pini	0	0	0	1
DIR				
Neodiprion sertifer	0	0	0	1
Diprion pini	0	+/0	-/0	10
Birch foliage				
RIR				
Epirrita autumnata	-	-	0	2,3,4
Dineura virididorsataa	0	0	0	3,5
DIR				
Epirrita autumnata	-	-	-	6,7,8
Dineura virididorsataa	+	?	?	9

*References: 1) Niemelä et al. (1984), 2) Haukioja and Niemelä (1977), 3) Haukioja and Niemelä (1979), 4) Haukioja and Hanhimäki (1985), 5) Neuvonen et al. (1988), 6) Haukioja et al. (1985), 7) Haukioja and Neuvonen (1985), 8) Neuvonen et al. (1987), 9) Neuvonen (pers. observ.), and 10) Niemelä (pers. observ.).

British experiments have concentrated on reporting chemical changes induced by foliage damage and their effects on the feeding preferences of herbivores (Wratten et al. 1984, Hartley 1988, Hartley and Lawton 1991). These studies have shown the existence of RIR, as evidenced by increases in phenolics, in British birch provenances, although the feeding bioassays have yielded variable results. Some British studies have also reported negative effects of foliage damage on the performance of insects (Bergelson et al. 1986, Fowler and MacGarvin 1986).

Delayed Inducible Resistance

Decreased quality of foliage during years following simulated or real insect attack, or delayed inducible resistance, can be triggered by mechanically damaging the birch leaves or by depositing feces of *Epirrita* larvae beneath/at the base of the birches (Haukioja et al. 1985). Insect damage induces a stronger delayed inducible response than does manual damage (Haukioja and Neuvonen 1985, Neuvonen et al. 1987). Both survival of *Epirrita* larvae and pupal weights were reduced on defoliated trees (Table 2). Performance, as measured by combined effects on survival and fecundity, of *E. autumnata* on partially defoliated trees may be over 70 percent below that on control birches. Mountain birches which had been artificially defoliated 2 to 4 years earlier still caused a reduction of 16 to 38 percent in fecundity (Haukioja and Neuvonen 1987). Birch provenances outside the usual outbreak range of defoliating insects may not express DIR (Haukioja 1980, Haukioja et al. 1983), and it is difficult to say whether this is a cause or a consequence of the distribution of outbreaks.

The foliage of defoliated mountain birches has lower nitrogen and higher phenolic content than that of control trees in the years following damage (Tuomi et al. 1984). Because of the high negative correlation between nitrogen and phenolic concentrations in birch foliage, it is difficult to evaluate which of these factors is more important in determining the success of *Epirrita* larvae. However, when the nitrogen content of birch foliage has been accounted for in models explaining variation in the pupal weight of *Epirrita*, the additional contributions of phenolic content have not appreciably improved the explanatory power of the models (Haukioja et al., unpubl. observ.).

Experiments on Pines

Studies of 20- to 25-year-old Scots pines in Finland have suggested that neither RIR nor DIR apparently develops in the mature foliage, the normal diet of diprionid sawflies (Niemelä et al. 1984). For example, four sawfly species survived and grew equally well on mature needles from control and defoliated (in the spring of the same and in previous years) branches. Geri et al. (1990) reached nearly the same conclusions working in France on the sawfly, *Diprion pini*. But, surprisingly, they discovered that female fecundity declined substantially on previously but not concurrently defoliated trees even though all other performance parameters (survival, growth, developmental rates, diapause rates) showed little response to defoliation. This is evidence for DIR, but not RIR. Because Niemelä et al. (1984) did not measure fecundity, which is usually positively correlated with insect growth, it is not known whether this performance variable declined due to defoliation. However, Sharov (this volume) found no changes in the fecundity of *Diprion pini* during outbreaks on Scots pine in the Rostov region of the U.S.S.R., as would be expected if there were strong DIR responses in pine.

In the case of other evergreen conifer species and other defoliators, there is some evidence for either weak RIR or DIR (Wagner and Evans 1985, Leather et al. 1987, Wagner 1988, Mattson et al. 1988). The study of Thielges (1968) has often been cited, though incorrectly, as an example of induced resistance. What he actually observed, however, was only that an "abnormal compound" occurred in the foliage of Scots pine heavily damaged by *N. sertifer*. It is not possible to evaluate whether this compound resulted from defoliation or existed prior to it, nor whether it was harmful to the larvae.

We conclude that there is at best only a weak DIR in Scots pine. Otherwise, one should be able to measure significant reductions in insect growth, developmental rates, and survival, none of which has been found.

HYPOTHESES EXPLAINING INDUCIBLE RESISTANCE

Owing to fundamental physiological differences between deciduous and evergreen coniferous trees (Dickson 1989), one would expect differences in their defensive responses to folivores. Tuomi et al.

(1988) suggested that the plants' carbon-nutrient balance (sensu Mattson 1980, Bryant et al. 1983) could largely determine the nature of the DIR occurring in the foliage. For example, an increase in resistance is expected when defoliation causes a relatively greater deficiency of minerals than carbon--leading to enhanced carbon-based secondary metabolism. This is presumably the case for deciduous trees growing on nutrient-deficient soils and having large carbon reserves in their stems and roots. On the other hand, for evergreens, old needles serve both as important sources of carbon reserves, and current photosynthates (Bryant et al. 1983), and hence their removal by herbivores may cause a relatively greater carbon than nutrient deficiency and hence suppress accumulation of carbon-based secondary metabolism. Furthermore, defoliation tends to increase the N content of the needles in evergreen conifer trees (Piene 1980, Piene and Percy 1984, Långström et al. 1990) which supports the thesis of a defoliation-induced carbon shortage. However, chronic, severe defoliation may eventually cause substantial rootlet mortality and result in a serious mineral deficiency thereby leading to enhanced secondary metabolite buildup.

Though differences in the effects of first defoliations on the plants' relative carbon/nutrient balance may explain differences in DIR in evergreen and deciduous trees, it is not sufficient to explain their apparent differences in RIR. Moreover, bioassays conducted with mountain birch have yielded results either difficult to predict from or inconsistent with the carbon/nutrient balance hypothesis (Haukioja and Neuvonen 1985, Haukioja et al. 1985). The facts that intensification of DIR is caused by cues from insects and that fertilization does not mitigate delayed inducible resistance triggered by manual defoliation are more consistent with a view of the responses as actual defenses against defoliators.

Although the carbon/nutrient balance hypothesis cannot explain all the details of delayed inducible resistance in birch, it is possible that the incidental responses suggested by it may have become truly more defensive in areas where heavy defoliations occur.

INDUCIBLE RESISTANCE AS A FACTOR IN THE POPULATION DYNAMICS OF PINE AND BIRCH DEFOLIATORS

The apparent absence of strong DIR in mature needles of Scots pine may explain why diprionid sawfly outbreaks can continue for several years in the same stands (Juutinen 1967, Juutinen and Varama 1986) and why several successive outbreaks are possible (Kangas 1963). Furthermore, the apparent lack of regular cycles in the population dynamics of diprionid sawflies is consistent with the lack of delayed negative feedbacks via foliage quality.

Some populations of pine defoliators show more or less regular cyclical fluctuations (Barbour 1988). It seems probable that other delayed feedback mechanisms than inducible changes in foliage quality are involved in these cases. The existence of DIR in those pine provenances has to be tested before any firm conclusions are possible, however.

As compared with other possible regulating factors, the importance of DIR is well established in birch/herbivore systems showing cyclical fluctuations in insect densities (Haukioja et al. 1988). These responses introduce time-lag negative feedback into the population dynamics of *Epirrita*. The importance of RIR is far less clear, on the other hand. DIR may be a key factor in the cyclical density fluctuations of birch defoliators in some areas, though this does not obviate the importance of other factors (e.g. parasitoids, diseases). DIR also contributes to the relatively short duration of *Epirrita* outbreaks.

SUMMARY

Both the presence and the absence of induced resistance in tree foliage can explain the population dynamics of defoliating insects. White birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) suffer large-scale defoliation in Fennoscandia. Outbreaks of birch defoliators have occurred at 9- to 10-year intervals. Duration of the outbreaks is short, 2 to 3 years. On Scots pine, local outbreaks occur every year, and large-scale outbreaks follow irregularly in 10- to 20-year intervals. That DIR produces time-lag negative feedback in the population dynamics of herbivores can explain the cyclical fluctuations. The absence of inducible responses in the mature foliage of Scots pine may explain why outbreaks can continue for several years in the same stands and why several successive outbreaks are possible.

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REPEATED DAMAGE OF LEAVES BY PHYLLOPHAGOUS INSECTS: IS IT INFLUENCED BY RAPID INDUCIBLE RESISTANCE?

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INTRODUCTION

It was discovered more than 10 years ago that toxic and repelling substances may increase in plant tissue in response to damage by phyllophages. Such rapidly inducible chemical changes may appear a few hours after leaf injury and then disappear in a few weeks or months (Walker-Simmons and Ryan 1977, Baldwin and Schultz 1983, Van Hoven 1974, Wratten et al. 1984). This phenomenon has been investigated in detail on mountain birch, ***Betula pubescens tortuosa***, in Finland (Haukioja and Niemelä 1977, 1979, Niemelä et al. 1979, Haukioja 1982, Neuvonen and Haukioja 1991). Research there has demonstrated that consumption of leaves from damaged shoots has detrimental effects on the development, fecundity, and sometimes the survival of several species of insects. The same adverse effects were found for insects feeding on damaged willow (Raupp and Denno 1984), larch (Niemelä et al. 1980), and other trees and shrubs. Although these effects may easily be demonstrated in laboratory and field tests, it is not clear what role they play in phyllophage population dynamics (Fowler and Lawton 1985). Are they a real defense against herbivores? If there are damage inducible defenses in plant leaves, it is reasonable to suppose that phyllophagous insects may have evolved mechanisms for coping with or rejecting damaged leaves. For example, laboratory trials have clearly shown that polyphagous lepidopteran larvae prefer to feed on intact birch leaves (Wratten et al. 1984). Arguments for the benefits of rapid inducible resistance (RIR) in plants are not so convincing. They emphasize the increased dispersion of insect injuries within a tree crown and the subsequent increase in mortality of the insects (Edwards and Wratten 1983, Silkstone 1987). However, this effect has been shown to be weak, and in many cases was not found at all (Silkstone 1987). Moreover, some laboratory experiments have shown that phyllophages are not capable of distinguishing damaged leaves and hence of avoiding them (Raupp and Denno 1984, Hartley and Lawton 1987).

I have investigated the effects of RIR on leaf choice by folivorous insects in Subarctic and southern taiga forests. In the Subarctic, different species of folivorous insects co-occurred on birch leaves more often than would have been expected according to the Poisson (random) distribution (unpubl. data). Initially, feeding wounds by chewing and sucking insects were distributed independently among leaves, but subsequently damaged leaves were more frequently and intensively attacked by insects than intact leaves. However, parallel observations made the same year in the southern taiga zone of the Urals gave quite different results. Co-occurrence of folivorous and sucking insects was more rare than expected according to the Poisson distribution, and some folivorous insects avoided certain leaf damage patterns (Bogacheva 1989). What is the reason for such a discrepancy between two different geographic regions? Why did we fail to demonstrate an over-dispersion of subsequent insect damage in

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the Subarctic? What are the main factors in leaf preference by phyllophagous insects: qualitative changes in damaged leaves or ecological conditions of leaf environment? In this paper I address these questions both in the field and in the laboratory (food choice experiments).

EXPERIMENTAL METHODS

Field Experiments

Experiments similar to those by Silkstone (1987) were done in 1988 at two sites: in forest tundra (66° 40'N) at the Labytnangi field station in the Low Ob' region, and in southern taiga (56° 50'N) near the city of Sverdlovsk in the Middle Urals. Around Labytnangi we worked with the *Betula pubescens* ssp. *tortuosa* growing in the small groves. Near Sverdlovsk we worked with *Betula pubescens*, the most common tree species in this region. I defoliated growing leaves using a 0.5 cm cork borer. One leaf from each intact dwarf shoot was so damaged, amounting to 3 to 4 percent of the mean leaf area on dwarf shoots. This was equal to the mean value of natural leaf consumption in the Subarctic, but in Sverdlovsk the mean consumption level averages 2 to 3 times higher.

I administered three kinds of treatments: 1) making one hole on one side of the leaf lamina, leaving the leaf margin undamaged (hereafter referred to as "middle hole"); 2) making two holes on one side of a leaf, but along the leaf margin, their total area and perimeter similar to those of the "middle hole" (this damage pattern hereafter referred to as "marginal holes"); and 3) keeping intact leaves as a control. All three leaves formed one replicate; they were similar both in size and in their position on a branch. Leaves were marked with dots of type-correction fluid. We used 20 replicates per tree, and there were 25 study trees at Labytnangi, 26 at Sverdlovsk. Unfortunately, some leaves were lost during the course of the experiments, 3 weeks at Labytnangi (6/30/88 - 7/24/88) and over 3 months at Sverdlovsk (5/27/88 - 9/12/88), i.e. until leaf fall. At the end of the experiments, mines and holes made in the leaves by insects were classified according to the list of 15 types of feeding damage earlier described (Bogacheva 1984). Amount of injury was measured using graph paper. Frequency distribution patterns of the damage size classes for each different damage type were compared using Chi-square tests. Galls found on leaves were recorded, but were rare; feeding injury by sucking insects was not recorded.

Laboratory Tests

We conducted laboratory tests at the Labytnangi field station in 1988 using the geometrid, *Epirrita autumnata* Bkh., and the weevil, *Phyllobius maculatus* Tourn. These two experimental insects were reared in the laboratory at room temperature (17 to 25°C) and natural photoperiod. Solitary insects were kept in Petri dishes on a damp filter paper. Two damaged and two intact leaves were placed in each dish daily. Each pair of leaves was similar in size and position within the tree crown, and all of the leaves used for each experimental series were collected from one birch tree. Only intact leaves from intact dwarf shoots were used. We artificially damaged one leaf in each pair 1 to 3 days before the experiments by creating the "middle hole" of the above-mentioned size. The food was changed every 24 hours and the amount of leaf lamina eaten was measured using graph paper. For weevils, the total number of feeding holes and their position within a leaf were also registered. Only last instar larvae were used in trials. *Epirrita autumnata* were very abundant in 1988, so they were changed every day or every two days during the experiments in order to rule out possible influence of individual induced preference. Weevils, on the other hand, were not abundant and thus were changed only in case of death or feeding refusal. In total, 53 specimens of geometrid larvae and 18 specimens of beetles were used; leaves for them were collected from 6 and 4 different birch trees, respectively.

RESULTS

Field Experiments

Only four birch leaves were lost in the field experiment at Labytnangi. Since incomplete replicates were excluded from the calculations, we had a total of 496 rather than 500 replicates (Table 1).

At Sverdlovsk a large number of leaves was lost and many replicates became incomplete so the calculations were carried out in two ways: 1) only on complete replicates, of which there were 347, and 2) on all the leaves of each treatment, including those of incomplete replications. Owing to the larger sample size (Table 2), more data appeared to differ significantly when the second method was used. However, the mean value of the data did not change considerably.

There were no differences among treatments at Labytnangi (Table 1). At Sverdlovsk, on the other hand, there were significant differences among treatments (Table 2). The data suggest that insect responses to the two patterns of artificial damage were not equal: insects apparently avoided leaves with marginal holes, preferring leaves with middle holes. Although these two damage patterns differed significantly from one another, neither differed significantly from the control (Table 2).

It is not clear why these two damage patterns are of different attractiveness for phyllophages despite the fact that the areas and perimeters of the holes are similar in both cases. One likely explanation is the differential detection of damaged leaves by insects using leaf blade shape outlines. Thus different positions of grazings on leaf blade surfaces appeared to cause different insect reactions. As for insect reactions to damaged leaves, they were found to be different at Labytnangi and Sverdlovsk, but, again, the reasons are not clear. Feeding damage of type 2 (large holes on leaves) is caused by insects of several families (many lepidopterans, some species of Tenthredinidae and Curculionidae species). At Labytnangi feeding injuries of this type are caused mainly by spring species of *Epirrita autumnata*, while at Sverdlovsk they are caused mainly by summer species of lepidoptera and Tenthredinidae. Feeding injuries of type 4 (small skeletonized spots on the underside of leaves) were caused by one summer tenthredinid species at Labytnangi and mainly by one late summer species of the Coleophoridae family at Sverdlovsk. Finally, feeding marks of type 7 (the tortuous grazings at leaf edge) were caused by Polydrusus weevils at both sites, though clearly by different species.

In summary, there were no differences in insects' responses to damaged and intact leaves at Labytnangi, but such differences did occur at Sverdlovsk, where insects were apparently attracted to leaves with middle holes and repelled by those with marginal damage. The latter damage pattern predominates in nature and our results thus run contrary to current theory, which predicts avoidance of all damaged leaves. Contrary to our results, on the other hand, Silkstone (1987) reported that middle lamina injuries decreased further insect damage. The reasons for this discrepancy will be discussed later.

Laboratory Tests

Under the conditions of our experiment, *Epirrita autumnata* larvae fed equally on both damaged and intact birch leaves (Table 3), while Phyllobius beetles preferred damaged leaves (Table 4). This suggests that different phyllophagous species may have different reactions to damaged leaves.

Table 1. Percent leaf damage and area of insect consumption per damaged leaf (mm^2) on *Betula pubescens* ssp. *tortuosa* trees in the field experiment at Labytnangi

Types of damage[a]	Leaf damage (%) and consumption (mm^2)	Treatment of leaves Middle hole A	 Marginal holes B	 Control C
General	Damage (%)	52.5	46.9	46.9
	Consumption	17.3	13.3	15.2
Type 2	Damage (%)	7.3	5.1	3.8
	Consumption	74.9	59.9	100.8
Type 4	Damage (%)	1.2	5.3	3.2
Type 7	Damage (%)	44.4	41.8	43.2
	Consumption	7.3	7.0	6.8
Total leaves		496	496	496

[a] Type 2 = large holes; type 4 = small skeletonized spots; type 7 = tortuous grazings at leaf edge (for details see Bogacheva 1984, and discussion in text).

Why should different species have different responses? First, taxonomically different species may have different chemoreceptors. Second, moths feed on leaves during the larval stage whereas weevils feed at the adult stage, and in that sense they are ontogenetically different. Third, rapidly induced responses may have different effects depending on the ecological peculiarities of insects (Edwards and Wratten 1983, Wratten et al. 1984). Both species involved here are considered generalists. In the Low Ob' region, I found *Epirrita* caterpillars feeding on mountain birch, *Betula nana*, *Alnus fruticosa*, *Salix*, *Populus tremula*, *Rosa acicularis*, and *Lonicera coerulea*. In the same region, I found *Phyllobius maculatus* on mountain birch and alder only, so, at that site at least it appears to be oligophagous. Finally, food choice may depend on insect mobility (Schultz 1983, Neuvonen and Haukioja 1991). The mobility of the two test species is also different: in 24 hours the weevils usually "travel" throughout an entire birch crown, *Epirrita* larvae only within a single branch, as a rule. This difference in mobility has been observed in experiments as well: *Epirrita* caterpillars damaged only two (1.81 ± 0.09) of four leaves available in Petri dishes, as a rule, inflicting four ($\bar{x}$ = 4.18 ± 0.40) holes. Phyllobius specimens often damaged all four leaves available ($\bar{x}$ = 3.21 ± 0.09), inflicting about nine ($\bar{x}$ = 9.88 ± 0.47 holes).

Table 2. Percent leaf damage and area of insect consumption per damaged leaf (mm^2) on *Betula pubescens* trees in the field experiment at Sverdlovsk

Types of damage	Leaf damage (%) and consumption (mm^2)	Treatment of leaves					
		A-1	B-1	C-1	A-2	B-2	C-2
General	Damage (%)	42.7	36.0	41.2	45.0	35.2	41.6
	Consumption	53.0	30.2	39.4	51.4a	29.8b	41.4
Type 2	Damage (%)	10.1	9.5	8.7	9.5	8.6	8.6
	Consumption	184.3a	73.2b	127.8	200.5b	72.8a	133.6
Type 4	Damage (%)	18.7	15.0	21.3	20.8	14.7c	22.7b
	Consumption	6.5	7.6	7.3	5.9a	7.7b	7.0b
Type 7	Damage (%)	18.7	13.5	14.1	17.3	13.9	12.8
	Consumption	8.8	7.1	7.4	8.6	7.1	7.6
Total leaves		347	347	347	400	397	406

a, b, and c indicate different treatments (see Table 1); 1 and 2 indicate different methods of calculation. Consumption data with different letter indexes differ significantly ($p \leq 0.05$).

Table 3. Consumption (mm^2) of damaged and intact *Betula* leaves by *Epirrita* larvae

Tree number	Replicates	Days after treatment	Damaged leaves (mm^2)	Intact leaves (mm^2)	Statistical significance
1	8	1	195.62	165.62	n.s.
2	10	2	179.30	104.00	n.s.
3	10	3	151.40	191.90	n.s.
4	10	2	284.80	298.80	n.s.
5	20	2-3	161.20	146.00	n.s.
6	9	2	131.67	296.67	n.s.
Total for all experiments	67	1-3	180.85	191.97	n.s.

Table 4. Consumption (mm^2) of damaged and intact *Betula* leaves by Phyllobius weevils

Tree number	Replicates	Days after treatment	Damaged leaves (mm^2)	Intact leaves (mm^2)	Statistical significance
7	20	1-2	50.65	33.95	n.s.
8	10	1	126.50	43.30	$p \leq 0.01$
9	20	1-2	60.70	60.10	n.s.
10	30	1-3	64.17	40.80	$p \leq 0.05$
Total for all experiments	80	1-3	68.34	44.22	$p \leq 0.001$

Furthermore, the experimental data suggest that different plants elicit different insect responses to leaf damage. Weevils showed a clear preference for damaged leaves from trees 8 and 10, but could not distinguish between damaged and intact leaves from tree 9 (Table 4). Heterogeneity of plants is an important source of variation (Fowler and Lawton 1985, Neuvonen and Haukioja 1985, Neuvonen and Haukioja 1991). When observing food selection by weevils, I learned that they prefer to begin eating at the artificial hole. The number of their feeding marks within 1 cm of the marginal hole was 4 to 5 times greater than that within 1 cm of the undamaged leaf edge (weevils' grazings were strictly marginal). The presence of the cork borer hole itself seems to account for the attractiveness of damaged leaves to weevils. It alone seems to facilitate grazing, although follow-up investigations are necessary to confirm this (Gibberd et al. 1988).

DISCUSSION

Two phyllophagous insects common in the Low Ob' subarctic region did not reject damaged leaves in the laboratory tests. Birch insect guilds are represented by dozens of species, but most of them are rare. Because I failed to find rejection of damaged leaves in two mobile, spring phyllophagous species, I would not expect to find it in summer or in less mobile species. It was not surprising that avoidance of damaged leaves was not detected in the field experiments for *Polydrusus ruficornis* Bonsd. (Curculionidae), the most abundant summer species in those sites (Table 1, type 7). When analyzing the course of natural leaf damage, I found already damaged leaves more likely to be damaged subsequently than the controls. Furthermore, subsequent insect grazing on the damaged leaves was more intensive (Bogacheva 1989).

The same was true for *Phyllobius maculatus* in laboratory tests at Labytnangi, but in nature this species is not the main consumer. One of the latter, *E. autumnata*, did not distinguish between damaged and intact leaves. Comparing my observations in nature with my experimental data, I conclude that insect preference for damaged leaves is caused not by leaf attractiveness (as a result of damage) but by some other property. All the comparisons were made between leaves from brachyblasts within one branch, i.e. with homogeneous plant material. Even within a single branch, however, some degree of heterogeneity does exist, including genetic fluctuations of defensive substances' content (Whitham 1981), uncertain variability in foliage feeding quality (Schultz 1983), and different light conditions in various twig parts can promote insect feeding on a certain leaves. Temperature (lighting of leaves) may be among the main factors determining insect food preference in the subarctic.

In the southern taiga zone at Sverdlovsk, the avoidance of damaged leaves by phyllophages was demonstrated in both laboratory and field experiments (Bogacheva 1989). The avoidance was rather weak, however, because the damaged and adjacent leaves were not free from subsequent insect damage. How can one explain the differences observed between the two sites? One possible explanation may be that in the subarctic forest, differences between damaged and intact leaves are not as important as some other factors, particularly ecological ones. In the south taiga, on the other hand, where the suppressing effects of low temperatures are eliminated, slight variations in leaf chemistry may be of greater importance. Nevertheless it is undeniably true that similar leaf damage patterns are caused at two sites by different insect species. However, even closely related species are known (Fowler 1984) to have different food preferences. The next step required to obtain an unambiguous explanation is experimentation with the same phyllophagous species at the two sites and/or chemical analysis of damage-induced leaf alterations.

With respect to the general significance of rapid inducible resistance against phyllophages, integrating my data and those of others, I believe that the pattern of responses by phyllophages to damaged-induced changes in leaves varies with many factors. The causes of these differences in phyllophages' responses can be classified into three large groups. 1) Given the inherent properties of a damaged plant, phyllophages' responses to injured leaves vary depending on (a) plant species (Edwards et al. 1986); (b) plant individual within the species (Fowler and Lawton 1985, Neuvonen and Haukioja 1985, Lawton 1986, Hartley and Lawton 1987, our observations); (c) site conditions (Baldwin 1988); (d) leaf age (Haukioja and Niemelä 1979, Edwards et al. 1986, Hartley and Lawton 1987); and (e) time span between damage and subsequent insect feeding (Fowler and Lawton 1985, Edwards et al. 1986, Hartley and Lawton 1987). Rapid induced response may be modified by the weather conditions during the growing season as well (Haukioja and Hanhimaki 1985); just as it may also modify the insects' responses. 2) Given the origin of the primary damage, phyllophages may respond differently if (a) primary damage is caused by insects of different ecological feeding modes (folivorous or sucking insects, miners, and so on) (Hartley and Lawton 1987); or (b) primary damage occurs within lamina position of grazing injury (e.g. middle or marginal wounds, etc.). Doubtless, these differences are realized for phyllophages through their host plant. 3) Different responses by phyllophages to similar leaf damage patterns are observed (a) in phyllophages of various ecological types, such as folivores, sucking insects, miners, and so on (Hartley and Lawton 1987, Neuvonen and Haukioja 1991); (b) in specialists and generalists (Edwards and Wratten 1983, Wratten et al. 1984, but see Fowler 1984); (c) in phyllophages of different mobility (Schultz 1983, Neuvonen and Haukioja 1991); and (d) at different developmental stages of a single phyllophage species which may be connected also with their mobility (Harrison and Karban 1986). Finally, in nature coexisting leaves can differ in food quality and ecological conditions, i.e. there are conditions both for food choice by insects and for repeated grazings on more favorable leaves (Baranchikov 1983, Bultman and Faeth 1985, Fritz et al. 1987, our observations).

Such a diversity of factors influencing responses by insects to damaged-induced leaf change enables us to say that the damaged leaf protects itself and adjacent leaves against subsequent injuries by only some herbivores. Damaged leaf rejection may be inherent in certain phyllophages species feeding on certain host plants. Though it may be possible to find damaged leaf avoidance among an entire insect guild on a certain plant, because the guild consists usually of few species, there is no justification for extending this response pattern to all plants and all consumers. I propose that the avoidance of injured leaves by insects does not exist as a general phenomenon. One can still ask, however, whether this effect, when it occurs, is beneficial for a plant. We have already mentioned that owing to the adverse effect of damaged leaves on insect performance, damaged leaf avoidance seems to be more necessary for insects than for plants. However, it is disputable even for insects. Is it more profitable for herbivores to continue feeding on damaged leaves, which retards their development (increased mortality due to carnivores and parasites) and decreases their fecundity, or to search for an intact leaf, thereby wasting energy (loss of body weight and fecundity) and increasing their chances of being detected by their natural enemies? Obviously, we are not ready to answer such a question.

Hartley and Lawton (1987) have studied the adaptive value of insect rejection of damaged leaves from the point of view of individual variability in plant chemistry. They found that foliar phenol content was so variable that it was sometimes higher in undamaged leaves than in damaged ones. "Hence, avoidance of damage is certainly no guarantee of better foliage quality" (Hartley and Lawton 1987). It is not surprising, then, that avoidance does not occur in all cases. When we state that a damaged leaf protects itself against subsequent damage, we consider the situation in terms of a leaf, though it is not the leaf but the plant that is the system to be protected. Let us consider rapid inducible defense in those terms. Increased dispersion of insect grazing throughout the tree crown and heightened mortality of phyllophages during their "traveling" in the canopy should not be considered a real benefit to plants because they also cause damage to previously intact leaves and may increase the fitness of the phyllophages. One can hardly characterize such consequences as a plant defense. I hypothesize that the alternate strategy, forcing insects to feed on damaged leaves, protecting the intact ones, and thus effecting deterioration of phyllophages' fitness, would be more beneficial to plants. Indeed, it requires that damaged leaves be attractive instead of repellent. When discussing rapid inducible resistance as a defense against subsequent, more serious damage to the whole plant, Rafes (1980, 1981) proposed that after the overall damage level attained a 60 to 70 percent threshold, there should follow a significant elevation in general resistance, such that the remaining 30 to 40 percent of the leaves would go undamaged. This phenomenon might be really profitable to a plant if it did indeed occur. One must consider, however, what would happen if insect feeding were not yet completed and the threshold damage level of 60 to 70 percent had been reached. The insect is not likely to die because mortality increases rather insignificantly in insects that feed on damaged leaves (Haukioja and Niemelä 1979). Many phyllophagous species are not readily able to change their host tree and will thus simply continue to feed. Foliage damage of 80 to 90 percent has often been recorded (Dmitrienko 1976, Petrenko and Petrenko 1981, Bogacheva 1989), even at low levels of leaf area consumption, to say nothing of the situation during insect outbreaks. Hence it appears that the existence of a threshold value of damaged leaves triggering resistance to inhibit subsequent damage is not supported by evidence.

SUMMARY

It was established earlier that in the Low Ob' region (forest tundra zone), damaged leaves of mountain birch received more frequent and more intensive subsequent phyllophages damage than intact ones, whereas in the Middle Urals the opposite trend was found. To obviate the factors of ecological heterogeneity and inherent leaf variability, field and laboratory experiments were carried out. Field studies in the forest tundra zone did not reveal different insect responses to damaged and intact leaves. On the other hand, in the south taiga, insects avoided leaves with marginal holes and were attracted to those with middle holes. In food choice experiments, neither of two phyllophagous species avoided injured leaves; in fact one insect, *Phyllobius maculatus*, preferred them. Although it is correct to view damaged leaf avoidance as a plant defense, one cannot consider it a general phenomenon.

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DOUGLAS-FIR NUTRIENTS AND TERPENES AS POTENTIAL FACTORS INFLUENCING WESTERN SPRUCE BUDWORM DEFOLIATION

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INTRODUCTION

Variation in levels of herbivory within and among plants can be attributed to many mechanisms, such as differences in a) host nutritional quality, b) suitability of the physical environment, and c) abundance of competitor consumers or natural enemies (Mattson et al. 1982, Denno and McClure 1983, Mattson and Scriber 1987, Clancy et al. 1988a, 1988b, Mattson et al. 1988). To test the hypothesis that variation in host plant nutritional quality is a significant mechanism in plant resistance against herbivores, I have selected western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and Douglas-fir, *Pseudotsuga menziesii*, for use as a model system.

C. occidentalis is one of the most abundant defoliators of true fir and Douglas-fir coniferous forests in western North America (Brookes et al. 1987). The larvae preferentially feed on the opening buds and the newly developing needles of their host trees. Several lines of evidence suggest that both foliar concentrations of nutrients, such as nitrogen, sugars, and minerals, and allelochemicals, terpenes in particular, could have important effects on budworm survival and reproduction (Harvey 1974, Kemp and Moody 1984, Redak and Cates 1984, Cates 1985, Wagner and Tinus 1985, Cates and Redak 1988, Clancy et al. 1988a, 1988b, Wagner et al. 1989, 1990).

This study was designed, therefore, to compare levels of foliar nutrients (N, sugars, and several mineral elements) and allelochemicals (terpenes) between phenotypically "resistant" and "susceptible" Douglas-fir trees. Differences in biochemical characteristics between trees that have experienced light versus heavy defoliation may provide clues to which nutrients or terpenes are connected with resistance to budworm attack. In addition, I compared the results with those from artificial diet experiments that were designed to ascertain the budworm's response curves to important host plant nutrients.

EXPERIMENTAL METHODS

Field Study

The study site was a high-elevation, mixed-conifer forest with a history of western spruce budworm infestation in the Pike National Forest near Deckers, Colorado. At the time of the study, in 1988, most of the trees at the site had sustained moderate to severe budworm defoliation for at least several years, as determined from their growth form and general condition.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

I selected 12 resistant trees by identifying mature (at least 20 years old, or well beyond juvenile stage) individual Douglas-fir trees with a full crown and good form, as distinct from most of the nearby trees that had clearly been defoliated for several successive years. The resistant trees were obviously healthy and vigorous and appeared to have sustained little or no defoliation. To pair with each resistant tree, I selected a nearby tree (within 30 m) of similar size (height and diameter) and microsite (slope and aspect) that was manifestly susceptible to budworm defoliation.

In late June of the 1988 growing season, corresponding to the late instar feeding period of the western spruce budworm, I collected current-year foliage from the 24 study trees for chemical analyses. One branch was clipped at random from the mid-crown area of the north, south, east, and west quadrants of each tree. All the current-year shoots were immediately removed, bagged, and stored on dry ice. The foliage was later transferred to an ultralow freezer and stored at -90°C until analyzed. The needles were pulled off the stems in preparation for the chemical analyses, and a composite subsample of all the current-year needles collected from each tree was analyzed.

Foliage samples were analyzed by the Analytical Services Laboratory of the Ralph M. Bilby Research Center, Northern Arizona University, for the following: total Kjeldahl nitrogen and phosphorus (colorimetrically); potassium, calcium, magnesium, and zinc (by flame atomic absorption spectroscopy); sugars--including xylose, fructose, glucose, galactose, mannose, sucrose, maltose, lactose, and erythrose (by high-performance liquid chromatograph); and terpenes--28 individual monoterpenes, sesquiterpenes, and oxygenated monoterpenes (by capillary column gas chromatograph) (Wagner et al. 1989). The same procedures were used to analyze nutrient concentrations in artificial diets.

Data were analyzed using paired *t*-tests ($P \leq 0.05$) to determine whether resistant and susceptible trees contained different concentrations of the several nutrients and of terpenes.

Artificial Diet Experiments

I evaluated the budworm's response curves to sugars, P, K, Ca, Mg, and Zn using a multiple generation bioassay and various artificial diets containing defined levels of the nutrients. My experimental base diet had concentrations of N, water, sugars, and most minerals similar to those provided by Douglas-fir foliage (Clancy in press).

I formulated other diets that encompassed the range of mineral (K, Mg, and Ca) and sugar concentrations typical for host foliage. However, the P and Zn experiments did not include responses at the lower limit because the concentrations of these minerals in the base diet were near the middle of the usual range for foliage.

My insect bioassay procedure measured survival and reproduction for three consecutive generations (Clancy in press). The P_1 generation of the experiments started with egg masses from my laboratory colony of nondiapausing western spruce budworm. Survival rates were determined for three periods: early to late larval instars, late instars to pupal stage, and pupal to adult stage. These rates were multiplied together to estimate cohort survival to the adult stage. I also incubated egg masses produced by the adult moths to determine the proportion that was viable. The bioassay for each treatment and generation started with 10 egg masses, which usually produced 200 to 300 first instar larvae. At the late instar stage, up to 150 live larvae were transferred to fresh diets to complete larval development. From 50 to 120 larvae typically pupated and produced about 40 to 100 moths, which laid a total of 25 to 75 egg masses on average. Pupae were weighed and the average female pupal mass for each treatment and generation was used to predict fecundity, e.g. the number of oocytes in the adult moth (Wagner et al. 1987). Experiments were replicated twice to evaluate repeatability.

Data obtained from these experiments were used in the following population growth model to get a composite measure of the effects on budworm performance of different nutrient levels:

no. F_1 larvae = (no. P_1 larvae) • (P_1 % cohort survival to adult stage) • (P_1 $\bar{x}$ female fecundity) • (F_1 % viable egg masses)

The number of F_2 and F_3 larvae was calculated using data for the appropriate generation. The model estimates the number of first instar larvae alive at the beginning of the F_1, F_2, and F_3 generations, assuming that all the treatments in an experiment have equal populations at the beginning of the P_1 generation, i.e. the number of P_1 larvae was 1 for all treatments. I plotted the number of F_1 to F_3 larvae against the nutrient concentrations for the different treatments in an experiment and determined the optimal concentration of each nutrient tested based on the level that produced the most F_3 larvae.

RESULTS

The foliage of trees susceptible to western spruce budworm defoliation contained lower levels of N ($P < 0.001$), sugars ($P = 0.004$), and P ($P = 0.009$), but higher levels of K ($P = 0.018$) than that of resistant trees (Table 1). Foliar concentrations of Ca, Mg, and Zn were not different between resistant and susceptible trees ($P \geq 0.265$) (Table 1).

I also examined ratios of sugars and minerals to N because experimental results had indicated that N may determine the amount of food a budworm larva ingests, which in turn affects the amount of other nutrients or allelochemicals consumed (unpubl. data). Susceptible trees had higher ratios of P, K, Mg, and Zn to N than resistant trees ($P < 0.001$) (Table 1) and a tendency toward higher Ca/N ratios ($P = 0.069$). The two types of trees did not differ in sugars/N ratios ($P = 0.487$) (Table 1).

The foliage of susceptible trees had concentrations of sugars and K, plus ratios of P, K, Ca, and Zn to N, which were closer to the optimal levels determined by artificial diet experiments than those of foliage from resistant trees (Table 1). The optimal Mg/N ratio estimated from diet studies was between the mean values for resistant and susceptible trees. Levels of P in resistant trees were nearer the diet experiment optimum. It should be noted, however, that for sugars, P, P/N, K, and Zn/N the optimal diet values either were barely contained in the ranges observed for trees or were outside the ranges. Furthermore, none of the optimal diet values would be included in 95 percent confidence intervals for average tree values.

Resistant trees had higher levels of foliar N than susceptible trees, contrary to findings by Cook et al. (1978) for *Picea glauca* and by Piene (1980) for *Abies balsamea*. I was not surprised at this result, however, because experiments conducted with varying levels of N in artificial diets had demonstrated that N alone is not a limiting nutrient for *C. occidentalis* (unpubl. data).

There were no detectable differences in foliar terpene concentrations between resistant and susceptible Douglas-firs ($P \geq 0.334$) (Table 2). Likewise there was no distinction in total terpene/N ratios ($P = 0.992$) (Table 2). The terpene concentrations were calculated on a fresh mass basis because the foliage from all the trees was collected at the same phenological stage and moisture contents were thus similar.

Table 1. Comparison of foliar nutritional chemistry for 12 pairs of Douglas-fir trees that appeared to be resistant versus susceptible to western spruce budworm defoliation and the optimal concentrations of sugars and minerals determined by artificial diet experiments

Response variable[a] (units)	Douglas-fir foliar chemistry[b]			Artificial diet experiment optimum[c]
	P[d]	Resistant	Susceptible	
N (%)				
$\bar{x}$	<0.001	1.14	0.93	--[e]
SE		0.031	0.021	
Range		1.02-1.39	0.80-1.07	
Sugars (%)				
$\bar{x}$	0.004	11.2	8.9	6.4
SE		0.43	0.49	
Range		9.5-14.0	5.7-11.9	
Sugars/N ratio				
$\bar{x}$	0.487	9.9	9.5	5.2
SE		0.39	0.39	
Range		7.6-12.4	7.1-11.8	
P (mg/g)				
$\bar{x}$	0.009	2.03	1.93	3.36
SE		0.042	0.044	
Range		1.84-2.32	1.71-2.23	
P/N ratio (x 10)				
$\bar{x}$	< 0.001	1.78	2.08	2.73
SE		0.024	0.056	
Range		1.67-1.97	1.71-2.40	
K (mg/g)				
$\bar{x}$	0.018	8.89	9.94	12.73
SE		0.180	0.369	
Range		7.80-9.65	8.16-12.2	
K/N ratio (x 10)				
$\bar{x}$	< 0.001	7.85	10.76	10.35
SE		0.232	0.521	
Range		6.54-9.23	8.08-14.13	
Ca (mg/g)				
$\bar{x}$	0.695	2.78	2.71	3.95
SE		0.191	0.154	
Range		1.80-4.01	1.91-3.82	

Table 1. Continued

Response variable[a] (units)	Douglas-fir foliar chemistry[b]			Artificial diet experiment optimum[c]
	P[d]	Resistant	Susceptible	
Ca/N ratio (x 10)				
$\bar{x}$	0.069	2.49	2.93	3.21
SE		0.212	0.188	
Range		1.59-3.71	2.15-4.29	
Mg (mg/g)				
$\bar{x}$	0.265	0.90	0.92	1.04
SE		0.030	0.022	
Range		0.73-1.07	0.80-1.02	
Mg/N ratio (x 10)				
$\bar{x}$	< 0.001	0.79	1.00	0.85
SE		0.026	0.039	
Range		0.68-0.98	0.79-1.17	
Zn (μ/g)				
$\bar{x}$	0.631	27.8	27.3	85.6
SE		0.90	0.53	
Range		24-36	24-30	
Zn/N ratio (x 1,000)				
$\bar{x}$	< 0.001	2.44	2.95	6.96
SE		0.052	0.084	
Range		2.24-2.75	2.43-3.30	

[a] All concentrations are based on the dry mass of the foliage or diet.

[b] Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

[c] The concentration that produced the best budworm survival and reproduction when larvae were reared on the diet for three consecutive generations.

[d] Probability level for a paired *t*-test comparing foliar chemistry for resistant and susceptible Douglas-fir trees, df = 11.

[e] Experiments conducted with different levels of N in artificial diets demonstrated that responses to N were dependent on levels of minerals in the diet. Thus I predict the optimal N concentration will vary according to levels of minerals (and other nutrients and allelochemicals) present in the food.

Table 2. Comparison of foliar terpene chemistry for 12 pairs of Douglas-fir trees that appeared to be resistant versus susceptible to western spruce budworm defoliation[a]

		Douglas-fir foliage[b]	
Response variable	P[c]	Resistant	Susceptible
		(μg/g fresh mass)	
Tricyclene			
$\bar{x}$	0.670	84.8	77.8
SE		14.54	11.24
Range		24-165	22-171
α-pinene			
$\bar{x}$	0.495	367.2	321.0
SE		66.05	42.01
Range		131-795	96-643
Camphene			
$\bar{x}$	0.495	544.0	471.0
SE		96.74	74.12
Range		190-1110	114-1097
β-pinene			
$\bar{x}$	0.351	275.3	207.5
SE		66.70	36.40
Range		82-813	0-359
Myrcene			
$\bar{x}$	0.920	56.9	55.7
SE		8.10	9.71
Range		22-98	25-142
Menthene-1			
$\bar{x}$	0.788	246.1	231.1
SE		32.06	44.67
Range		121-411	82-626
Bornyl acetate			
$\bar{x}$	0.922	471.2	461.5
SE		81.75	85.50
Range		105-924	99-1194
Total monoterpenes			
$\bar{x}$	0.334	1742.2	1411.9
SE		279.52	199.56
Range		590-3347	404-3100

Table 2. Continued

Response variable	P^c	Douglas-fir foliage[b]	
		Resistant	Susceptible
		(µg/g fresh mass)	
Total oxygenated monoterpenes			
$\bar{x}$	0.981	477.4	475.1
SE		84.93	89.67
Range		105-978	99-1248
Total terpenes			
$\bar{x}$	0.437	2219.6	1887.0
SE		357.62	285.63
Range		775-4325	503-4348
Total terpenes/N ratio		ratio x 1,000	
$\bar{x}$	0.992	202.1	201.7
SE		35.26	28.66
Range		68.6-408.0	55.9-430.5

[a] Concentrations of six monoterpenes (tricyclene, α-pinene, camphene, β-pinene, myrcene, menthene-1) and one oxygenated monoterpene (bornyl acetate), the principal components of the oleoresin of these trees, are presented. Additional monoterpenes (α-phellandrene, Δ-3-carene, ℓ-limonene, terpinolene) and oxygenated monoterpenes (cis-β-terpineol, ℓ-borneol) that were minor components of the oleoresin were included when calculating terpene totals.

[b] Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

[c] Probability level for a paired *t*-test comparing foliar chemistry for resistant and susceptible Douglas-fir trees, df = 11.

CONCLUSIONS

Foliar analyses of 1988 new growth revealed that defoliation susceptible Douglas-fir had lower levels of N and sugars in their foliage than nearby defoliation resistant trees. Susceptible trees, moreover, had higher mineral/N ratios for P, K, Ca, Mg, and Zn. These field data are consistent with predictions made from laboratory diet experiments that high mineral/N ratios favor spruce budworm population growth. In other words, the susceptible trees had sugar concentrations and mineral/N ratios closer to the optimal levels for the spruce budworm than did the resistant trees. The results, therefore, support the hypothesis that variations in levels of foliar nutrients among individual trees may be an important mechanism in Douglas-fir resistance to *C. occidentalis* damage. Resistant trees may suffer low defoliation because they provide a food source that is poorly matched to the budworm's nutritional requirements with respect to concentrations of sugars and balances of key minerals to N.

A potential caveat must be attached to these results, however. Although there were detectable differences in sugar concentrations and mineral/N ratios between apparently resistant and susceptible trees, neither group was close to the optimal levels estimated from diet experiments. This implies that host plants rarely provide a food resource which closely matches the budworm's most favorable conditions for growth and reproduction.

Terpenoid compounds did not appear to be related to resistance to budworm attack because there were no detectable differences between monoterpene concentrations in putatively resistant and susceptible trees. This result was somewhat surprising because terpene compounds have frequently been implicated as important determinants of western spruce budworm performance (Redak 1982, Cates et al. 1983a, 1983b, 1987, Perry and Pitman 1983, Redak and Cates 1984, Cates 1985, Shepherd 1985, Wagner and Tinus 1985, Cates and Redak 1986, 1988, Campbell 1987, Hermann 1987, Wulf and Cates 1987, Wagner et al. 1989, 1990). However, the sample size was small (12 pairs of trees) and observations were highly variable, so the significance of the failure to detect differences may be open to question. Moreover, I only measured monoterpenes and sesquiterpenes, not larger terpenoids such as resin acids.

Several possible alternatives may explain why foliar nutrients were different between susceptible and resistant Douglas-fir trees. First, the susceptible trees may truly have inherently different nutrient levels owing to their genetic make-up. Second, the foliar chemistry of resistant versus susceptible trees may have been induced by the dissimilar defoliation histories, which are a consequence of some unmeasured tree properties (Piene 1980). If this is the case, it implies that budworm defoliation has a positive feedback for subsequent generations, as in the "resource regulation hypothesis" proposed by Craig et al. (1986). Third, it is possible that resistant trees support budworm populations equal to those supported by susceptible trees, but the larvae consume less of the annual foliage increment because a) the food contains more N and b) the trees produce more foliage. In other words, resistant trees suffer substantially less defoliation. A fourth plausible explanation involves phenology of budbreak. Resistant trees may break bud later than susceptible trees and consequently be consistently asynchronous with budworm emergence. I am investigating these alternative explanations in greenhouse bioassay experiments with replicated isogenic lines of resistant and susceptible trees.

SUMMARY

The western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir (*Pseudotsuga menziesii*) provide a good model system by which to test the hypothesis that variation in host plant nutritional quality is a mechanism for plant resistance to herbivore attack. In this study I compared levels of several nutrients (nitrogen, sugars, phosphorus, potassium, calcium, magnesium, and zinc) and terpenes in foliage of Douglas-fir trees that were phenotypically resistant and susceptible to western spruce budworm defoliation. The field results were compared with the results of artificial diet experiments designed to determine the budworm's response curves to individual nutrients.

This first year's (1988) field data revealed that susceptible Douglas-fir trees had lower levels of foliar N and sugars than resistant trees, agreeing with predictions made from laboratory diet studies. Moreover, the susceptible trees had mineral/N ratios (for P, K, Ca, and Zn) which were closer to the optimal levels established in artificial diet studies. There were no detectable differences in monoterpenes between susceptible and resistant Douglas-fir trees.

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PATTERNS OF NUTRIENT UTILIZATION IN THE NEEDLE-FEEDING GUILD

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INTRODUCTION

It is well known that large differences in performance parameters such as growth rate, survival rate, or fecundity rate are found between various insect guilds, e.g. root feeders and sapsuckers (Slansky and Rodriguez 1987, Slansky and Scriber 1985). Within guilds and even within a given host plant, the variability of the plant material may also result in considerable differences in the performance parameters of insect larvae feeding on the plant (Whitham 1983, Jensen 1988).

Under constant laboratory conditions, variability in performance depends primarily on the nutrient and secondary compound content of the host plant material. Positive correlations between performance parameters and the carbohydrate, amino acid, or total nitrogen content can be found, while negative correlations have often been made between performance and the presence of phenolics, tannins, or alkaloids.

With a limited number of insect species such correlative analyses might be tested by using artificial diet studies. In such studies, however, it is extremely difficult to mimic the true composition of the various chemicals in the plant tissue. Another method is to study the fate of various biochemicals when ingested by a certain insect.

In the present investigation, the content of various biochemicals in the needles of conifers (*Pinus* and *Picea* species) was compared with the content of the same compounds in larval feces for a number of insect species within the needle-feeding guild. These species comprise conifer specialists within the Lepidoptera (*Bupalus pinarius*, *Dendrolimus pini*, *Panolis flammea*) and Hymenoptera (*Diprion pini*, *Neodiprion sertifer*, *Pristiphora abietina*, *Gilpinia hercyniae*, *Pachynematus scutellatus*, *Cephalcia abietina*) as well as the generalists, mainly Lepidoptera (*Orgya antiqua*, *Lymantria monacha*), known to use host plants other than the conifers.

EXPERIMENTAL METHODS

All insects were reared under standardized conditions, at 20°C and with 18 hr daylight, on whole branches cut from 40 to 60-year-old spruce and pine trees. First instar larvae were kept in groups, later instars singly. Most individuals were wild-captured or first generation laboratory-reared with the exception of *Diprion pini*, which came from the stock maintained at the University of Turku, Finland.

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Samples of needles were taken at the start and in the middle of the experimental period, and larval feces samples were collected 2 to 3 days after the needle samples were taken. Needles and feces were freeze-dried, ground, and stored in a desiccator in the dark at room temperature.

Polar compounds were extracted three times with methanol, 2 ml for 15 min at 65°C, each time with subsequent centrifugation, 5 min 2800 U/min at room temperature. The methanol extract was derivatized by oxime formation followed by silylation and applied to a gas chromatographic column (2m x 4mm) packed with SE52 on Chromosorb G. The internal standard method was used to determine the quantities derived from the chromatograms.

The total nitrogen content of the freeze-dried material was determined by means of the modified micro-Kjeldahl method.

RESULTS

Total Nitrogen

As expected, the total nitrogen content in conifer needles differs between old and young needles, highest values (ca. 4 percent dwt) being found in the newly flushed needles and decreasing as the needles grow old. Even at the start of the growing season, old needles have a very low ($\leq$ 1 percent dwt) nitrogen content.

Fig. 1 shows the concentration of nitrogen in spruce and pine needles compared with the concentration of nitrogen in the feces of several insect species. The consensus for all species and all types of food is that nitrogen utilization is low. The concentration of nitrogen in the feces is only slightly lower than that in the needles. Even in cases where the food has a content of about 1 percent, the concentration in the feces is close to the value in the needle. When the metabolic quotient is taken into account, the general utilization of nitrogen in these species is in the order of 45 to 55 percent.

Carbohydrates

In the present investigation, the concentrations of fructose, alpha- and beta-glucose, and sucrose were measured individually and the total amount of hexose-equivalents calculated as:

$$\text{Chex} = \text{Fru} + \text{Glu} + 2(\text{Suc})$$

In pines few differences in carbohydrate concentrations were found between old and young needles, whereas among spruce somewhat higher concentrations were found in old than in the younger needles.

Fig. 2 shows the level of carbohydrates in the feces of all insect species investigated. The consensus for all species on all food resources is utilization is very high, 95 to 100 percent. Even when carbohydrate concentrations are very elevated, the utilization is almost complete. Carbohydrate values from insect consumption of male flowers are not included in the figure, but male flowers can have carbohydrate concentrations of 600 to 1,300 nmoles/g dwt, and in such cases the utilization is still 95 to 100 percent.

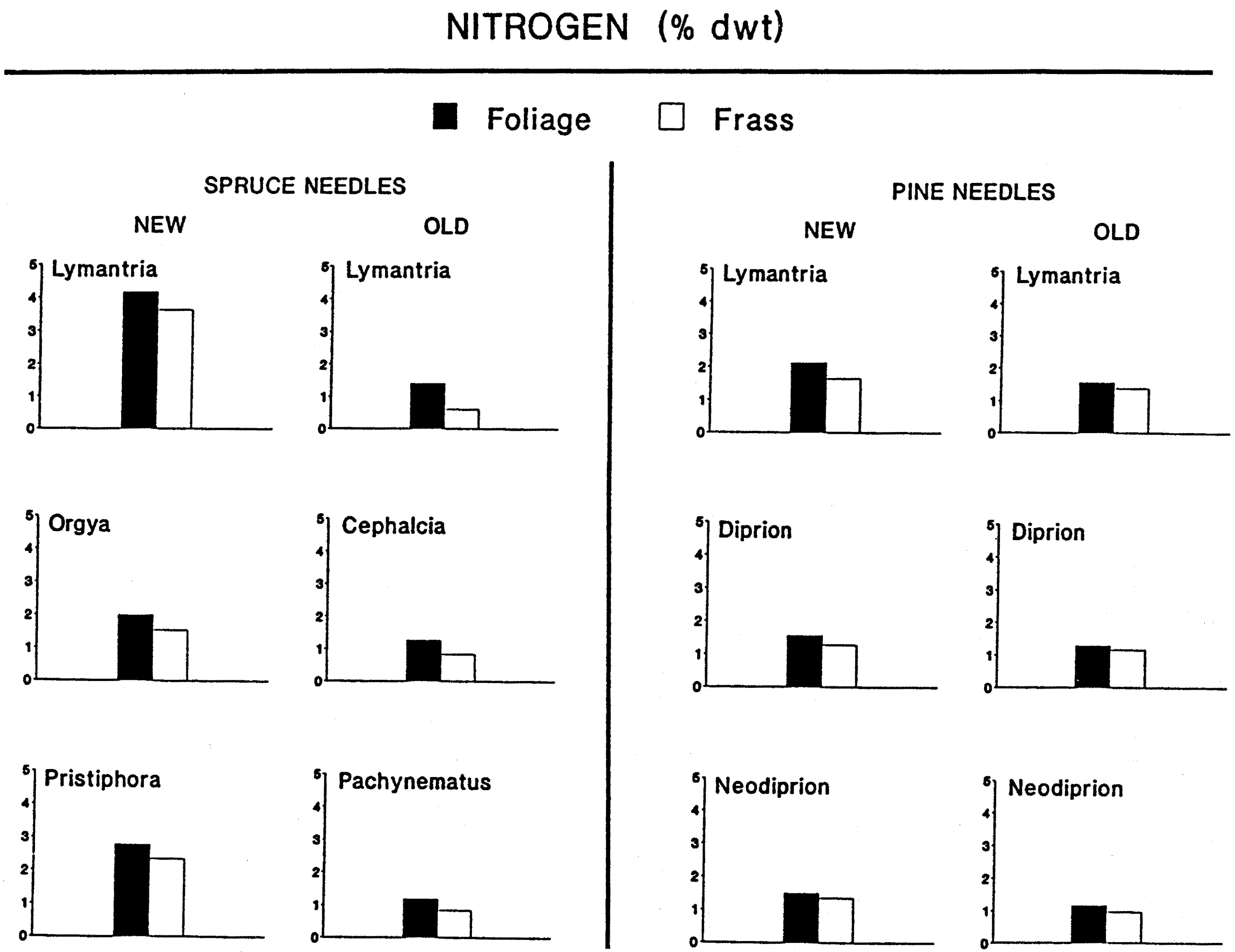

Figure 1. Concentrations of total nitrogen in new and old needles of spruce and pine, and in frass of insect herbivores.

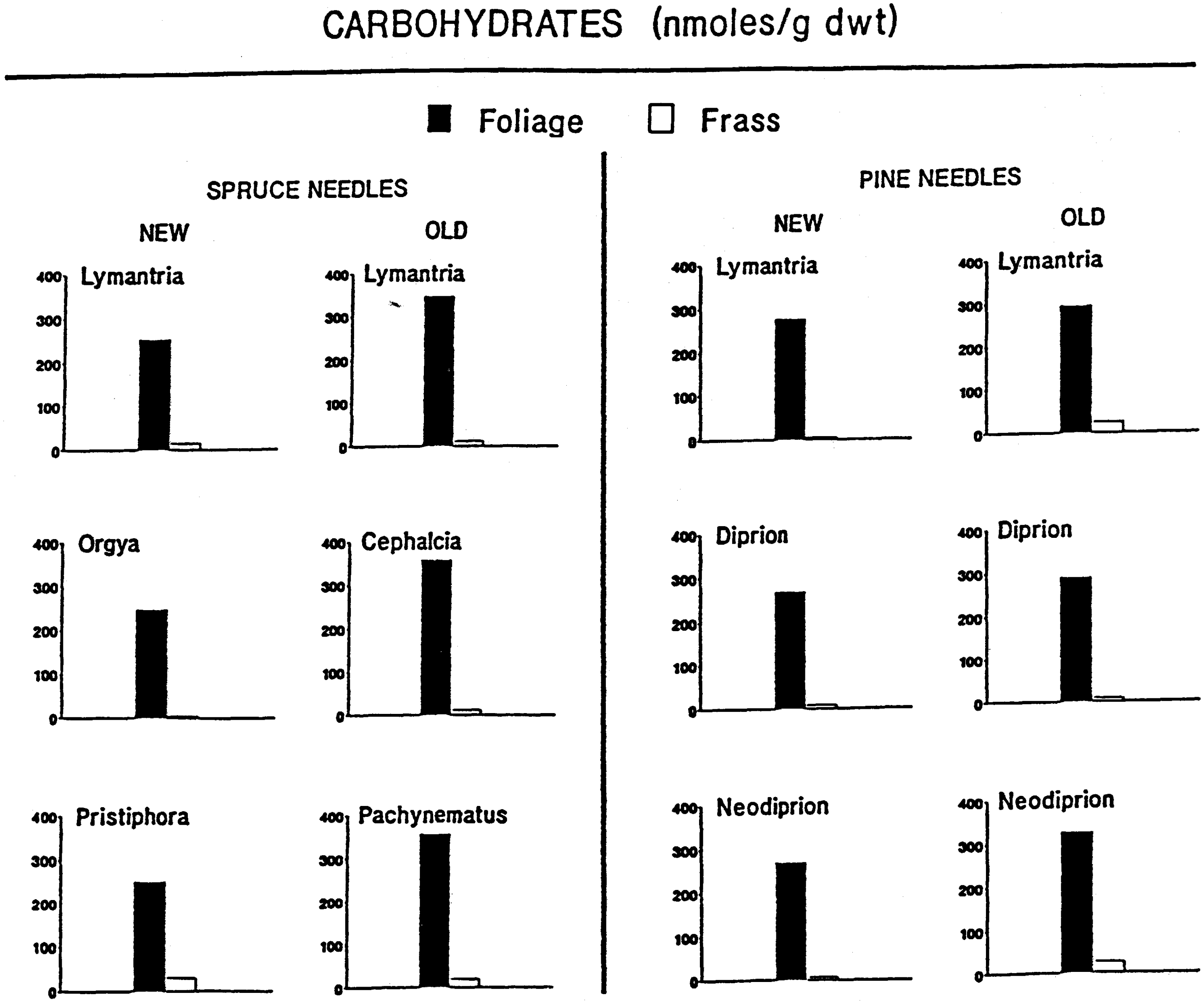

Figure 2. Concentrations of carbohydrates (hexose-equivalents of sucrose, fructose, and glucose) in new and old needles of spruce and pine, and in frass of insect herbivores.

Cyclites

Fig. 3 shows the concentrations of the conifer-specific cyclite (sugar alcohol), pinitol. Pinitol occurs in rather high concentrations, highest in the new needles. Male flowers also contain high amounts of pinitol. In most insect species there seems to be an almost complete utilization of this compound, although *Lymantria monacha* has a somewhat lower assimilation level/rate when eating old needles. When the concentration of pinitol in the food is very high, however, utilization seems to decrease.

The other cyclite, inositol, occurs in much lower concentrations (7 to 25 nmoles/g dwt) in the needles and in the male flowers. At low concentrations, all inositol is utilized, but at higher concentrations in the food, inositol can occur in concentrations of up to 17 nmoles/g dwt in *L. monacha* feces.

Phenolic Acids

Quinic acid is the low-molecular compound in conifer needles found in probably the most variable concentrations, ranging from 35 to 1,000 nmoles/g dwt. The high concentrations are found in newly flushed needles and in the male flowers of spruce and the lower concentrations in old pine needles.

Fig. 4 shows that the pattern of utilization of quinic acid is highly variable, depending on the insect/host plant system. The generalist *L. monacha* seems to tolerate this compound, quinic acid being present in the feces in concentrations equal to or even higher than in the needles. Taking the metabolic quotient into account, one may infer low or zero utilization.

The same pattern is found in the other generalist lepidopteran, *Orgya antiqua*, feeding on new spruce needles. The specialist pine lepidopterans, *Bupalus pinarius* and *Dendrolimus pini*, seem to follow the same pattern as well, and with them higher concentrations in the feces than in the old pine needles clearly indicate that quinic acid passes through the intestine unaltered.

In striking contrast, the specialist sawflies seem to utilize at least a part of the quinic acid when reared on their proper host. When *Diprion pini* and *Neodiprion sertifer* feed on old pine needles, concentrations of quinic acid in the feces are quite low. However, when these species are forced to feed on new needles with a higher content of quinic acid, the concentrations in the feces are higher, but still below the value in the needles.

The spruce specialist sawflies seem to follow this pattern. Although given higher concentrations of quinic acid in spruce needles, higher levels are also found in the feces, utilization seems to be similar.

Shikimic acid also shows a variable pattern between plant species and plant parts, highest values being found in old spruce needles and in *Pinus contorta* and lowest values in new spruce needles and male pine flowers (Fig. 5).

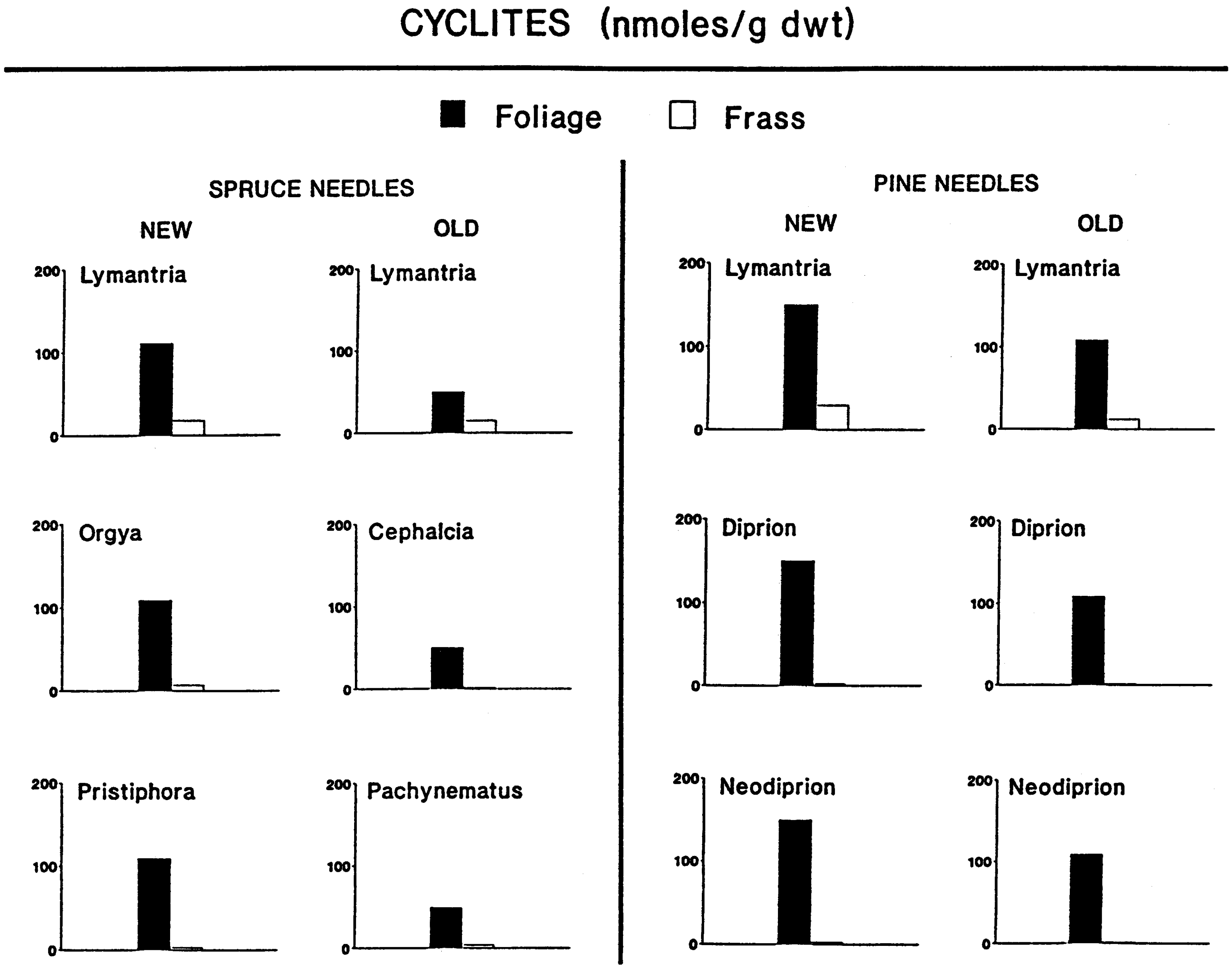

Figure 3. Concentrations of the cyclite, pinitol, in conifer needles and in herbivore frass.

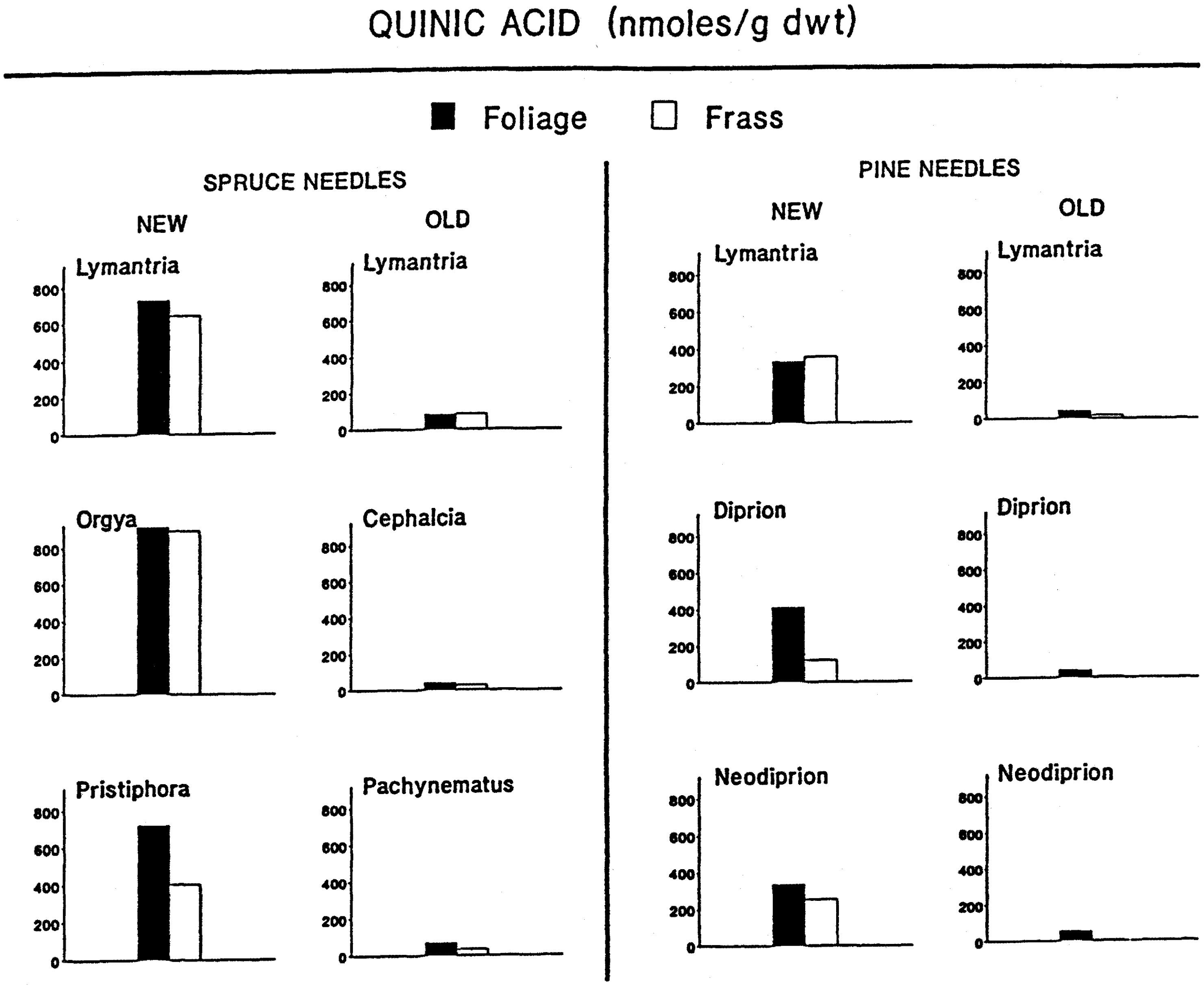

Figure 4. Concentrations of quinic acid in conifer needles and in herbivore frass.

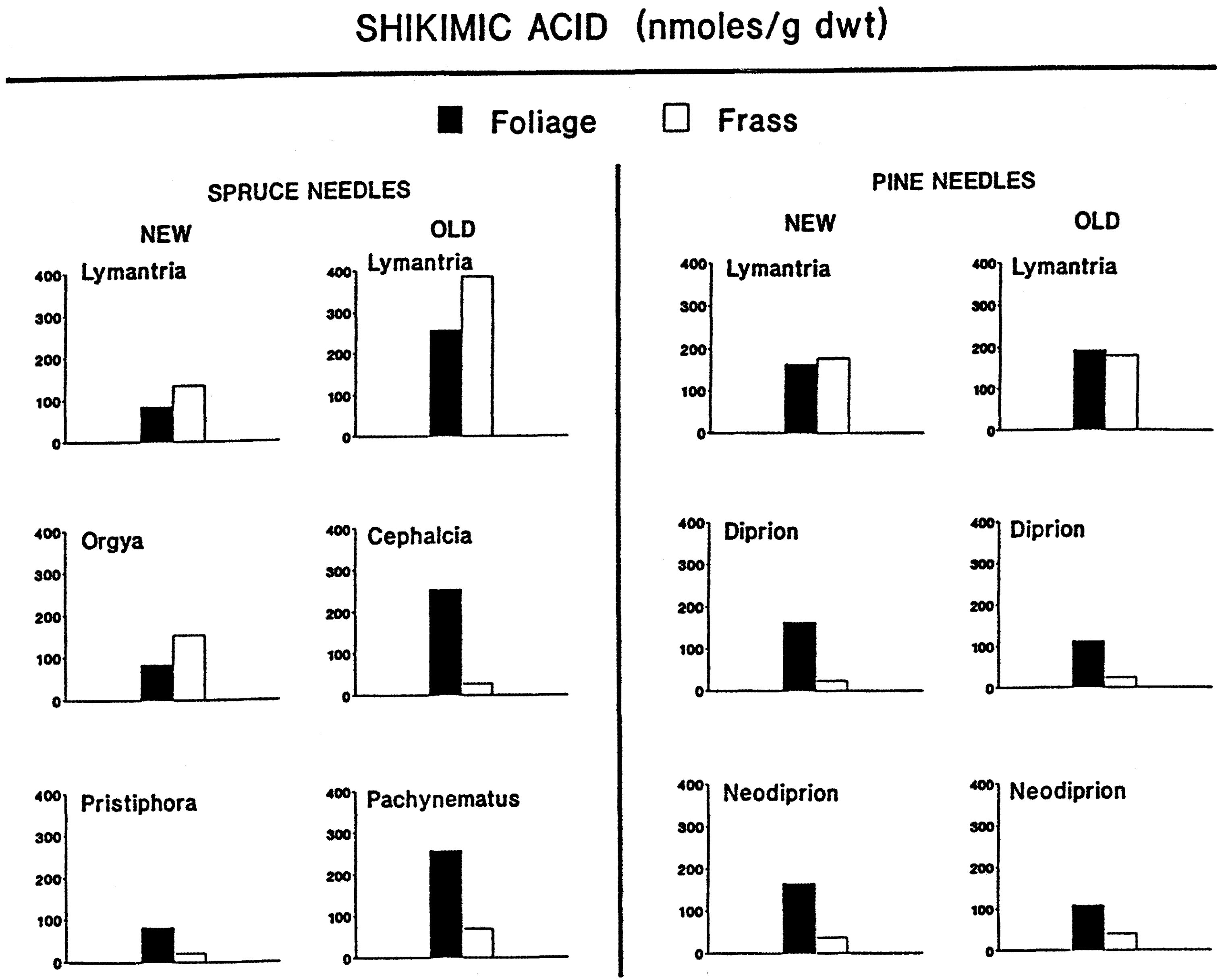

Figure 5. Concentrations of shikimic acid in conifer needles and in herbivore frass.

Likewise the variability of shikimic acid utilization by needle-feeding insects is considerable. The concentration of shikimic acid in the feces of *L. monacha* is often higher than in the food, indicating that the compound passes through the intestine unmetabolized. The same holds for another generalist lepidopteran, *Orgya antiqua*, and the pine specialist lepidopterans, *Bupalus pinarius*, *Dendrolimus pinus*, and *Panolis flammea*.

In contrast, all specialist sawflies, irrespective of host plant and plant part, show fairly high utilization of shikimic acid.

DISCUSSION

The results of our analyses clearly show that in all conifer insect species investigated, the utilization of carbohydrates (fructose, glucose, and sucrose) was almost 100 percent. This strongly suggests that demand for carbohydrates in the concentrations found in conifer needles is high among needle-feeding herbivores. It also suggests that carbohydrates may be a limiting factor in certain performance parameters for those insect species consuming the most carbohydrate-poor diet.

Studies of insect performance in relation to carbohydrate concentrations have so far given rather different results, however. Positive correlations have been found in *Gilpinia hercyniae/Picea abies* (Schopf 1986, Jensen 1988), *Sphinx pinastri/Pinus silvestris* (Otto 1970), and *Choristoneura fumiferana/Picea glauca* (Harvey 1974, McLaughlin 1986). Nonsignificant correlations have been described in *C. fumiferana/Abies balsamea* (Shaw et al. 1978).

Although cyclites are carbohydrates, they seem to differ from them in having a somewhat lower utilization rate. In particular, pinitol, when highly concentrated in the needles, is sometimes found in high concentrations in the feces as well. In any case, the cyclites add to the general pool of energy available to the herbivores.

Nitrogen is one of the compounds most often related to insect performance (Mattson 1980, Mattson and Scriber 1987). Thus it is interesting to note that in the present investigation nitrogen was found to be utilized only to a limited degree by the foliage-feeding herbivores. This may be due to the indigestible nature of the N compounds or to large concentrations of digestibility-reducing compounds, e.g. tannins or resins, which can lower the bioavailability of the proteins in the needles (Rhoades 1983). As nitrogen utilization was low and the concentration of nitrogen high in the feces of species eating newly flushed needles, however, concentrations of digestibility-reducing compounds should also be high in these new needles. This is not consistent with general theory and not supported by available data. By way of explanation, one could argue that the results obtained here are derived mainly from later instar larvae and that newly hatched larvae would have a greater demand for and therefore a higher utilization of nitrogen.

The highly variable utilization of quinic acid and shikimic acid may be interpreted in relation to their potential role as secondary compounds. Utilization of these acids is rather low among generalist and specialist lepidopterans, and the part of the compounds excreted. Accordingly, these insect species do not receive the potential carbon-energy from the compounds in question, but have, on the other hand, developed a tolerance for acidity and merely excrete the acids.

The specialist sawflies, unlike the lepidopterans, seem to metabolize part of the acids and hence obtain carbon-energy, probably by means of microbial activity in the mid-gut (Schopf 1986), but this adaptation often limits them to a very specific host-range, some of the species being unable to tolerate needles of a certain age class even from their favorite host. *Gilpinia hercyniae* often dies on immature spruce needles (Jensen 1988). *Neodiprion sertifer* and *Diprion pini* have a high preference for old, pine needles, though if forced to eat new needles, they are able to survive.

CONCLUSIONS

Results of the present investigation seem to indicate that the main differences in utilization of nutrients and secondary compounds within the needle-feeding guild exist along taxonomical lines (Hymenoptera-Lepidoptera) rather than generalist-specialist lines. Both orders have developed a high capacity of carbohydrate utilization and perhaps a lower capacity of nitrogen utilization. Both specialist and generalist lepidopterans seem unable to metabolize, but able to tolerate certain secondary compounds, whereas hymenopterans, all specialists, utilize these compounds to varying degrees.

SUMMARY

The nutrient content and the content of certain low molecular secondary compounds of conifer needles and flowers from *Picea* and *Pinus* species were quantified by means of gas chromatography and micro-Kjeldahl analysis. The same compounds were also quantified in the feces of conifer insects (Lepidoptera and Hymenoptera) within the herbivore guild. Carbohydrates and cyclites in the needles and in the flowers were almost totally utilized by these insect species, whereas only 45 to 55 percent of the total nitrogen content was utilized. Among specialist and generalist lepidopterans, secondary compounds such as shikimic acid and quinic acid were utilized only to a very low degree, whereas among specialist hymenopterans (sawfly species), utilization of these compounds was high.

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THE FOLIVORE GUILD ON LARCH (LARIX DECIDUA) IN THE ALPS

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In memoriam Christian Auer

INTRODUCTION

The term "guild" describes a group of organisms that exploit the same class of resources in a similar manner (Root 1967, Mattson et al. 1988). This study focuses on six members of the folivore guild of subalpine larch, *Larix decidua*, in Switzerland--five lepidopterans and one hymenopteran. From 1949 to 1979, Auer (1977) sampled populations of the larch bud moth, *Zeiraphera diniana* L., and at the same time collected associated larvae. I have analyzed these 30 years of insect sample data for the six different species and now offer it to the scientific literature. In spite of some methodological shortcomings, the data have tremendous value because of their historical import. There are precious few long-term data sets of this kind.

The spectacular population cycles of the larch bud moth (LBM) and the ensuing periodic severe defoliations of the subalpine larch forests have provided an interesting opportunity to analyze possible interspecific competition among members of the larch folivore guild owing to varying degrees of depletion of their common food source. The impact of defoliation on each member of the guild is evaluated by comparing trends (immediate and delayed) in the population index of each with the larch bud moth (LBM) cycle.

By analogy to what happens to the LBM, "immediate impact" is understood as increased larval mortality and reduced fecundity due to loss of shelter and starvation, whereas "delayed impact" results from the "induced response" which is mediated by the lower food quality in years subsequent to defoliation and results in drastically increased mortality of the small larvae for several succeeding generations. I used Chi-square analysis to compare the trends in fluctuation patterns of the guild members with the LBM. I examine the hypothesis that interspecific competition driven by the LBM contributes to the quantitative structuring of the guild.

EXPERIMENTAL METHODS

Biology and Phenology of Guild Members

Although there are many insects associated with the large larval instars of the LBM, only the six most frequent phytophagous species are considered (Fig. 1).

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

1) Tortricidae

a) *Exapate duratella* Heyd. is polyphagous on mountain ash (*Sorbus aucuparia*), shrubs (*Vaccinium*, *Rhododendron*, and *Cotoneaster*), or herbs (*Thalictrum*) growing underneath larch (Thomann 1947). It occurs throughout the alpine region and overwinters in the egg stage. Hatching occurs somewhat later than the LBM. It has five larval instars which construct fascicles similar to those of the LBM. Rather agile when disturbed, they descend on silken threads to lower branches or to the ground. If not disturbed, *E. duratella* pupates on larch. The species is sexually dimorphic: males are winged and white; females are wingless and dark gray. Females are very cold-hardy, surviving temperatures as low as -18°C, and are active at air temperatures as low as 5°C (Baltensweiler 1961).

b) *Ptycholomoides aeriferana* H.-Schaeff. is oligophagous on *Acer platanoides*, *Larix*, and pine (Raigorodskaya 1963). Palearctic in distribution, it is found from Europe to Japan. This species hatches from the egg in fall, molts to the second instar without feeding, and overwinters in diapause. It starts to feed in the spring, simultaneous with the LBM. After the fifth larval instar, pupation takes place between the needles. The female attaches her eggs to the needles by means of an adhesive substance. Highest densities usually occur at altitudes below 1700 m.

c) *Spilonota laricana* Hein. is monophagous on larch and palearctic in distribution (Bovey 1978). The eggs are deposited on needles in June to August, depending on altitude. The first instar larvae hatch after 2 weeks and overwinter as second instar larvae in a hibernaculum. Emergence takes place during needle growth of larch. The larvae construct a fascicle similar to that of the LBM. Pupation occurs between needles and the moths emerge after 2 to 3 weeks. Highest densities usually occur at altitudes below 1700 m.

2) Geometridae

Oporinia (Epirrita) autumnata Bkh. is polyphagous, living on birch, larch, fir, and spruce. Extensive outbreaks occur on birch in Scandinavia (Tenow 1972). The species being univoltine, eggs are deposited singly on branches, where they overwinter. Hatching occurs in early spring. The five larval instars live openly along the branch axis and feed on needles without spinning a fascicle. Thus the larvae are very easily dislodged when the branch samples are collected if precautions are not taken. Losses of 30 percent and 53 percent were observed when the branch samples were thrown to the ground from the lower and middle to upper crown levels respectively (Bidaud 1970). Pupation occurs on the ground. The moths are not very good flyers.

3) Gelechidae

Teleia saltuum Z. is oligophagous and palearctic in distribution. Its biology is not very well known, but the insect seems to occur primarily at low altitudes. It is a biennial species, overwintering both as L2- and L5-larvae. Eggs are deposited on needles.

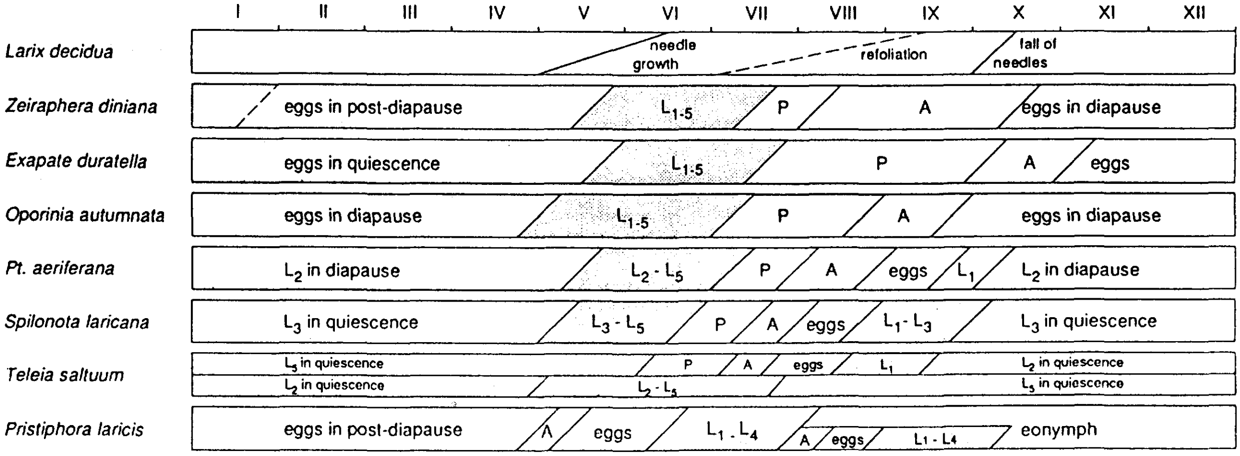


Figure 1. Phenology and biology of the folivore guild on larch (*Larix decidua* Mill.) in the European Alps.

4) Tenthredinidae

Pristiphora laricis Htg. is monophagous and palearctic in its distribution. At lower altitudes two generations occur per year; above 1700 m only a partial second generation is observed. Overwintering as an eonymph in a cocoon, it transforms to a pronymph in January (Lovis 1975), and the adults emerge toward the end of May and beginning of June. Eggs of the first generation are laid on the growing needles and hatch after 10 days at 16°C or 21 days at 10°C.

Larval Population Sample

The sampling methodology for the LBM and its associated guild members (Kälin and Auer 1954, Auer 1961) relies on a sampling scheme stratified according to topography (altitude and exposure) and host tree density per unit area in the subalpine forest, e.g. *Larici-pinetum-cembrae* (Ellenberg and Klötzli 1972). The proper sample provides a basic population estimate for the larval stage of each generation on a weight basis, i.e. number of larvae per kg of larch twigs with foliage. It is comprised of three branches cut at three levels within the crown of the tree. The samples are taken when the LBM is in its fourth or fifth instar. This coincides phenologically with the time at which the larch needles cease to grow.

Five outbreak areas along the alpine arch, covering 2120 to 6280 ha of montane and subalpine forests, were sampled between 1949 and 1976 with 100 to 500 sample trees for various periods (Auer 1977):

1) the region of the Briançonnais in the western Alps (Department Hautes Alpes, France)
2) the Goms in the Upper Rhone River Valley (Kanton Wallis, Switzerland)
3) the Oberengadin (Kanton Graubünden, Switzerland)
4) the Valle Aurina (Provincia Autonoma di Bolzano-Alto Adige, Italy)
5) the Lungau (Land Salzburg, Austria).

Evaluation of the Defoliation Impact on the Guild Members

Two negative effects of defoliation on the fluctuations of the guild members are conceivable.

1) An immediate impact. Assuming that the destruction and depletion of the common food resource in the current generation t induces immediate larval mortality due to malnutrition or lack of shelter and reduces, therefore, the egg potential of the following generation, the immediate impact is a lower larval density in generation t+1:

   [If Density $\mathrm{LBM}_t > 100$ larvae/kg: Density $x_{t+1} <$ Density x_t].

   Pristiphora laricis, whose first generation larval period coincides exactly with the large larval stages of the LBM, might suffer heavy mortality in the same generation t, and therefore the immediate impact is defined by [Density $\mathrm{Pl}_t <$ Density Pl_{t-1}].

2) A delayed impact. Defoliation of the larch lowers the long-term nutritional quality of the larch needles in subsequent generations, a condition which may relax only over the course of several years (Baltensweiler 1984, Baltensweiler and Fischlin 1988). This impact is defined as follows:

   [If Density $\mathrm{LBM}_t > 100$ larvae/kg: Density $x_{t+2} <$ Density x_{t+1};
   Density $\mathrm{Pl}_{t+1} <$ Density Pl_t].

   The differences in density are evaluated as trends only, and the occurrence of cases is tested by Chi-square analysis. The error probabilities are given as percentages.

RESULTS

The densities for the LBM and its associated species on larch in five different subalpine regions are presented in Tables 1 through 7. The fluctuation pattern of the guild as a whole is remarkably similar at all five subalpine sites. In four to five generations, the LBM increases by five orders of magnitude and transgresses the defoliation threshold of 100 larvae/kg twigs at regular intervals of 8 to 9 years (Baltensweiler et al. 1977). Conversely, the numbers of the other guild members vary with a moderate amplitude between 0.01 and 5 larvae/kg twigs, but without exhibiting any particular trend. This is somewhat surprising since one might have assumed that the severe and widespread defoliation by the LBM would synchronize the fluctuations of the other phytophagous species with each other.

Table 1. *Zeiraphera diniana* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			4.174		
1953			68.797		
1954			331.760		
1955			126.541		
1956			21.280		
1957			2.246		
1958		0.049	0.085		
1959		0.090	0.080		
1960	4.422	0.458	0.371	0.040	
1961	48.303	1.774	1.638	0.140	0.090
1962	361.879	10.902	22.878	2.420	0.560
1963	53.440	151.132	248.817	39.260	8.760
1964	70.770	175.215	184.272	180.460	107.870
1965	0.475	3.235	3.116	21.880	234.576
1966	0.024	0.013	0.020	0.280	38.540
1967	0.041	0.025	0.002	0.020	0.290
1968	0.335	0.025	0.059	0.050	0.040
1969	2.152	0.180	0.197	0.150	0.183
1970	10.114	1.495	1.068	0.752	0.707
1971	81.913	10.338	10.569	3.810	3.170
1972	245.787	76.355	173.932	8.330	29.820
1973	1.371	78.225	249.612	4.255	36.060
1974	0.396	8.075	176.050	4.029	118.450
1975	0.258	0.190	4.749	4.740	18.380
1976	0.618	0.050	0.014	0.441	3.760
1977	3.600		0.008	0.118	0.830
1978	36.144	0.600	0.056	0.068	0.240
1979	209.531	1.616	0.204	0.130	0.170

Table 2. *Exapate duratella* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.018		
1953			0.282		
1954			0.826		
1955			0.134		
1956			0.018		
1957			0.002		
1958		0.012	0.004		
1959		0.050	0.070		
1960	1.402	0.497	0.220	0.090	
1961	2.945	0.241	0.166	0.100	0.040
1962	5.556	0.451	1.228	0.160	0.090
1963	3.500	1.130	5.573	0.490	0.250
1964	0.330	0.960	2.830	0.280	0.200
1965	0.030	0.207	0.388	0.170	0.212
1966	0.008	0.010	0.011	0.010	0.140
1967	0.055	0.010	0.022	0.010	0.050
1968	0.413	0.050	0.034	0.070	0.050
1969	0.432	0.170	0.099	0.020	0.069
1970	0.530	0.325	0.619	0.163	0.100
1971	1.258	0.798	1.411	0.310	0.310
1972	1.179	0.615	6.833	0.220	0.150
1973	0.210	2.145	2.844	0.118	0.190
1974	0.028	0.530	0.798	0.128	0.100
1975	0.220	0.060	0.042	0.110	0.090
1976	0.542	0.045	0.008	0.039	0.110
1977	1.360		0.010	0.176	0.080
1978	1.288	0.040	0.015	0.078	0.010
1979	6.133	0.101	0.050	0.010	0.050

Table 3. *Oporinia autumnata* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.287		
1953			0.669		
1954			0.994		
1956			0.202		
1957			0.106		
1958			0.134		
1958		0.531	0.361		
1959		0.668	0.838		
1960	1.074	1.047	0.707	0.960	
1961	0.780	0.670	0.417	0.310	0.530
1962	0.414	3.284	2.185	0.930	0.850
1963	0.560	6.320	2.354	1.260	0.900
1964	0.600	10.388	0.850	0.980	1.650
1965	0.530	2.530	0.286	0.40	1.151
1966	0.412	0.328	0.124	0.330	0.610
1967	2.950	0.450	0.248	0.490	0.420
1968	4.883	1.445	0.888	1.385	0.580
1969	2.472	2.205	1.063	2.730	0.752
1970	0.225	1.795	0.788	1.693	1.153
1971	0.255	1.581	1.047	1.360	1.360
1972	0.168	1.085	0.912	0.290	1.370
1973	0.196	0.990	0.572	0.216	0.440
1974	0.458	3.035	0.508	0.676	1.040
1975	0.740	1.060	0.128	0.880	0.570
1976	0.570	0.550	0.361	0.667	0.590
1977	3.760		0.229	2.197	0.590
1978	18.394	1.590	0.696	1.255	0.690
1979	5.449	0.909	0.240	0.485	0.240

Table 4. *Ptycholomoides aeriferana* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.001		
1953			0.018		
1954			0.006		
1955			0.002		
1956			0.001		
1957			0.001		
1958		0.001	0.002		
1959		0.001	0.002		
1960	0.225	0.007	0.002	0.010	
1961	0.037	0.001	0.002	0.010	0.010
1962	0.667	0.113	0.026	0.070	0.020
1963	0.160	0.085	0.032	0.250	0.010
1964	0.090	0.093	0.016	0.210	0.560
1965	0.010	0.010	0.016	0.110	0.101
1966	0.004	0.003	0.002	0.060	0.160
1967	0.005	0.005	0.002	0.010	0.030
1968	0.065	0.005	0.002	0.095	0.020
1969	0.221	0.010	0.007	0.115	0.064
1970	0.040	0.085	0.007	0.118	0.127
1971	0.240	0.061	0.053	0.310	0.310
1972	0.026	0.050	0.019	0.070	0.070
1973	0.019	0.220	0.012	0.029	0.110
1974	0.028	0.055	0.006	0.098	0.020
1975	0.001	0.010	0.002	0.070	0.140
1976	0.092	0.040	0.002	0.069	0.110
1977	0.150		0.002	0.088	0.080
1978	0.356	0.040	0.002	0.010	0.050
1979	0.327	0.010	0.002	0.010	0.010

Table 5. *Spilonota laricana* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.031		
1953			0.065		
1954			0.125		
1955			0.103		
1956			0.017		
1957			0.009		
1958		0.142	0.026		
1959		0.150	0.022		
1960	0.451	0.593	0.043	0.070	
1961	0.404	0.084	0.027	0.070	0.010
1962	0.273	0.255	0.039	0.060	0.007
1963	0.400	0.220	0.043	0.190	0.270
1964	0.180	0.113	0.138	0.220	0.110
1965	0.265	0.397	0.174	0.430	0.889
1966	0.092	0.065	0.041	0.120	0.550
1967	0.486	0.160	0.029	0.110	0.250
1968	1.644	0.175	0.086	0.160	0.220
1969	0.085	0.295	0.091	0.145	0.173
1970	0.115	0.275	0.035	0.118	0.060
1971	0.828	0.121	0.070	0.450	0.450
1972	0.124	0.060	0.101	0.200	0.470
1973	0.201	0.110	0.151	0.157	0.160
1974	0.134	0.210	0.136	0.382	0.810
1975	0.150	0.040	0.155	0.270	0.290
1976	0.127	0.105	0.084	0.539	0.290
1977	0.230		0.049	0.127	0.100
1978	0.182	0.130	0.022	0.088	0.110
1979	0.163	0.061	0.030	0.019	0.030

Table 6. *Teleia saltuum* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.297		
1953			0.166		
1954			0.162		
1955			0.033		
1956			0.024		
1957			0.042		
1958		0.234	0.018		
1959		0.185	0.112		
1960	0.338	0.500	0.056	0.580	
1961	0.321	0.240	0.040	1.310	0.430
1962	0.111	0.363	0.125	0.590	0.280
1963	0.130	0.360	0.061	3.050	1.450
1964	0.030	0.080	0.028	0.110	0.210
1965	0.040	0.105	0.073	1.210	1.354
1966	0.028	0.143	0.026	0.180	0.270
1967	0.202	0.130	0.046	0.210	0.950
1968	0.680	0.100	0.038	0.420	0.310
1969	0.452	0.215	0.113	0.940	0.391
1970	0.065	0.325	0.060	0.497	0.313
1971	0.169	0.197	0.034	2.340	2.340
1972	0.051	0.050	0.068	1.950	1.200
1973	0.024	0.030	0.006	0.206	0.230
1974	0.013	0.060	0.010	2.274	1.140
1975	0.040	0.010	0.013	0.410	0.190
1976	0.077	0.010	0.008	0.559	0.970
1977	0.080		0.006	0.608	0.670
1978	0.058	0.040	0.007	0.225	0.850
1979	0.041	0.020	0.220	0.010	0.220

Table 7. *Pristiphora laricis* density (larvae/kg)

Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.181		
1953			0.198		
1954			0.352		
1955			0.084		
1956			0.225		
1957			0.887		
1958		1.901	2.587		
1959		1.345	2.657		
1960	0.525	2.500	1.986	4.500	
1961	0.514	0.394	0.949	1.920	2.340
1962	0.929	1.402	2.284	1.880	5.010
1963	0.360	0.400	0.939	1.450	3.730
1964	0.730	0.345	0.262	1.130	2.080
1965	1.820	0.667	1.000	1.160	0.545
1966	2.936	0.642	1.872	0.850	0.880
1967	1.694	2.115	2.477	2.550	0.610
1968	1.952	3.620	3.551	2.985	0.970
1969	1.422	1.720	1.753	2.195	1.278
1970	1.805	1.815	3.198	3.431	3.740
1971	0.562	1.263	2.787	1.430	1.430
1972	0.336	1.335	3.001	1.170	1.840
1973	0.708	2.125	0.739	0.961	1.080
1974	0.239	2.090	0.322	3.010	1.000
1975	4.350	1.710	1.292	2.570	0.530
1976	16.585	4.790	0.247	4.382	0.790
1977	1.730		3.465	1.912	2.110
1978	1.404	1.050	1.988	1.156	1.880
1979	2.878	1.283	1.780	1.942	1.780

Table 8. Significance tests (Chi^2, error probabilities in %) of the immediate or the delayed impact due to defoliation of the larch by the LBM on the fluctuations of the guild members (for further explanation see text).

	Immediate response			Delayed response		
	Yes	No	%p	Yes	No	%p
Exapate duratella	13	2	0.45	14	1	0.08
Oporinia autumnata	11	4	7.07	9	6	43.86
Pt. aeriferana	10	5	19.67	10	5	19.67
Spilonota laricana	5	10	19.67	10	5	19.67
Teleia saltuum	8	7	79.63	8	7	79.63
Pristiphora laricis	11	4	7.07	8	7	79.63

By examining possible immediate and delayed effects of defoliation on the fluctuation patterns of the individual species, one obtains a more revealing insight (Table 8). For ease of interpretation, the fluctuation patterns of the six species are compared to the LBM cycle in the Oberengadin (*Z. diniana*: mean density 58.31 larvae/kg; coefficient of variation (CV) 167 percent), as shown in Figs. 2a and 2b.

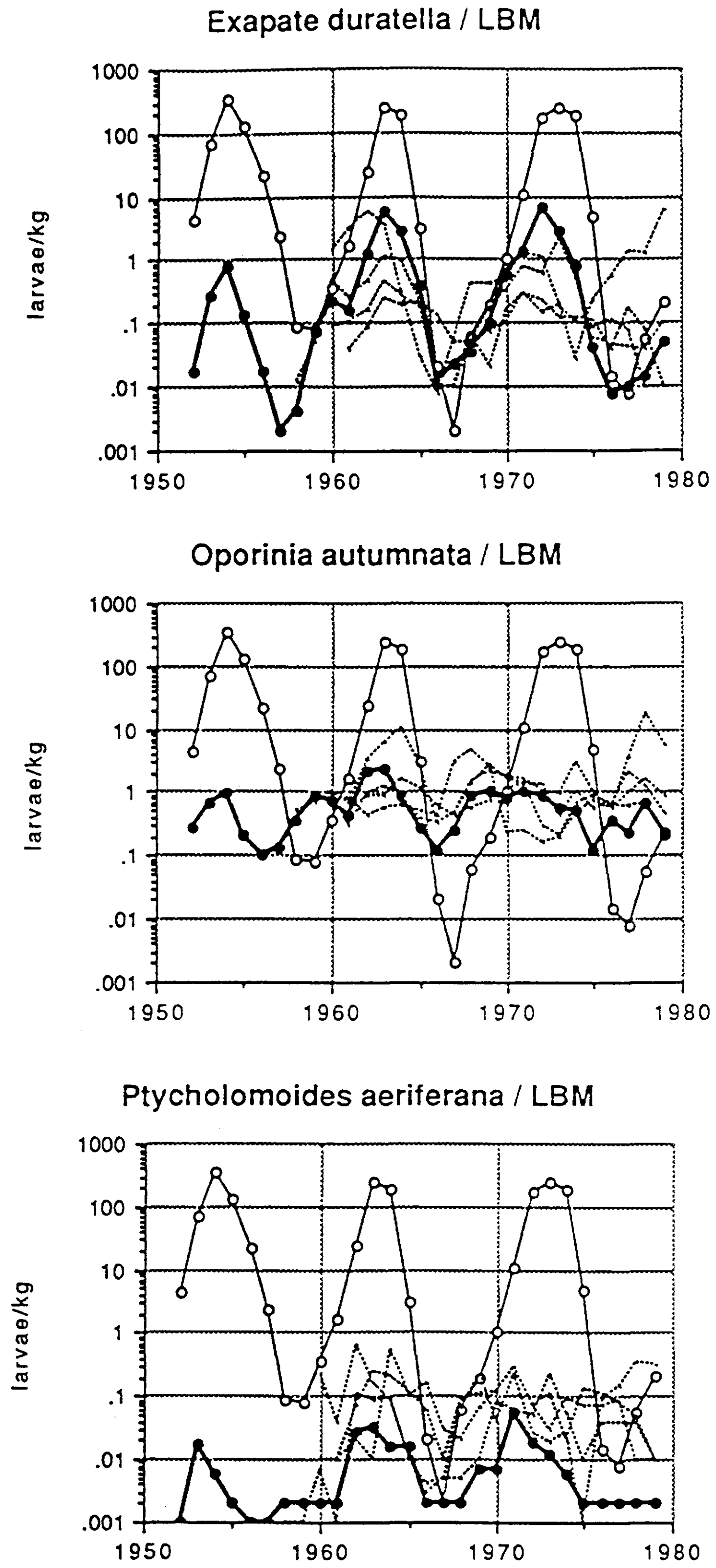
1) *Exapate duratella*. Mean density 0.88 larvae/kg. Exhibits a cycle synchronous to the LBM and of large amplitude (CV 194 percent). The hypothesis of a significant immediate impact is accepted ($p < 0.01$), but there is also a highly significant delayed impact ($p < 0.10$). In two of the three cycles, *E. duratella* exhibits the highest densities of all associated species.

2) *Oporinia autumnata*. Mean density 0.65 larvae/kg; CV 85 percent. In all three LBM cycles, the immediate impact is apparent, but there are three more minor peaks asynchronous with the LBM maxima. This suggests that processes other than the interspecific impact of the LBM (immediate impact: $p = 0.07$), but of similar efficiency, regulate the densities of *O. autumnata*. In the Briançonnais, maximal densities of *O. autumnata* are observed when LBM densities range from 0.3 to 36 larvae/kg.

3) *Ptycholomoides aeriferana*. Mean density 0.009 larvae/kg; CV 136 percent. The fluctuation of the Engadine population suggests coincidence with the LBM cycle, but because in 15 out of 28 years no larvae were recorded, no further comment is made.

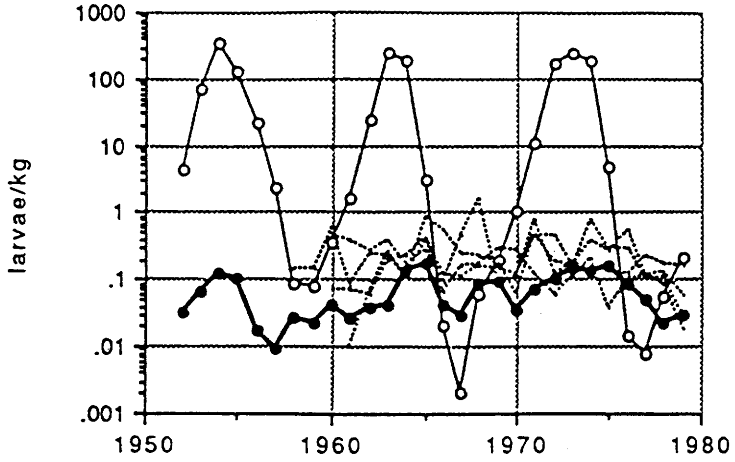
4) *Spilonota laricana*. Mean density 0.07 larvae/kg; CV 70 percent. The species fluctuates at a minor amplitude, so the hypothesis of an immediate impact has to be rejected ($p = 0.20$), whereas the hypothesis of a delayed impact shows an error probability of only 0.07, inclining one toward acceptance.

5) *Teleia saltuum*. Mean density 0.07 larvae/kg; CV 105 percent. Population increases and decreases alternate rapidly and independently of the LBM densities, so both impact hypotheses have to be rejected ($p = 0.80$).

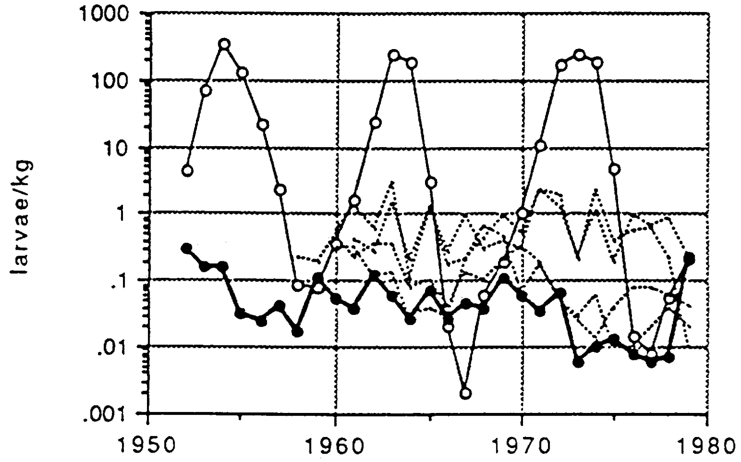


Figures 2a. Fluctuation patterns of guild members on larch from five subalpine regions in the European Alps (•••••) compared with the fluctuations of the larch bud moth (LBM) (o——o) and the relevant species (•▬▬•) in the Oberengadin from 1952 to 1979. Sampling unit: larvae/kg larch twigs.

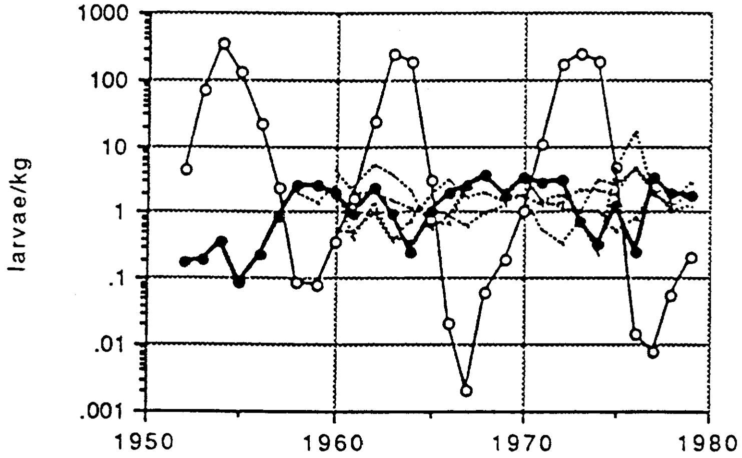
Spilonota laricana / LBM



Teleia saltuum / LBM



Pristiphora laricis / LBM



Figures 2b. Fluctuation patterns of guild members on larch from five subalpine regions in the European Alps (•••••) compared with the fluctuations of the larch bud moth (LBM) (o——o) and the relevant species (●——●) in the Oberengadin from 1952 to 1979. Sampling unit: larvae/kg larch twigs.

6) *Pristiphora laricis*. Mean density 1.54 larvae/kg; CV 73 percent. The fluctuation of Pl in the Engadine (Fig. 2b) suggests that an immediate impact is exerted by the LBM, i.e. the density of Pl is reduced already during the year of defoliation from that of the previous generation. This tendency is confirmed when all the data from the alpine arch ($p = 0.07$) are considered, whereas the hypothesis of a delayed impact is a chance event ($p = 0.80$).

CONCLUSIONS

Analysis of an immediate and a delayed interspecific impact of defoliation of the larch by the LBM on the fluctuation of six guild members reveals that out of 12 possible cases only the two related to *E. duratella* are significant ($p < 0.01$), and two more cases show a mere "close to significant" probability. In spite of methodological constraints, such as the evaluation of densities related to the biology of the LBM and not related to the individual species, or the grossly generalized assumption of the near to complete defoliation of larch forests over large areas, this result is surprising. Although comparison of the fluctuation curves clearly shows a parallel negative population trend (with the possible exception of *T. saltuum*), the nonsignificance is due to the asynchrony in population trends with the cycle of the LBM. This asynchrony is caused by the fluctuations at much lower densities which result in smaller amplitudes. Maximal densities of *Oporinia*, *Ptycholomoides*, *Spilonota*, and *Pristiphora*, which correlate with minimal densities of the LBM or densities well below defoliation threshold, suggest that these guild members are not regulated by interaction with the food quality. This conclusion was confirmed on two occasions when the LBM failed to transgress the defoliation threshold--in the Valle Aurina in 1973 and 1975 (Fig. 3) and Goms in 1972--but the guild members did not deviate from their general pattern of fluctuation. Furthermore, it is interesting to note that, with the exception of *Exapate*, trends indicating an interspecific impact (*Oporinia* and *Pristiphora*) are related to the immediate impact, i.e. to the lack of food and loss of shelter, but not to the delayed impact due to reduced food quality.

Clearly, the folivore guild feeding on larch trees may be classified into two groups: those species which respond to the self-induced change in food quality by a drastic decline in population (LBM and *Exapate*); and those species which lack such a specific response (*Oporinia*, *Ptycholomoides*, *Spilonota*, *Teleia*, and *Pristiphora*). This finding is next discussed as a function of the plant carbon/nutrient balance (Bryant et al. 1988, Tuomi et al. 1988).

Aspects Relevant to the Host Plant

A pioneer species, *Larix decidua* has evolved in harsh climates and environments of low productivity which make for inherently slow growth and are thought to favor the evolution of constitutive antiherbivore defenses (Bryant et al. 1988). Unfortunately, allelochemicals have not yet been investigated in larch needles, but several other criteria serving as food value indices, such as growth rate (Baltensweiler 1984, 1985) and nitrogen and fiber concentrations (Benz 1974, Omlin and Herren 1976), are known to be strongly correlated with growth responses of the larch to abiotic or biotic constraints. As water consumption, photosynthetic capacity, and nitrogen concentrations are positively correlated with each other, the growth rate of needles responds immediately to the prevailing weather conditions. Consequently, growth conditions and nitrogen concentrations are reflected in an integrated manner by the shape of the growth curve and the final length of the needles (Fig. 4). Much more drastic effects on the physiology of the tree are to be expected from defoliation. Late frosts in spring may kill the new needle biomass and necessitate refoliation, whereas early frosts in fall may destroy needles and prevent the resorption of nutrients into the stem. In either case the flush of needles in the following spring remains short and stiff. Precisely the same effects are observed after artificial and/or natural defoliation by the LBM (Benz 1974, Omlin 1980, Baltensweiler 1985). The reduced food value of such needles for lepidopteran larvae is due not only to the physical properties of the needles, but also to their reduced nitrogen content (Benz 1974, Fischlin and Baltensweiler 1979, Omlin 1980). These effects are all in agreement with the predictions derived from the model of plant carbon/nutrient balance (Tuomi et al. 1988).

Aspects Relevant to the Insects

LBM and *E. duratella* display the highest mean densities in the subalpine forests. They both show developmental and behavioral adaptations to low temperatures--LBM in the egg stage (Bakke 1969) and *E. duratella* in oviposition (Baltensweiler 1961)--which enables them to cope successfully with the harsh subalpine environment. But even more relevant in this context are characteristics such as the early hatching, and the feeding of the first two instars close to meristematic plant tissue, which reflects their adaptations to exploit one of the most nitrogen-rich food resources in the subalpine environment (Baltensweiler in prep.).

In contrast to LBM and *E. duratella*, the four guild members *Ptycholomoides*, *Spilonota*, *Teleia*, and *Pristiphora* show highest mean densities on larch near Zürich at 600 m a.s.l. (Auer, unpubl.). *Spilonota*, *Teleia*, and *Pristiphora* are "late season species" (Fig. 1), which means in general that they are obliged to be much more tolerant of low food quality, considering the usual maturational decline in foliar nutrients (Clancy et al. 1988). It is thus not at all surprising that reduced nutritional quality of larch foliage due to LBM defoliation does not constrain the population dynamics of these guild members appreciably. In accord with this conclusion is the finding that the trends in interspecific impact due to LBM defoliation (*Oporinia* and *Pristiphora*) are due more to the immediate impact, which is mainly quantitative lack of food and loss of shelter, and not to the delayed impact, which consists of reduced food quality. These findings, then, allow us to conclude that the trophic interrelation between larch and the two food specialists LBM and *E. duratella* may be interpreted as an adaptation of the insects to the physiologic responses of the larch to its abiotic environment. Thus the hypothesis of a quantitative defense reaction of the larch tree to the impact of specialistic herbivores would violate rules of parsimony.

No specific and detailed studies have been made to determine the processes which might regulate the various guild members on larch in the subalpine region. Information on the fecundity of subalpine populations is scarce (e.g. *P. aeriferana* 51.8 ± 5.08 eggs/female, n = 6). Polyphagy and voltinism would be important mechanisms to buffer the various species against negative impact by the LBM. Parasitism of the guild members has been investigated in order to evaluate their possible role as alternative hosts to *Z. diniana* (DeLucchi et al. 1974, Lovis 1975). Eighty-one species of parasitoids have been obtained from eggs, larvae, and pupae of the associated species. Twenty-nine of these species also parasitize the LBM, but at a very insignificant rate. One hundred and nine species of primary and secondary parasitoids are known from LBM in the European Alps. However, since its 10 most important parasitoids are monophagous, they cannot exert any direct regulative influence on the population dynamics of the guild members (DeLucchi 1982).

We may conclude that five of the six most important species belonging to the folivore guild on *Larix decidua* exhibit population dynamics remarkably independent from the apparently dominant fluctuation cycle of the LBM. These five species have evolved as trophic generalists, whereas the LBM and *E. duratella* have apparently specialized to exploit the most nutritive niche available. Given the longevity of the larch, defoliation by the LBM does not have an excessively detrimental effect on the population dynamics of its host plant. On the contrary, it could be argued that the larch and the biocoenose would on the whole profit from the faster recycling of the needle biomass and its nutrients. This argument needs to be considered by those who would contend that the physiologic reaction of the larch to defoliation is a defensive reaction to folivores which may have evolved through coevolutionary steps.

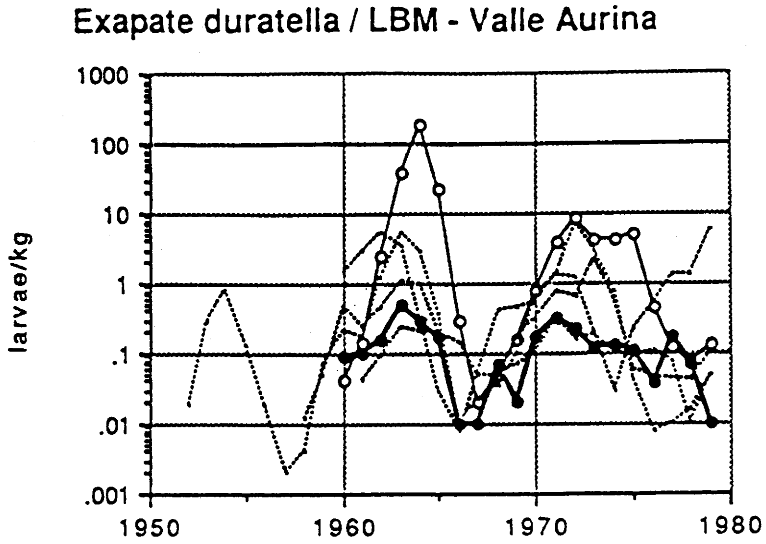


Figure 3. Comparisons of the fluctuation patterns of *Exapate duratella* and the larch bud moth (LBM) in the Valle Aurina (legend as in Figs. 2a and 2b).

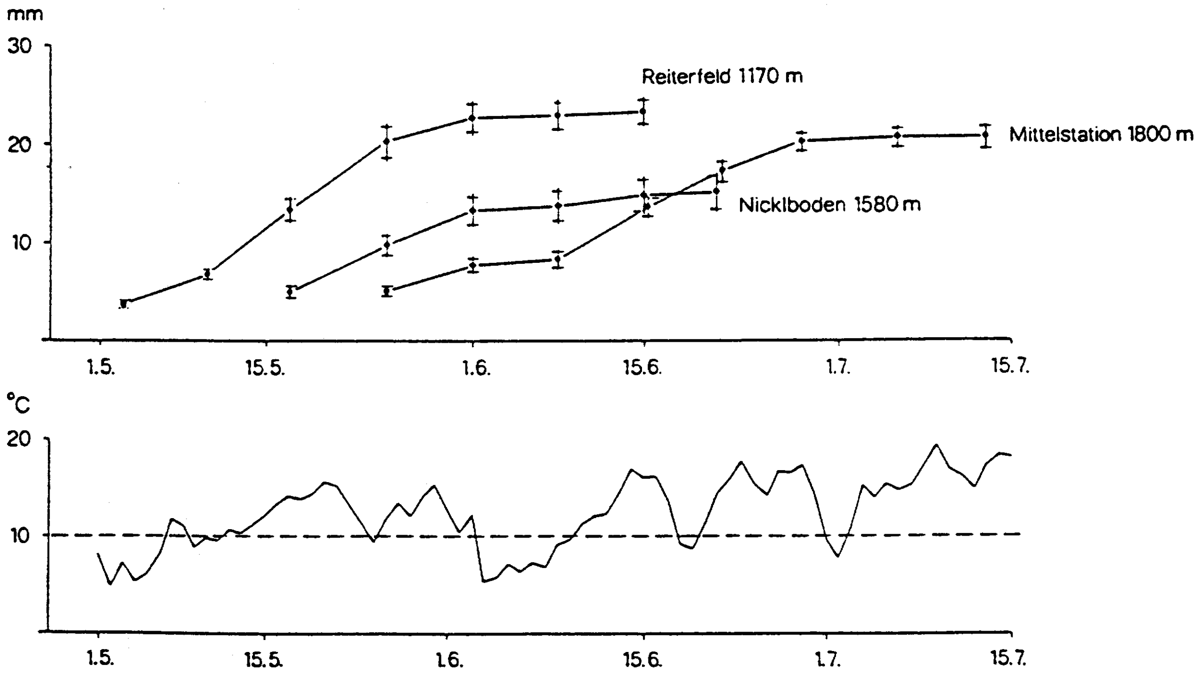


Figure 4. Growth curves of larch needles (mm: x ± s_x) in the Lungau at three altitudes in 1975 compared with the daily mean temperature (station Tamsweg, 1021 m a.s.l., °C, min + max/2).

SUMMARY

Population data obtained from a larval census of the larch bud moth, *Zeiraphera diniana*, and six associated insects feeding on larch needles are presented for five subalpine regions in the European Alps. The fluctuations of these folivore guild members are analyzed vis-a-vis their response to the spectacular periodic defoliation of the larch forests by the larch bud moth. The tortricid species *E. duratella* suffers from a significant impact and exhibits, therefore, a cyclic fluctuation similar to that of the larch bud moth, whereas the other five guild members show a remarkable independence in their fluctuations. It is concluded that their population dynamics in the subalpine zone are not regulated by the variability of the trophic resource, but by different processes. The relationship between the folivore guild and the larch is considered in an evolutionary context.

ACKNOWLEDGMENTS

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OUTBREAK OF ZEIRAPHERA RUFIMITRANA ON SILVER FIR HITHERTO UNKNOWN IN SOUTHWEST GERMANY

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INTRODUCTION

The most important defoliator of the silver fir, *Abies alba*, is *Choristoneura murinana* (Lepidoptera: Tortricidae) (Bogenschütz 1978). The fact that *Zeiraphera rufimitrana* H.-S. (Lepidoptera: Olethreutidae) (Bovey 1978) often occurs simultaneously with *C. murinana* has, in practice, frequently led to misidentification. The larvae of both species feed exclusively on juvenile needles in the upper, sun-exposed tree crowns and cause an identical type of defoliation. Foraged needles discolor reddish-brown in the early summer and are later shed. Once the brown needles have been shed, one can assess the severity of the infestation, over the course of previous years as well as more recently. Damage inflicted by the two species can be distinguished on the basis of morphological and behavioral differences between them. In this paper I present the results obtained from studies pursued since an outbreak of *Z. rufimitrana* in the Black Forest in 1986. It represents the first outbreak of this particular pest observed in southwest Germany to date.

METHODS

The population dynamics of *Z. rufimitrana* can be determined in two ways: 1) indirectly, by appraisal of needle loss on yearly shoot orders, and 2) directly, by studies of population densities of various developmental stages. Both procedures have advantages and disadvantages. The indirect method is universally applicable, allowing a relatively large area to be surveyed quickly. The direct method can be applied only during a very short, specified time period and is highly work intensive. It is used to determine not only changes in population density but also the factors influencing population dynamics.

Using the indirect method, we examined a stand on the western slopes of the Black Forest which had been severely damaged in 1988. The age of the trees in the stand ranges from 95 to 115 years. The stand is comprised of 85 percent silver fir, the remainder divided between beech and oak and has an average height of 23 m. Sloping to the southeast, it lies at roughly 550 m above sea level.

In the winter of 1988-89, two field assistants using binoculars appraised the degree of defoliation in the discernible portions of the crown. Damage estimates based on yearly growth were rated in three categories: 1) low, up to a maximum of 1/3 defoliation, 2) medium, up to a maximum of 2/3 defoliation, and 3) high, up to complete defoliation. In addition to the stand thus assessed, a heavily infested selection forest with a high proportion of silver fir was singled out in the upper Black Forest

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region, at about 850 m above sea level. In both of the stands, direct methods were used to collect data on population dynamics. To determine the density of the hibernating eggs, it is necessary to fell the sample tree. Sample branches from the upper crown area were then searched for eggs under the microscope. To determine the density of the descending larvae, a procedure was used whereby funnel traps (0.25 m^2), whose containers were filled with litter and humus, were placed directly under the tree crowns. In 1989, the year our data were collected, the feeding period was completed in the first half of June. Larvae were collected from the crown on different dates during the feeding period to determine the degree of parasitism, either by dissection or by rearing.

RESULTS

In the forest district of Staufen the outbreak of *Z. rufimitrana* began in 1986. The years following showed a steady increase in the number of trees attacked, the area of infested stands approximately 600 ha in 1988, and the intensity of defoliation (Fig. 1). The eggs were found singly or in small groups between the bud scales of the year's shoots and to a lesser degree, between the scales at the base of the male flowers. Shoots located in the upper half of the crown were favored. In the initial phase of the study, we removed branches from the uppermost eight to 12 branch whorls of four dominant or codominant trees and sampled 10 shoots, both middle and secondary, from each whorl.

The number of eggs found on each branch whorl sampled fluctuated greatly (Fig. 2), especially in the two uppermost whorls. Below the eighth branch whorl a clear reduction in egg numbers was found. As a result, the survey of fir stands will be limited to the third through seventh whorls, thereby yielding a sample of 5 x 10 = 50 shoots per tree. Table 1 shows that the rather consistent results obtained from four sample trees in the forest district of Staufen. In contrast, the results obtained from the forest district of St. Blasien showed greater variability. It must be noted that in the latter area, the old sampling method, examining the full upper crown, was still used. However, the order of magnitude of the results coincided in both regions.

Less than half of the eggs found during the winter were intact and consequently developed to young larvae in the spring. On the average 8 or 11 percent respectively had a black discoloration. These eggs had been parasitized. The remaining eggs were empty (Table 2).

Table 1. Egg density.

Forest district	Number of sample trees	Eggs/shoot			
		Min.	Max.	$\bar{x}$	s
Staufen	4	10.2	13.7	12.3	1.6
St. Blasien	9	4.0	13.3	7.4	3.6

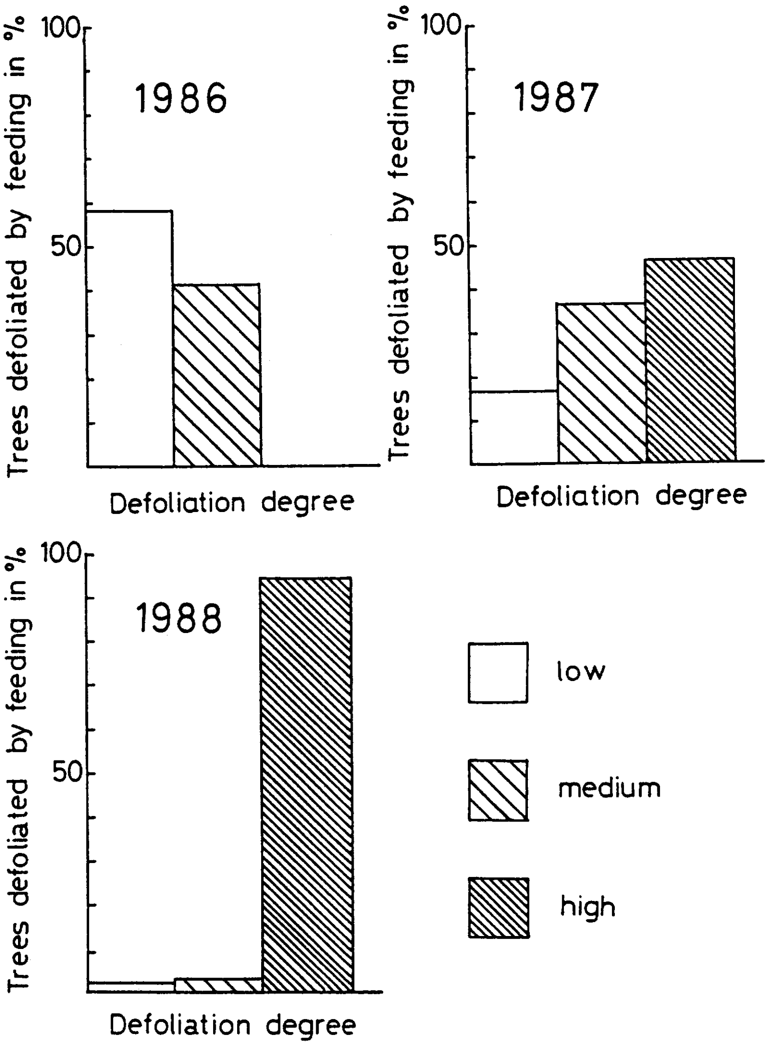

Figure 1. Increasing defoliation by *Zeiraphera rufimitrana* in the forest district of Staufen.

Table 2. Condition of the eggs.

Forest district	Number of eggs	Ratio (%)		
		Healthy	Paras.	Empty
Staufen	4085	29.8	8.4	61.4
St. Blasien	3514	42.7	10.9	46.4

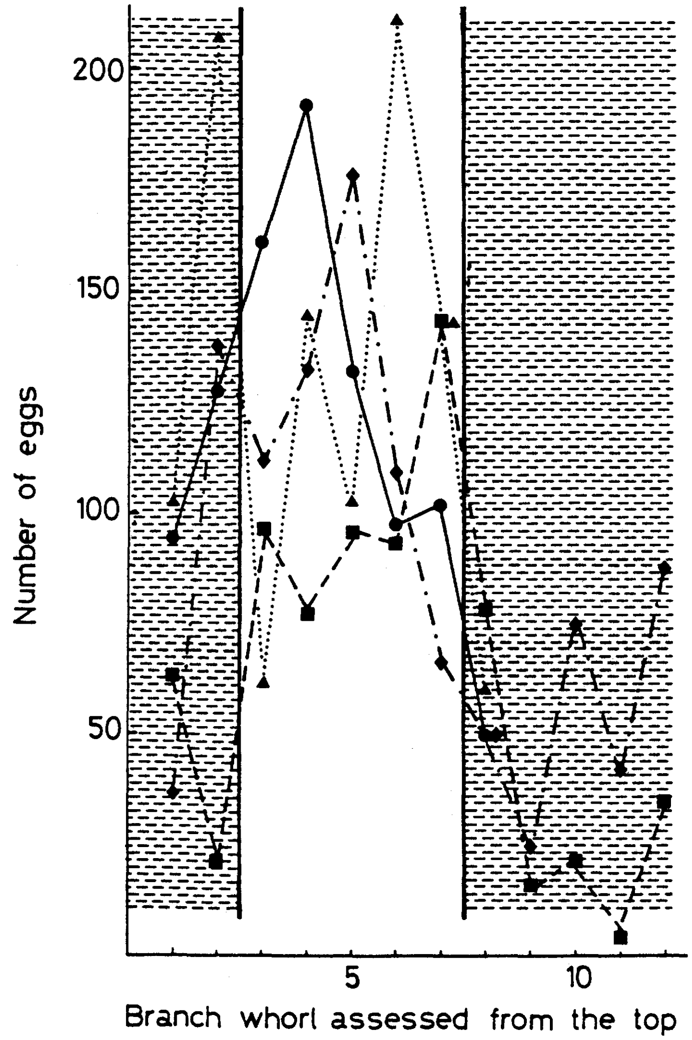

Figure 2. Distribution of the egg density (eggs/shoot) of *Zeiraphera rufimitrana* within the crown of four individual silver fir trees (whorl 1 was uppermost).

Table 3. Density of the descending larvae.

Forest district	Number of funnel traps	Larvae/m^2
Staufen	45	15
St. Blasien	9	110

Although egg density did not differ much in the two study areas, the number of descending larvae per m^2 sampled at Staufen was only 14 percent of the amount sampled at St. Blasien (Table 3).

Although parasitoids have been found to be important factors in the mortality of the larvae, they are not responsible for the different population declines. At least two hymenopterous species produced notable degrees of parasitization, reaching almost 60 percent (Table 4), but they have yet not been identified. Species 1 is a parasitoid originating from former larval instars. It leaves the host during or prior to the fourth instar to spin a cocoon in the crown. Species 2 to 4 were found relatively seldom. Species 5--an ectoparasite of late larvae--had a degree of parasitization of up to 50 percent. Parasitoids of pupae were also found.

Table 4. Parasitization of the larvae (estimated by dissection).

Forest district	Sampling date	Larval instar (%)					Total paras. (%)	Frequency per species in % of the total parasitization				
		L1	L2	L3	L4	L5		1	2	3	4	5
Staufen	08/05/89	77	9	12	2	0	32	100	0	0	0	0
	24/05/89	0	0	13	74	13	43	92	0	0	8	0
	08/06/89	0	0	1	8	91	59	16	0	0	0	84
St. Blasien	19/05/89	3	19	29	47	2	39	95	2	3	0	0
	29/05/89	0	0	17	61	22	40	93	0	7	0	0
	20/06/89	0	0	0	3	97	43	5	0	3	0	92

DISCUSSION

As with *C. murinana*, the regional distribution of *Z. rufimitrana* corresponds with the distribution of its host *Abies alba*. Since 1945 five outbreaks have been documented, occurring both within and outside the natural habitat of the silver fir (Fig. 3). These outbreaks have a noticeably broad elevational range, from sea level to 1400 m, and occupy an area extending from northern Germany to northern Italy, a fact which indicates that outbreaks of *Z. rufimitrana* are not site specific. That is further verified by the current outbreak in southwest Germany, where numerous isolated populations have been discovered, occurring in different growth zones each in turn possessing a broad range of site conditions (Fig. 4). The type of stand management applied, furthermore, had no influence on the outbreaks, which were detected both in even-aged monocultures and in mixed forests. Outbreaks can usually be found on mature and overmature trees. Defoliation occurs exclusively on the sun-exposed portions of the tree crowns. Because of its obvious attraction to warmth, we can assume that climatic conditions are a factor in outbreaks of *Z. rufimitrana*. Tests are currently being conducted to determine whether a positive correlation exists between extraordinary weather conditions and outbreaks of *Z. rufimitrana*.

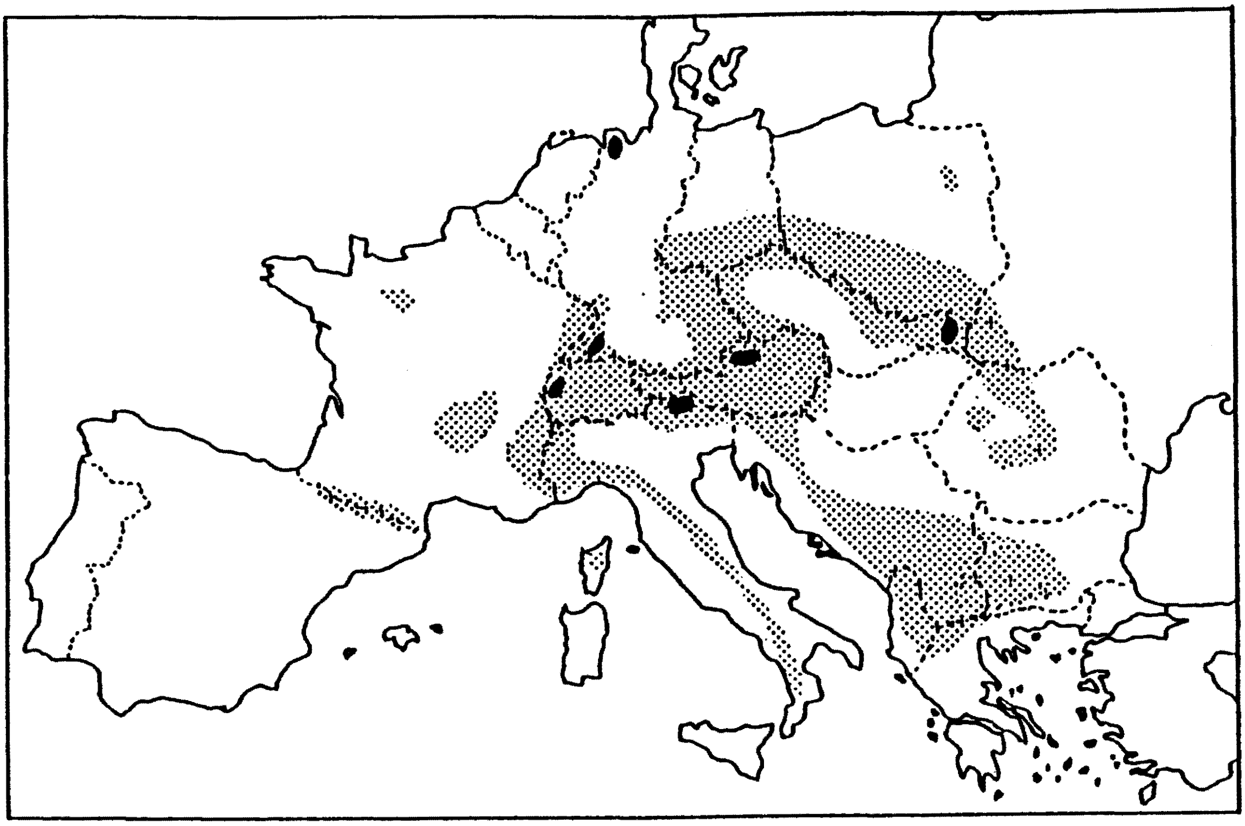

Figure 3. Natural habitat of *Abies alba* (dotted area) and zones of outbreaks of *Zeiraphera rufimitrana* since 1945 (shaded black).

The outbreak of *Z. rufimitrana* in the forest district of Staufen began in 1986, and a noticeable decline in the damage was observed in 1989. That means that the culmination of the defoliation in 1987 and 1988 was followed by a collapse of the population in the fourth year of the outbreak. A clear population decline has been shown in the differences between the densities of the eggs and the larvae. Effective parasitism is one reason for this decline. Other factors may be the lack of synchrony of the larval hatching and the budding of silver fir, or the influence of predators, especially on the stages descending to or living on or in the ground. Future studies should concentrate on these factors about which we know little as yet.

Another question to be studied arises from the empty eggs found in winter. Had the larvae already hatched in summer or fall, or had they been emptied by a predator? The fate of eggs prior to the winter is currently being researched.

SUMMARY

The first observed outbreak of *Zeiraphera rufimitrana* was recorded within the natural habitat of the silver fir in southwest Germany in 1986. The larvae feed exclusively on needles of May shoots. By assessing needle loss from preceding shoot orders, it is possible to reconstruct the course of the outbreak. The peak of the outbreak was observed in two districts within the Black Forest in 1988. Although egg counts reached 12.3 and 7.4 eggs per shoot respectively in the two districts, only 15 and

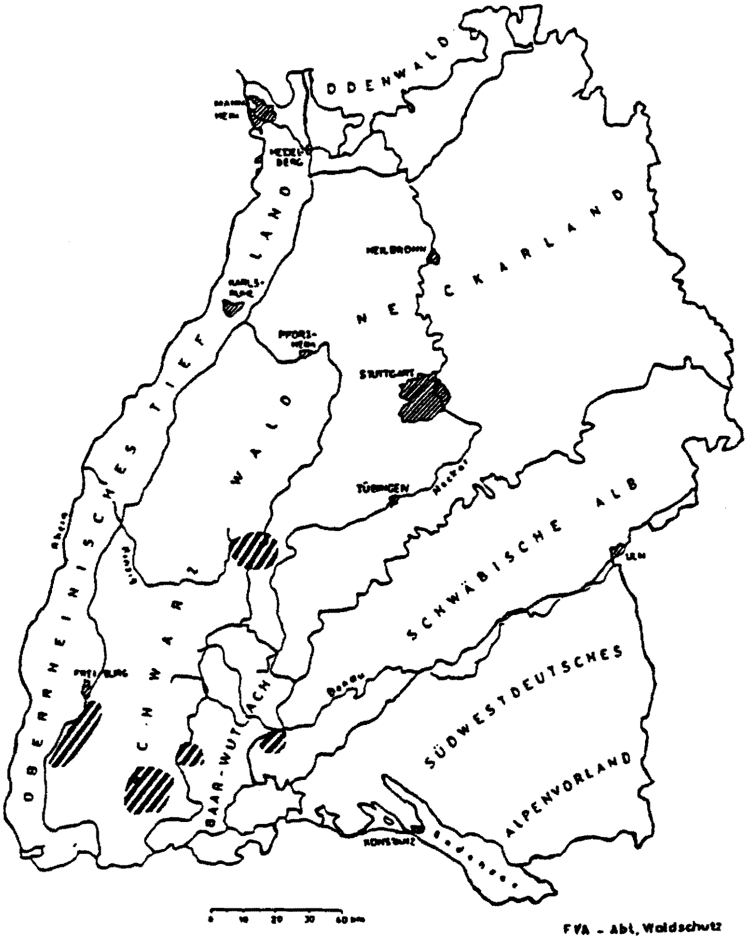

Figure 4. Growth zones of Baden-Württemberg and a real distribution of *Zeiraphera rufimitrana* outbreaks (hatched area) since 1987.

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110 larvae per m^2, respectively, reached the pupal stage. Parasitoids accounted for a substantial portion of the decrease in population density, with a mortality rate of 8 to 11 percent of the eggs and 43 to 59 percent of the larvae parasitized. Additional factors relating to mortality are discussed.

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AN INSECT OUT OF CONTROL? THE POTENTIAL FOR SPREAD AND ESTABLISHMENT OF THE GYPSY MOTH IN NEW FOREST AREAS IN THE UNITED STATES

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INTRODUCTION

The gypsy moth, *Lymantria dispar* L., was introduced from Europe into North America near Boston, Massachusetts, in 1869, and is now well established as a serious defoliator of forest, shade, and fruit trees over much of the eastern United States. Despite substantial efforts to eradicate, contain, or control this pest, the gypsy moth has persisted and continues to extend its range. The generally infested area currently extends from the northeast corner of North Carolina along a diagonal line that extends through Virginia, West Virginia, and the northeast corner of Ohio into Michigan. These five states are referred to as the transition zone, and states to the east of this line represent what is referred to as the generally infested area. A vast area of suitable habitat for the gypsy moth, much of which is valuable commercial hardwood forest, lies to the south and west of the generally infested area. This paper assumes that the gypsy moth will if not checked expand its range into that area and therefore proposes a management strategy for preventing this from occurring.

THE HISTORICAL RECORD

The original infestation increased and spread gradually until, by the summer of 1889 (30 years after its introduction), the insect was so abundant and destructive that it attracted public attention. The first outbreak encompassed forested lands that included 30 towns and cities in the greater Boston area and prompted the state of Massachusetts to implement an intensive program to eradicate the insect. The program was so successful in reducing the infestation that the state legislature chose to abandon the effort in 1900. Many people considered that action to be a fatal mistake.

During the next 5 years, gypsy moth populations increased tremendously in Massachusetts and new infestations were subsequently discovered in the neighboring states of Rhode Island, New Hampshire, Vermont, and Connecticut. From 1906 to 1912, the federal government financed the importation of natural enemies of the gypsy moth from several European countries and from Japan

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(Brown and Sheals 1944). Efforts to prevent the shipment of gypsy moth-infested products into outlying areas were intensified and led eventually to enactment of a federal domestic quarantine against the insect in 1912. The quarantine has been modified over the years, but remains in effect today and credited with greatly reducing the accidental long-range transport of gypsy moth on regulated commodities.

Between 1906 and 1920, the gypsy moth spread westward at an estimated rate of 9.6 km a year. Isolated infestations were discovered on estates in New York, New Jersey, and Ohio. In 1923, a barrier zone extending from Canada to Long Island and encompassing some 27,300 km^2 was established through a cooperative effort by the federal government and the state of New York to prevent the westward spread of the insect. Infested territory to the east of the zone was to be treated by the responsible state; infestations found within and to the west of the barrier zone were to be eradicated. Despite these efforts, the barrier zone became generally infested by 1939, and the effort was terminated in 1941.

Gypsy moth infestations seemed to explode in 1951-52, when 0.6 million ha were defoliated, as a result of which yet another thorough appraisal of the problem was made by state and federal officials.

A seven-point plan to re-establish the barrier zone was formulated in 1953, and the Congress made funds available to initiate an eradication program using DDT in 1956. By 1958, defoliation by the gypsy moth was recorded on only 50 ha within the totally infested area. However, concerns about the environmental persistence of DDT became paramount and use of the chemical was discontinued. Hopes of eradicating the gypsy moth were abandoned and a long-overdue emphasis was placed on research. The areas of infestation and defoliation increased substantially thereafter, which provided impetus for accelerated programs of research on the gypsy moth beginning in 1971 and continuing to the present.

MEANS OF SPREAD

Current distribution and spread of the gypsy moth in the United States (Fig. 1) is a product of both the natural spread of wind-blown first-stage larvae, and the inadvertent human transport of life stages from the generally infested area throughout the U.S. Historically, the extent of artificial introduction has probably been underestimated and the significance of natural spread overestimated. The following discussion offers a synthesis of what is known about both methods of spread.

Windblown Dispersal of Larvae

The distance that newly hatched larvae can disperse has been a controversial question for years. Early workers were convinced that long-distance dispersal of larvae was widespread in the Northeast and that larvae were readily blown up to 40 km by the winds (Collins 1917). However, Mason and McManus (1981) concluded that in nonmountainous terrain 99 percent of airborne larvae would be deposited within one km of their source. Even in mountainous areas, where mechanical turbulence and updrafts are more pronounced, an atmospheric dispersion model predicted that most larvae would be deposited within 3 km downwind.

Taylor and Reling (1986) conducted extensive aerial sampling of first-stage larvae over heavily infested ridges in Pennsylvania and suggested that 0.3 percent may get the opportunity to travel up to 19 km in one episode. More recently, Fosberg and Reling (1986) modeled the dispersal of gypsy moth larvae in mountainous terrain using a three-dimensional wind and dispersion model with real time climatological data from coastal California. Their model predicted that larvae would be carried aloft and transported more than a few hundred meters in only 2 percent of the cases. When long-range transport did occur, larvae were deposited 7 to 21 km away, but in very low concentrations. The

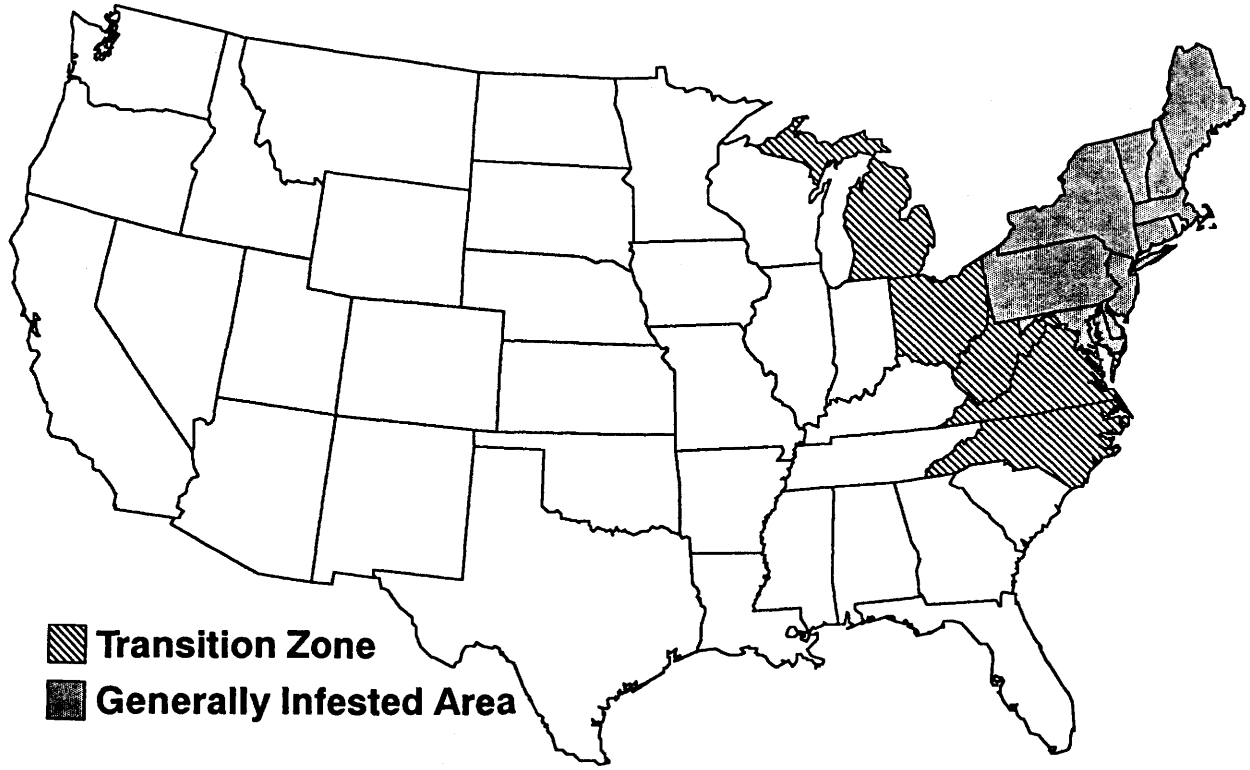

Figure 1. Current gypsy moth distribution

evidence suggests that although some larvae may be transported long distances when source populations are dense and hatch periodicity and optimal meteorological conditions are synchronized, most larval dispersal is a relatively short-range phenomenon. Support for this conclusion can be found in the documented record of isolated infestations that have occurred beyond the generally infested area. Of more than 264 isolated infestations that have been detected by the Animal and Plant Health Inspection Service, only 47 (18 percent) exceeded ca. 2.6 square km (1 sq mi) in area, even though these incipient populations may have persisted for several years prior to their detection. This suggests that under normal circumstances, the extent of larval dispersal and subsequent survival is minimal.

We recognize however that the Appalachian mountain range has been a factor in the accelerated rate of natural dispersal of the gypsy moth to the south. Susceptible ridgetop stands favor gypsy moth reproduction and survival, and complex wind fields associated with mountainous terrain increase the probability of greater dispersal. In the generally infested area, larval dispersal probably accelerates the redistribution and coalescence of local populations that have already begun to increase over broad areas.

Inadvertent Introduction of Life Stages

State and federal officials recognized in the early 1900s that spread of the gypsy moth out of the infested area around Boston was expedited by the transport of egg masses and other life stages on vehicles and commodities carried by major roads and thoroughfares. This led to enactment of a federal quarantine against the insect in 1912. Despite that regulatory effort, infestations were again discovered far beyond the infested area. In retrospect, it appears that the gypsy moth was probably introduced and reintroduced into both contiguous and distant areas and yet went undetected since there were no pheromone traps in those years and scouting for egg masses at low densities was and is an imperfect science.

The dimensions of the problem are best demonstrated by reviewing the circumstances of an isolated infestation detected in Somerville, New Jersey, in 1920. This infestation originated from a separate introduction of infested blue spruce trees from the Netherlands in 1910, prior to enactment of the federal quarantine. At the time it was discovered, the infestation was scattered over 1,040 km^2 around Somerville. A record of shipments of trees from the Somerville estate indicated that, prior to 1921, 261 shipments had been sent to 15 states from Connecticut south to Florida and west to Minnesota and Missouri. Follow-up inspections revealed that the shipments had led to new infestations in at least three of the states. The Somerville infestation was finally eradicated in 1931 at a total estimated cost of $2.5 million (Felt 1942). When one considers that this incident involved only commodity originating from a single small infestation at a time when transportation was somewhat limited, one can better appreciate the magnitude of the task to contain the gypsy moth today.

The regulatory quarantine is still in effect, although it has been modified over time to emphasize detection of life stages in commercial household moves. Historically, most new infestations have been traced to the transport of life stages on backyard furniture and related articles (dog houses, firewood, recreational equipment). Under new regulations implemented in 1983, shipments of household goods from designated high risk areas through or into nonregulated areas must be inspected at the point of origin and certified free of gypsy moth life stages.

Since 1980, California officials have initiated an aggressive program to supplant the federal quarantine on gypsy moth since they see the insect as a serious threat to the fruit and nut industry in the state. The California Department of Food and Agriculture maintains 16 border stations where personnel conduct inspections of recreational vehicles (campers, motorhomes, boat and house trailers) entering the state and identify shipments of household goods from states known to be infested by the gypsy moth. Recreational vehicles are known to be carriers of gypsy moth life stages. A survey conducted by APHIS in 1980 determined that 33 percent of all RVs leaving seven infested New Jersey campgrounds were carrying gypsy moth life stages. Under the California program, shipments of household goods are allowed to proceed through the border station but inspection of all outdoor items is conducted by destination county commissions after the moving van is unloaded. Documented results of this program are dramatic in that they illustrate the enormous potential for artificially introducing the gypsy moth into one of the most distant states from the generally infested area (Fig. 2). More than 2,000 interceptions of gypsy moth life stages from 14 states and Canada have been recorded since the program began in 1980. Most of the border interceptions occurred on recreational vehicles, although from 70 to 210 interceptions annually were recorded from county inspections of household goods at their destination. Egg masses were the life stage most frequently encountered, and in approximately 38 percent of the cases the life stages encountered were viable. As a result of this concerted effort to exclude the gypsy moth from California, the number of established infestations requiring treatment with pesticides declined from 10 in 1983 to only one in 1987, thus saving California taxpayers millions of dollars in treatment costs. The state estimated the cost of chemically treating the 10 infestations identified in 1983 at $1.5 million.

The increasing number of interceptions recorded since 1980 is obviously related to the extent and severity of the initial infestation in the generally infested area (Fig. 3). The number of interceptions recorded annually on recreational vehicles at California border stations, coupled with the fact that from 26 to 30,000 shipments of household goods from infested areas have been logged annually since 1984, demonstrates the potential for introduction of the gypsy moth into previously uninfested states (Fig. 4). These data also suggest that the gypsy moth is repeatedly being introduced into states both adjacent to and far removed from the generally infested region.

Since 1978, pheromone traps have been used extensively to detect isolated infestations throughout the United States and serve as the basic tool of the regulatory program. When pheromone traps are deployed according to APHIS protocols (1 trap/9 sq mi, depending on the terrain, setting, whether forest or residential, and so forth), new infestations are frequently detected and delimited within 2 to 3 years of their establishment and can then be more readily eliminated. As mentioned earlier, 72 percent of new infestations are less than 2.6 km in area when they are delimited. Those more extensive infestations that have been discovered in recent years in the states of Oregon (1984), Idaho (1987), and Utah (1988) apparently went undetected for several years because those states did not deploy a systematic grid of pheromone traps. The success of state detection programs is contingent upon the intensity of the trapping effort that each state initiates and maintains.

FACTORS THAT LIMIT ESTABLISHMENT IN NEW AREAS

Based on the statistics previously cited from the California gypsy moth exclusion program, there is no doubt that gypsy moth life stages have been transported to many uninfested states every year and that the number of such incidents has increased dramatically since the 1980-82 outbreak in the generally infested area. Yet judging from the relatively small number of infestations that have occurred and required APHIS to apply eradication treatments, we have to conclude that the probability of the gypsy moth becoming established in new areas is quite low. If this were not the case, the gypsy moth would by now, undoubtedly, have become entrenched in the oak-hickory and oak-pine forests throughout North America and in residential areas from coast to coast.

HOST AVAILABILITY AND SUITABILITY

In this section we attempt to elucidate those factors that affect the establishment of gypsy moth in new areas and will ultimately determine the future distribution of the insect in North America.

Unlike most other forest defoliators, the gypsy moth is a polyphagous insect that can feed successfully on over 200 species of trees that grow in the continental United States. Historically, however, outbreak areas have been characterized by an abundance of preferred host species, mainly oaks and aspen. Given the known distributions of oak-hickory and oak-pine types in the United States, the gypsy moth has the potential for establishing itself and thriving in several states to the south and west of the current generally infested area. The severity of the problem will be exacerbated by the availability of the contiguous forested area occupied by preferred food species, mainly oaks. The state of Pennsylvania, for example, contains over 4 million ha of oak forest, especially along the Appalachian mountain range that traverses the state. The state has experienced repeated outbreaks since 1970, as the gypsy moth has slowly spread to the south and west. Since oak remains the dominant species in Pennsylvania forests, the gypsy moth will be a recurring problem there in the years ahead. Similarly, the oak-pine forests on Cape Cod, Massachusetts, have sustained severe and repeated episodes of defoliation since the early 1900s and are still considered highly susceptible. Missouri, Tennessee, Kentucky, and West Virginia contain extensive areas of oak forests and have been identified as susceptible to the gypsy moth. The unglaciated regions of several midwestern states also contain extensive forests of oak and other susceptible species.

States further west and south have not been considered at risk to the gypsy moth because in them coniferous forests predominate. Hardwood species, including oaks, are scattered throughout these forests, however, especially along the waterways, and there they offer a suitable habitat for the gypsy moth. A case in point is Lane County, Oregon, where in 1987, 121,000 ha of mainly Douglas-fir forest were treated to eradicate an extensive but isolated infestation of gypsy moth that went undetected for several years. This infestation was successfully eliminated over a period of 3 years during which state/federal agencies applied multiple Bt treatments to the residual population.

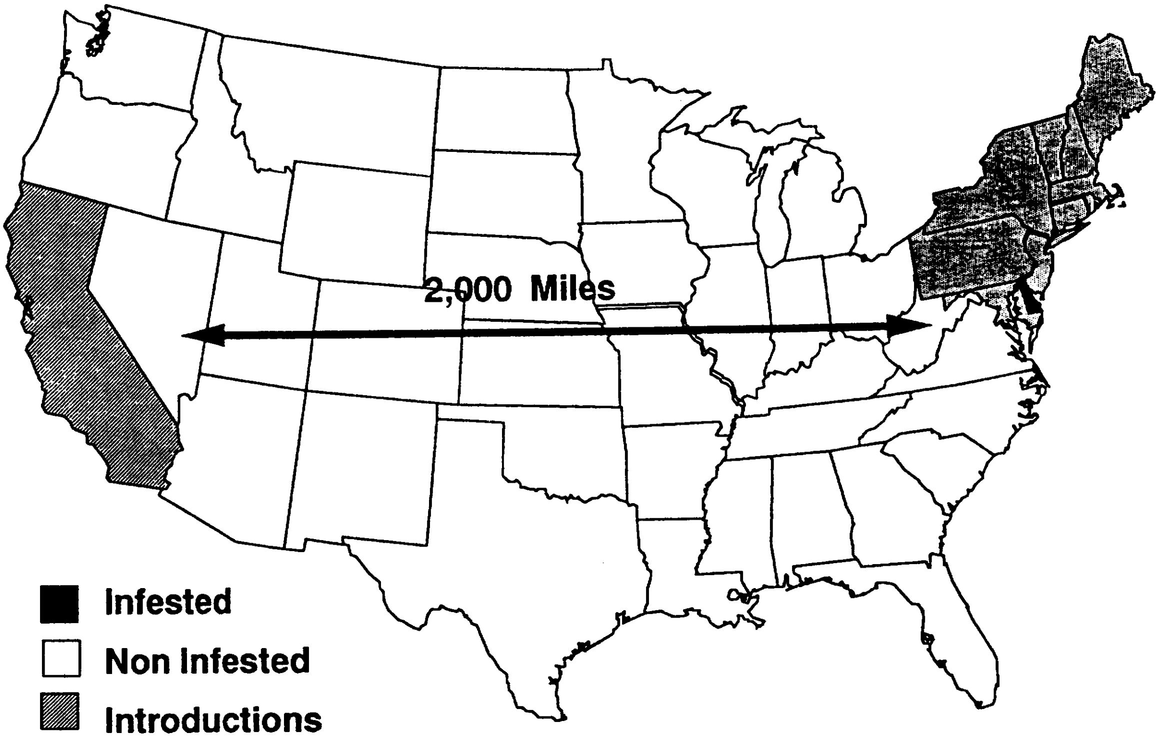

Figure 2. Introduction of gypsy moth into California

We must emphasize that although host availability may restrict the geographical extent of the problem when the gypsy moth is introduced beyond the natural range of oak, most successful establishments in places far removed from the generally infested region occur in urban residential areas and result from the introduction of life stages on household goods. In these areas, extensive plantings of preferred food species such as oaks, aspen, and ornamental fruit trees can support the establishment and expansion of gypsy moth populations.

Although considerable effort has been directed toward defining the range of host suitability for gypsy moth (Mosher 1915, Barbosa et al. 1983, 1986, Lechowicz and Mauffette 1986, Miller and Hanson 1989), most of these studies have been restricted to laboratory preference tests conducted on individual tree species common to the eastern United States. These studies confirm that although gypsy moth feeding preferences are extremely catholic, many tree species are not favored or rarely fed upon, such as black locust, *Robinia pseudoacacia*, ash, *Fraxinus* spp., and yellow poplar, *Liriodendron tulipifera*.

In general, the range of host suitability is narrowest for the early larval instars and broadest for the late larval instars, which can successfully feed and complete their development on most hardwoods and conifers. We do not fully understand the suitability of all species to all instars, especially when host switching occurs in the field. Gansner and Herrick (1985) reported on the preferences of gypsy moth for host species exhibited in the defoliation that occurred over a 5-year period on 575 plots in Central Pennsylvania. Although their data provide an index of preference, the results were somewhat compromised because less than half of the plots sustained moderate to heavy defoliation (> 30 percent), and that occurred in one year. Consequently, hemlock, a coniferous species readily defoliated

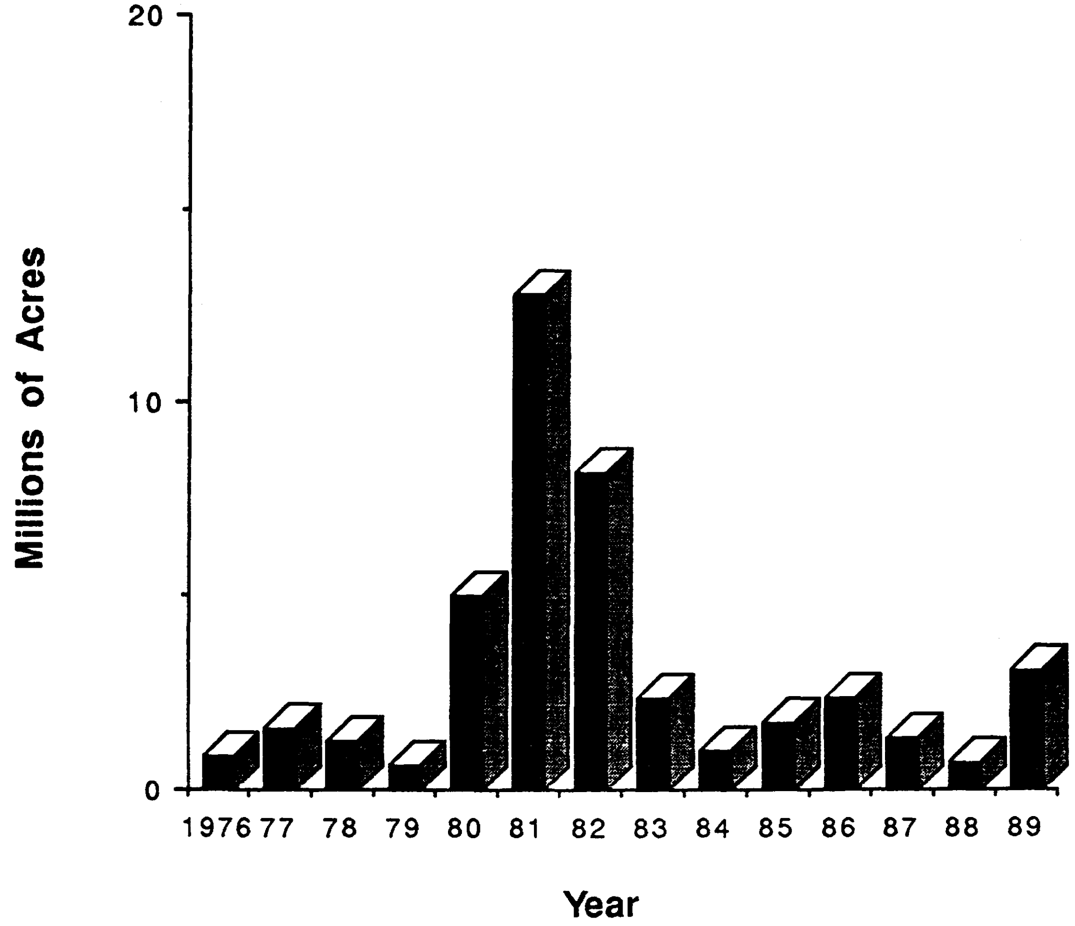

Figure 3. Acres defoliated by gypsy moth

by the gypsy moth and among which mortality often results, was the least preferred species in their study. This suggests that host preference in the field will be affected by initial distribution of the gypsy moth, relative density of the population, and proximity to other infested stands. There are still many unanswered and puzzling questions. For example, Barbosa et al. (1983) found that gypsy moth larvae reared on sweetgum, *Liquidambar styraciflua*, had the shortest developmental period, the highest pupal weights, and the largest mean fecundity, yet we observe mature native sweetgum trees in Maryland that are fully foliated while adjacent oaks are completely stripped. Obviously, more research is needed on gypsy moth/host plant relationships.

OTHER FACTORS

In addition to host availability and suitability, other variables such as climate, natural enemies, and losses due to dispersal affect the successful establishment of gypsy moth life stages that have been introduced into new areas. Given the known distribution of the gypsy moth worldwide (Giese and Schneider 1979), the insect is probably capable of surviving anywhere in the United States where

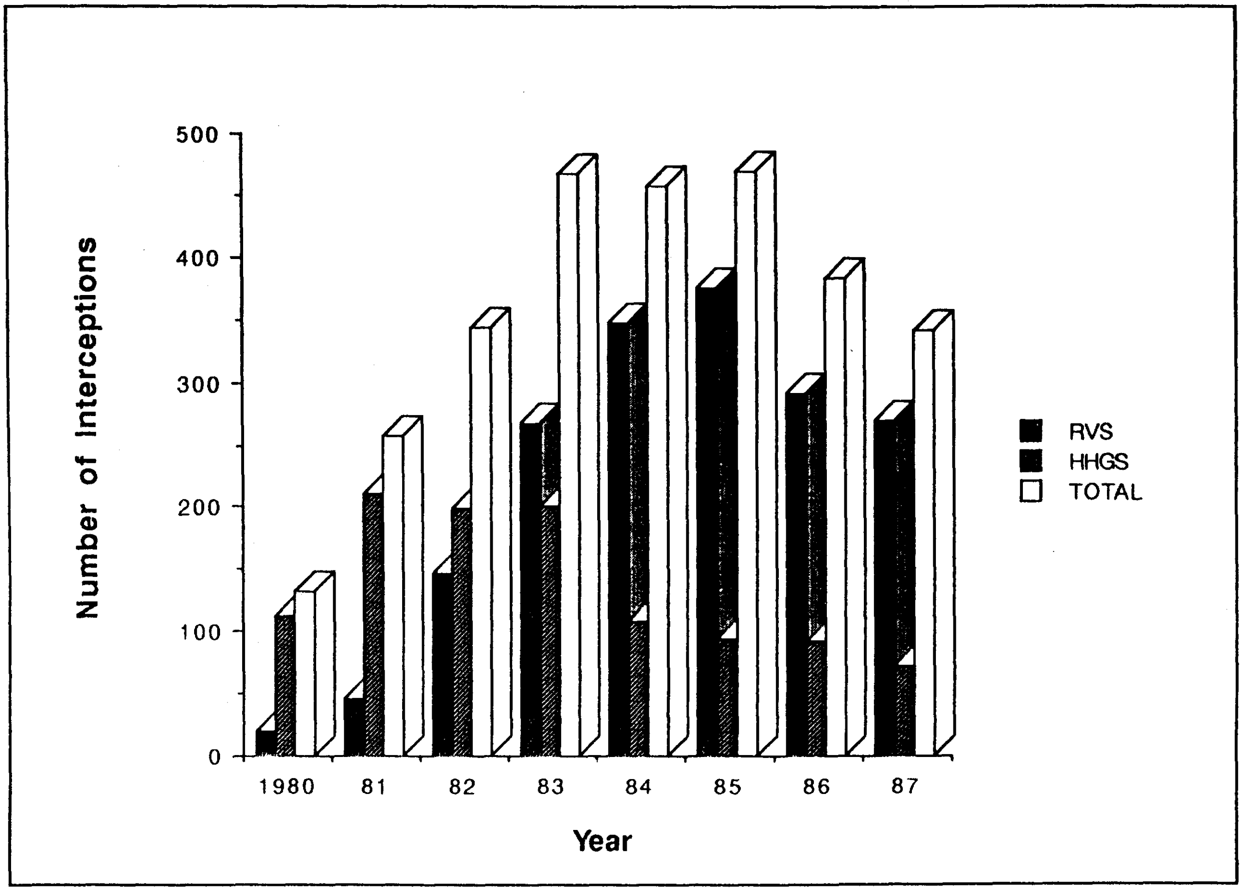

Figure 4. California interceptions from 1980-1987

suitable hosts exist. The gypsy moth is distributed as far north as Leningrad (60 N), as far south as North Africa (30-32 N) and the Far East (20 N). However, the area where periodic outbreaks occur lies between 0 and 50 E. longitude and 40-55 N. latitude and typically receives 25-100 cm of precipitation annually. Since the continental U.S. lies between 25 and 50 N. latitude, climate should not be a major factor limiting establishment by the gypsy moth.

The gypsy moth has an obligatory egg diapause whereby the egg stage must experience a period of exposure to chilling below a threshold temperature (ca. 5°C) in order to satisfy diapause requirements prerequisite to successful eclosion. The egg stage is better protected against severe cold than against mild or fluctuating temperatures. Outbreaks have occurred as far north as southern Quebec, where Madrid and Stewart (1981) concluded that lack of hosts in the province to the north are more limiting to the insect than extreme winter temperatures.

Experience with isolated infestations in the Pacific Northwest, Santa Barbara, California, and in Myrtle Beach, South Carolina, indicates that diapause requirements were satisfied in these climatically marginal areas. However, eclosion occurred much earlier in the spring and extended over a period of 4 to 8 weeks. This fact complicates the timing of eradication treatments and usually warrants repeated applications of pesticides at intervals throughout the hatch period.

Although we know little about the fate of gypsy moth life stages in new habitats, recently both parasitism and predation of life stages have been documented in instances where sterile insect releases were made to eradicate isolated infestations. In Berrien County, Michigan (1983), birds, especially blue jays, preyed heavily on releases of sterile male gypsy moths; in Bellingham, Washington (1985), where sterile eggs were released, 21 percent of the larvae collected had been parasitized by either *Cotesia melanoscelus* or *Compsilura concinnata*. Pending information from detailed studies, we can only assume that a complement of generalist parasites and predators or their ecological equivalents would attack the gypsy moth in isolated infestations.

One would think that passive dispersal of first-stage larvae would result in a high incidence of larval mortality. Hatching larvae frequently rest on or near the egg mass for hours if not days without feeding when meteorological conditions are not conducive to their dispersal. The longer they are prevented by adverse weather from dispersing, the more subject they are to predation and the lower their chances of successfully establishing on suitable foliage. Periods of rain can also drown the first-stage larvae. Windblown larvae must first survive the physical environment during the dispersal process, then locate and establish on suitable foliage after they are deposited. Airborne larvae are particularly vulnerable to desiccation. In a study by Taylor and Reling (1986), those larvae that had been collected aerially were all dead. Larvae deposited in hostile or nonforest environments obviously will not survive. The probability of establishment of those first-stage larvae that do reach forested environments is largely dependent upon the structure and composition of the vegetation in the area where they are deposited. Although estimates of gypsy moth mortality attributed to larval dispersal are not available, estimates are available for the eastern spruce budworm, another passively dispersed species. Miller (1958) estimated that the average mortality rate of first-stage budworm over a 6-year period was 64 percent and varied from 48 to 82 percent. Dispersal losses were greatest in open, mature stands and least in dense, middle-aged stands.

Many if not most introductions of gypsy moth life stages do not produce new infestations, and many factors acting in concert probably contribute to the demise of the gypsy moth in these remote situations. This conclusion is supported by the relatively few isolated infestations that have been reported in the past 13 years despite the large number of artificial introductions that apparently occur annually in states as far removed as California.

POTENTIAL IMPACT OF GYPSY MOTH ON FORESTS TO SOUTH AND WEST

On review of the approximate range of the oak-hickory and oak-pine forests beyond the currently infested area, it is apparent that there is abundant, highly suitable gypsy moth habitat to the south and west. A workshop held in West Virginia in 1987--"Coping with the gypsy moth in the new frontier"--was organized to provide the latest information on forest effects and management strategies to forest managers in states along the advancing front. This update was deemed necessary because the forests in the "new frontier," the Appalachian region, contain both a large oak component and a more valuable timber resource than those previously inhabited by the gypsy moth. In order to understand the potential impact of the gypsy moth on forests, we must shift our thinking from effects on individual trees to effects on stands of trees.

Stand Susceptibility

The term "susceptibility" refers to the potential for a forest stand to be defoliated by the gypsy moth, while "vulnerability" is the probability of mortality occurring after a stand has been defoliated. Bess et al. (1947) classified forest stands in New England as susceptible or resistant to defoliation on the basis of species composition and their history of disturbance. Species composition is the single most important factor that determines a stand's susceptibility; the higher the basal area in oaks and other preferred species such as aspen and birch, the more susceptible is the stand. Houston and

Valentine (1977) recognized the need to identify in advance of the gypsy moth those forest stands that are likely to be defoliated often and those where tree mortality is likely to be significant. They used ordination techniques to compare forest stands based on certain structural tree features known to influence gypsy moth larval behavior and survival and larval host food preferences. Later, Valentine and Houston (1984) developed discriminant functions for identifying mixed-oak stand susceptibility based on the measurement of diameters of preferred host trees and those trees that possess deep bark fissures or bark flaps between the ground and 1.83 m (6 ft). Herrick and Gansner (1986) also developed a rating system based on the basal area of oaks and that of trees with good crown condition. Mason (1987) reviewed both rating systems and provided an in-depth discussion of the merits of both approaches. It is important to recognize that susceptible stands are probably defoliated both more frequently and more severely than stands designated as resistant. However, Bess et. al. (1947) noted that resistant stands can be defoliated if they are adjacent to susceptible ones; furthermore, resistant stands that incur severe defoliation can themselves become more susceptible.

Stand Vulnerability

Stands defoliated by the gypsy moth have incurred tree mortality, growth loss, and changes in understory composition (Hicks and Fosbroke 1987). The magnitude of these impacts depends upon the number and severity of defoliations on individual trees. When trees are defoliated 50 to 60 percent or more, they respond by refoliating in midsummer. This creates stress on trees and predisposes them to attack by secondary agents (other insects and pathogens) that are the direct cause of subsequent mortality. Other stresses such as drought or frost along with site and stand conditions and incidence of secondary organisms, contribute to tree mortality and complicate the task of predicting the vulnerability of individual stands.

Although the results of studies to assess mortality after episodes of gypsy moth defoliation and to rate stand vulnerability have been somewhat variable, we can make some statements on which there is a consensus: 1) stands that contain the most oak incur the highest mortality; 2) trees that sustain two or more moderate to heavy defoliations (> 60 percent) are most likely to die; 3) trees with poor crown conditions are more vulnerable to defoliation than healthy trees; and 4) there is a "first wave effect" such that stands in newly infested areas realize the highest mortality rates after their first severe episode of defoliation. This pattern held true in New England (Campbell and Sloan 1977), New Jersey (Kegg 1973), and Pennsylvania (Quimby 1987) and appears likely to occur in the mid-Atlantic states of Maryland and West Virginia.

It is difficult to compare the published results of these studies because losses are expressed variably as value loss per acre, volume of pulpwood and sawtimber, dead trees per acre, or basal area per acre. Campbell and Sloan (1977) summarized results from the first major outbreaks in New England (1911-1931) and reported that the mortality of oak was 48 percent of total basal area and ranged from minor losses to catastrophic losses in some stands. In the aftermath, species composition of the stands was altered; they contained fewer oaks and more nonfavored species. Gypsy moth outbreaks still occur in these stands, but do not result so much in mortality as in deterioration of growth, yield, and wood quality.

The first severe outbreak in New Jersey occurred from 1968 to 1971 on the Newark watershed, where stands sustained 3 consecutive years of defoliation (> 75 percent). Net basal area loss was 44 percent; by 1972 oak mortality had reached 63 percent and another 28 percent of stems was left in declining condition (50 percent or more of canopy dead). Gansner et al. (1983) and Herrick and Gansner (1988) measured changes in forest conditions after gypsy moth defoliation in northeastern and central Pennsylvania and concluded that oak basal areas were reduced in both areas, but that timber stands outgrew most losses. These studies concentrated on the effects of defoliation on timber volume and value over a broad resource area rather than on individual stands, and since less than 40 percent of the plots in central Pennsylvania experienced even one year of moderate to heavy defoliation, mortality was properly not anticipated.

In another Pennsylvania study, where appraisals were conducted only on forest land known to have sustained repeated defoliations and tree mortality, Quimby (1987) reported tree mortality rates of 27.6 percent for pulpwood and 32.5 percent for sawtimber over nearly 350,000 acres, and 51.3 percent for both pulpwood and sawtimber over another 341,000 acres. Summer droughts during the period from 1980 to 1983 were thought to exacerbate the defoliation stress and resultant mortality. Preliminary reports on tree mortality in the ridge and valley system in western Pennsylvania and from the panhandle of West Virginia suggest that oak mortality is variable by species, but exceeds 25 percent in most areas (Twery, pers. comm.). Collectively, these studies indicate that oaks are most vulnerable to gypsy moth defoliation and incur the highest mortality rates. However, there is no consensus on which species of oak are most affected nor on whether trees growing on poor, stressed sites are more vulnerable to defoliation than those occupying better, mesic sites.

Although forest managers are primarily concerned about mortality, we should not discount the effects of defoliation on growth loss and regeneration. Hicks and Fosbroke (1987) have reviewed this subject and discussed the need to develop models from site and stand data that can predict mortality after episodes of defoliation. By linking stand vulnerability with susceptibility models, forest land managers can develop a basis for sound pest management decisions.

As the gypsy moth moves into the oak-pine forests of the South and the mixed-hardwood stands of the Midwest, questions arise about the dynamics of the insect in these stands and its ultimate impact. Several midwestern states are using available susceptibility models to rate their stands in advance of the gypsy moth. Although the species composition of these stands is more diverse, the native oak species are similar to those found in the generally infested area; consequently, these models may adequately classify stand susceptibility.

The picture in the South is more complex because oak-pine mixtures there consist of conifers and oaks that do not occur in the susceptible oak-pine stands of southern New Jersey and Cape Cod. At a recent conference on the management of pine-hardwood mixtures, presentations by Gottschalk and Twery (1989) and Montgomery et. al. (1989) synthesized what is known about the impact of gypsy moth on pine-oak stands to the north and discussed implications for management of these commercially important stands in the South.

In 1988-89, the Gypsy Moth Research and Development Program funded several projects designed to evaluate the suitability of native southern species to the gypsy moth both in the lab and in field plots established along the advancing front of the infestation. Similar evaluations are being conducted in the highly susceptible native aspen stands of central Michigan. These studies will provide data needed by forest managers to assess the potential susceptibility and vulnerability of stands in newly infested areas.

It seems likely that the gypsy moth will indeed continue to spread south and west until it runs out of suitable hosts. While large areas of southern pine will undoubtedly be resistant to defoliation, extensive commercial forest lands to the south and west of the currently infested zone are at considerable risk. Affected states must be prepared either to alter stand composition to reduce their susceptibility/vulnerability or to apply pesticide treatments more extensively than we are now capable of financing. If these management costs are deemed prohibitive, then we should consider initiatives to slow or even halt the spread of the gypsy moth in the immediate future.

CONTAINMENT: A VIABLE OPTION THEN AND NOW

Historically, there has been considerable debate on the merits of instituting a containment policy. Detractors say that since the natural spread of the moth cannot be halted, containment efforts would be futile and, furthermore, the cost of such a program would be prohibitive. Proponents argue that every year that a state remains uninfested translates into savings in pest management costs and spares the citizenry a year's worth of nuisance and damage.

Major programs have been undertaken to eradicate, control, or contain the gypsy moth since it was introduced into North America (Perry 1955). As mentioned earlier, the barrier zone that was deployed from 1923 to 1942 is credited with restricting distribution of the gypsy moth to New England east of the New York line. Felt (1942) estimated that maintenance of the barrier zone cost $210,000 annually. In 1940, the chief of the Bureau of Entomology and Plant Quarantine commissioned a blue ribbon committee to conduct a thorough appraisal of the gypsy moth problem. The committee's report strongly urged maintaining the barrier zone to prevent the spread of the moth to the central hardwood, southern Appalachian, and Piedmont regions (Korstian and Ruggles 1941), but funding for the barrier zone was drastically reduced in 1941, when resources were redirected to the war effort.

In 1952, a study group appointed by the Secretary of Agriculture initiated a program to assemble the facts needed for evaluation of the problem and for determining a future combative policy (Perry 1955). A seven-point plan for the prevention of spread and reduction in damage was formulated, including re-establishment of the barrier zone. The plan was implemented to the extent permitted by available funds, but eventually discontinued. In 1978 the Expanded Gypsy Moth Program initiated a contact with Ketron, Inc. to develop a cost/benefit analysis for gypsy moth containment. The report (Blacksten et al. 1978) concluded that significant expenditures are justified even to slow the spread of the moth and that the existing APHIS program projected a quite favorable benefit/cost ratio.

The advancing front of gypsy moth infestation is now located in the states of Michigan, Ohio, West Virginia, Virginia, and North Carolina. Any further advances into the next tier of states will greatly increase the cost of control and magnify proportionally the area from which artificial introductions can emanate. The 1952 appraisal documented that between 50 and 80 percent of the forest land in the states of Ohio, Tennessee, Kentucky, and Missouri was classified as susceptible to gypsy moth damage, based on proportion of favored food species, dry sites, poor stocking, and a history of land abuse. Clearly, there is much at risk beyond the advancing front.

A meeting of state and federal officials was recently held in Raleigh, North Carolina, to discuss the feasibility of containment given available technology and current distribution of the insect. A series of recommendations was drafted, one of which states that "a comprehensive research, development, operational plan should be developed that is specifically designed to culminate in a containment trial." The group concluded that containment is a potentially viable management strategy because of the limited mobility of the insect and because of the existence of a number of technologies that could be utilized in a containment program.

In essence, a containment program already exists. In 1988, the Appalachian Integrated Pest Management Program (AIPM) was implemented in a 38-county area of Virginia and West Virginia encompassing 5.2 million ha. One of the stated goals of this project is to minimize the spread of the gypsy moth through the AIPM area. A 2-3 km grid of pheromone traps is used to monitor populations throughout the project area. Data from these traps provide a measure of the distribution of the gypsy moth and identify areas where more intensive surveys are needed to detect possible outbreaks. Control tactics can then be deployed against spot infestations before they expand and cause economic damage. Treatments in the designated "transition zone" (Fig. 1) are analogous to the tactics used in the barrier zone in New England, though the pheromone traps now being used are far superior to the labor intensive practices used earlier. Furthermore, whereas treatments in the barrier zone consisted of creosoting egg masses and ground spraying with lead arsenate (neither of which is environmentally acceptable), we now have at our disposal biological and chemical pesticides, sterile insects, and pheromone technology that are environmentally acceptable by today's standards.

For those who may be skeptical that biological pesticides alone can eradicate an established infestation, three aerial applications of Bt coupled with intensive pheromone trapping to delineate residual populations were successful in eliminating the large infestation in Oregon over a 3-year period beginning in 1984. The area requiring treatment declined from 225,000 a in 1985, to 190,000 a in 1986, and to 12,000 a in 1987, when only 40 male moths were trapped. By expanding the existing AIPM pheromone trap network in Virginia and West Virginia through North Carolina to the east and through Ohio to the west, we could establish a containment zone within which gypsy moth populations could be delineated and suppressed as deemed necessary.

Perhaps the greatest deterrent to a containment strategy is the lack of a concerted federal commitment. At present, the Animal and Plant Health Inspection Service (APHIS) maintains the federal regulatory quarantine mainly by regulating the shipment of household goods out of the infested region and by detecting and eliminating isolated infestations, but funding for APHIS programs has not kept pace with inflation and their success has been compromised. APHIS programs must be continued and strengthened. As argued in the Ketron report, an effective containment strategy must be implemented to eliminate all artificial spread and eliminate natural spread. There must also be a federal commitment to provide the funds needed to suppress gypsy moth populations along the advancing front when densities exceed a threshold level. This is lacking in the current federal policy providing states only with matching funds. During actual outbreaks, funds available to the states are sufficient to treat only the highest priority forested lands.

To offset the high cost of containment, states in the second and third tiers beyond the advancing front should contribute to the effort as an investment in the future. A projected cost of $10 million per year is much more affordable when divided between 12 or more states as opposed to the five that make up the advancing front.

In the final analysis, if the costs are not prohibitive, the technology is adequate, and a shared state and federal commitment is made, there is every reason to believe that a containment program to slow the spread of the gypsy moth can be successful. Moreover, if we maintain the gypsy moth status quo for 5 to 10 years, there is a good possibility that ongoing bio-technological research will provide us with more effective tools for coping with the gypsy moth problem.

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INTEGRATING HOST, NATURAL ENEMY, AND OTHER PROCESSES IN POPULATION MODELS OF THE PINE SAWFLY

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INTRODUCTION

Explanation of population dynamics is one of the main problems in population ecology. There are two main approaches to the explanation: the factor approach and the dynamic approach. According to the first, an explanation is obtained when the effect of various environmental factors on population density is revealed. Such analysis is performed using well developed regression methods (Poole 1978). The resulting regression equations can be used for prediction of population density and their coefficients indicate the role of each factor in population change. This method of explanation considers the population as a black box with inputs and outputs. Population predictions obtained by regression are relevant only for stationary systems and only if mechanisms of population dynamics do not change.

The dynamic approach is oriented to the analysis of mechanisms of population change. It can predict the consequences of deliberate change of these mechanisms and, thus, it is more useful for population management than the factor approach. The dynamic approach deals with a system consisting of a population and its environment, a life system (Clark 1964). When applying the dynamic approach one must distinguish between factors and processes. A factor is a characteristic of the life system state. Clark et al. (1967) used the term "codeterminant" instead of "factor." But I prefer the term "factor" because its has became traditional in ecology. A process is a flow of similar ecological events that are taking place in a life system. Reproduction, mortality, growth, development, and migration are examples of ecological processes. There exist different mortality processes in each population. These processes correspond to different developmental stages of dying organisms and to different causes of mortality. For example, spontaneous larval and pupal mortality of a certain insect are different processes. Also, population decreases caused by predation and parasitism are the result of two different processes.

Life tables are widely used for the analysis of mortality in animal populations (Harcourt 1969, Varley et al. 1973). In these tables, mortality processes are termed as "mortality factors." This term is quite ambiguous because it includes both death processes and the factors affecting the rate of this process (Sharov 1985). But factors and processes cannot be identified for two reasons. First, there is no one-to-one correspondences between them. For example, insect mortality caused by predation depends not only on predator density but also on prey density, refuge capacity, temperature, and other factors as well. Temperature is a factor affecting the rates of many other processes: growth, reproduction, migration, and so on. Second, factors which influence the process rates may interact so that mortality levels cannot be attributed to individual factors. Thus, we reject the term "mortality factor."

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A life system can be described formally by a simulation model which uses the information about factor influence on process rates and factor change in the course of ecological processes. Simulation models are considered to be the basis for scientific explanation of population dynamics (Clark et al. 1967, Berryman 1981). But the behavior of a simulation model is often difficult to explain like the behavior of a real population.

Therefore, in practice the explanation of population dynamics is usually based not on simulation models but the statistical analysis of life tables. Using k-factor analysis one can reveal key mortality factors (Varley and Gradwell 1960, Podoler and Rogers 1975). Regression methods allow us to distinguish density-dependent factors which are believed to play a regulative role in population dynamics (Morris 1959, Varley et al. 1973). These methods have two main drawbacks. First, they use the term "mortality factor" which, as has been shown, leads to wrong interpretation. For example, temperature and humidity are usually not given in life tables and, therefore, they cannot be key factors despite their strong effect on population. Second, traditional methods of life table analysis do not provide us with sufficient information about life system structure. For example, the regulative role of ecological process in population dynamics is evaluated on the base of its density dependence, while ignoring its interaction with other processes. The possibility that density regulation is performed by process interaction is not taken into account. Thus it is not surprising that in many relatively stable populations, density dependent factor have not been revealed (Dempster 1983). The fact that some mortality factor is a key or density dependent one tells nothing about what will happen after its deliberate change.

Thus the dynamic approach, in spite of its advantages as compared with the factorial one, does not provide methods for evaluating factors and processes in population dynamics.

In this work I attempt to evaluate the role of factors and processes depending on their contribution to quantitative characteristics of population dynamics. This method allows us to reveal the role of process interactions.

Two approaches (empirical and simulational) can be applied in the analysis of the role of factors and processes in population dynamics. Using the empirical approach one should change factor values or process trends in the real life system and then consider the response of quantitative characteristics of population dynamics. In the simulational approach such experiments are simulated by a computer mathematical model. The latter approach is less expensive. Moreover, it is possible to simulate such changes of the life system that are not possible or not desirable in practice. However, the simulational approach is indirect, its precision depends on the validity of a simulation model. In this work we use the simulation approach.

The proposed method of a population analysis is applied to the common pine sawfly, *Diprion pini* L., a dangerous pest of pine plantations. It overwinters as an eonymph (prepupa) in cocoons in the litter or the upper soil layers. Eonymphs having visible rudimentary pupal eyes are called pronymphs. There are 2 to 34 percent pronymphs among hibernating sawflies (Avramenko 1970). Overwintered sawflies have two flight periods: late April to early May and late July to early August (Sharov and Safonkin 1982). Sawflies hibernated as pronymphs emerge in both periods (about 60 percent in the first period and about 40 percent in the second period), while sawflies hibernated as eonymphs emerge only in the second period (about 35 percent). The remaining eonymphs maintain their diapause during the next whole year or longer.

Female sawflies oviposit into a split made along the edge of the pine needle. Eggs laid by one female usually occupy a needle cluster (Dusaussoy and Geri 1966). Larvae hatched from an egg cluster form a colony. In July eonymphs make cocoons in pine crowns and from September to October in the litter and soil. Emergence of sawflies from summer cocoons nearly coincides in time with the second flight period of the overwintered generation. Thus in August there are larvae of the first and second generations. To avoid confusion, we use the term "wave of development" instead of "generation."

Sawflies developing in May to June belong to the first wave of development, and the sawflies developing from August to October belong to the second wave. In the Rostov region the common pine sawfly has outbreaks of mass reproduction within 3 to 6 years (Kharlashina 1984). Outbreaks usually follow those years with hot, dry summers.

METHODS

Simulation Modelling

The model proposed in this paper is based on our previously published data on the life cycles and survival of the common pine sawfly and its parasitoids (Sharov 1982, 1983, 1986b, 1987, 1988, Sharov and Safonkin 1982). Principles of modelling were adopted from the model of winter moth (Varley et al. 1973). The mean temperature in May to September is an input variable. Parameters of the model were partially taken from experimental data and partially found by the maximum likelihood procedure. The model validity was evaluated on a qualitative level by its ability to predict pest outbreaks. Information about sawfly outbreaks in the Rostov region (Kharlashina 1984) and temperature from 1956 to 1983 were used as a test.

Quantitative Characteristics of Sawfly Population Dynamics

Sawfly population dynamics as a whole was characterized by the mean level and standard deviation of a log-transformed (natural logs) late-instar larvae density in the second wave of development. Pest density in the first wave of development has not been considered because it was smaller than the density in the second wave. Log-transformation is necessary because of a log-normal distribution of population density. Mentioned characteristics were estimated using the simulation of a population dynamics. The real mean temperature from May to September during the 28-year-period from 1956 to 1983 was taken as an input variable.

The population dynamics pattern of the common pine sawfly is complex because of repeated outbreaks of the pest. We analyzed each period of an outbreak separately. Isaev and Khlebopros (1974) distinguished five periods in the phase portrait of an outbreak cycle of forest insect pests: period of stability, increase, maximum, collapse, and depression. The common pine sawfly has a very short period of maximum, and thus we considered only the other four periods.

The period of stability is characterized by coefficients of m- and v-stability (in previous publications (Sharov 1986a) they were called coefficients of buffering and homeostasis, respectively), describing different aspects of population density regulation. They were estimated using the simulation model with the mean temperature from May to September being constant and equal to 18.6°C, which is the average temperature in non-drought years. Let $\bar{x}$ be the mean log-transformed late-instar larvae density in the second wave of development and $\bar{z}$--the mean log-transformed larvae survival in the same wave of development before the measurement of population density. In both cases, averaging was performed across a number of years. If the value $\bar{z}$ becomes lower due to additional mortality, the value $\bar{x}$ decreases. The coefficient of m-stability is defined as

$$MS = (d\bar{x}/d\bar{z})^{-1} \qquad (1)$$

It indicates how difficult it is to suppress the population density. The greater its value, the more additional mortality is needed for population suppression.

Another important aspect of population regulation is the v-stability, which prevents the increase of the amplitude of density fluctuations. It is described by the coefficient of v-stability:

$$VS = (ds^2_x/ds^2_z)^{-1} \tag{2}$$

where s^2_x and s^2_z are variances of the log-transformed sawfly larvae density, x, and the log-transformed survival, z . When s^2_z is infinitesimal and the system is in a stable state, then:

$$VS = s^2_z/s^2_x \tag{3}$$

The rate of an increase of sawfly density at the beginning of the outbreak is characterized by the index $\ln(N_o/N_s)$, where N_s and N_o are late-instar larval densities in the second wave of development per 1 m^2 in the period of stability and during the outbreak, correspondingly. The rate of density decrease at the period of population collapse is characterized by the index $\ln(N_o/N_c)$, where N_c is the larval density after an outbreak.

Rates of population density fluctuation were estimated using the simulation model. We assumed that the mean temperature from May to September was 18.6°C and it did not change from year to year (the period of stability); then it increased up to 21.1°C for only one year (the simulation of a drought) and after that it was stable at the initial level. The density N_s was measured in the year before the drought, N_o in the next year after drought and N_c in the second year after drought.

In a period of depression of a sawfly population, drought generally does not cause repeated outbreak; if it does, outbreak is less intensive. This property is characterized by the coefficient of "refractoriness"

$$R = \sum_{i=2}^{4} \ln(N_o/N_i) \tag{4}$$

where N_o is the larval density in the next year after the first drought and N_i is the same density in the next year after the second drought which happens i years after the first drought. For i more than 4 the refractory effect is lost. The coefficient R was estimated using the simulation model. The drought was simulated by rising the mean May to September temperature from 18.6°C to 21.1°C.

Confidence limits for all quantitative characteristics estimated using the simulation model were found by the following method: a set of versions of the initial model was obtained by independent stochastic variation of the 32 most important parameters of the model. Standard deviations of these parameters were equaled to their standard errors. For selection of adequate model versions the population dynamics was simulated assuming the droughts occurred periodically every 4 years. Then the estimated parasitization rate of sawfly eggs and eonymphs was compared with our empirical data obtained from 1977 to 1979. As a result 10 model versions, including the initial one, were selected for simulation of the dynamics of the sawfly's parasitization rate.

Each quantitative characteristic was estimated using all 10 model versions and then the mean value, standard deviation "s" (in this case it is taken as standard error) and half of the confidence interval "ts" ("t" is the student's criterion for P = 0.05) were found for each characteristic. In the following text half of the confidence interval is given after the signs "±".

Analysis of Process and Factor Contributions to the Quantitative Characteristics of Population Dynamics

The contribution of individual processes and their interactions to the quantitative characteristic y_i of population dynamics was evaluated using the equation:

$$y_i = \beta_o + \beta_1 v_1 + \beta_2 v_2 + \beta_{12} v_1 v_2 + \beta_3 v_3 + \ldots , \tag{5}$$

where v_j is an integer variable indicating the dependence of the j-th ecological process on factors, and β_j is the coefficient representing the contribution of the j-th ecological process or process interaction (if the coefficient has more than one index) to the value y_i. The variable v_j has only two meanings: $v_j = 1$ if the rate of j-th process naturally depends on factors and $v_j = 0$ if this rate is fixed at the equilibrium level peculiar to the period of stability. Process rates were fixed only in that period of an outbreak cycle, in which we wanted to examine the role of these processes. The value y_i was estimated using the model with different combinations of processes having the fixed rate. Then coefficients β_j were obtained by the multi-factor regression technique (Maximov 1980).

The "refractoriness" of the sawfly population is associated with a special postoutbreak state of the life system. We analyzed what factors peculiar for this state gave the greatest contribution to the coefficient of refractoriness R. In the course of simulation the value of different factors was changed in winter following the outbreak of the sawfly population. Values peculiar to the period of stability were given to these factors. The refractory role of factors was evaluated by the response of the coefficient of refractoriness to factor change.

The role of parasitoids in sawfly population dynamics was examined by simulation of their exclusion from the life system. The change of the mean value and standard deviation of the log-transformed sawfly larvae density was analyzed.

RESULTS

Simulation Model

The proposed model simulates the multiple year dynamics of the common pine sawfly population. It has been described in detail (Sharov 1986b). A year is the basic time unit. There are four blocks describing the sawfly population, its host tree *Pinus sylvestris* L., and two groups of parasitoids developing in sawfly eggs and eonymphs. The model describes the change of population density of the sawfly and its parasitoids in their life-cycle and the dynamics of the amount of needles on the pine trees. Sawfly mortality caused by parasitoids was described by the modified model of Rogers (1972). In this model I assumed that the area of discovery (a) depends on the parasitoid density (P) in accordance with the model of Hassell and Varley (1969): $a = Q\ P^{-m}$, where Q and m were parameters. Sawfly-host plant interaction was described by the model of Semevski (1971). According to this model the pest space distribution is log-normal. The number of surviving larvae on each tree was assumed to be equal to the number of food units on the tree. If food is in plenty there is no mortality due to food shortage. The initial distribution of needles on trees was assumed to be uniform.

Sawfly fecundity is constant. Young larval survival increases with the size of a colony, the group effect (Sharov 1988). The size of a colony, in turn, depends on egg mortality due to parasitism. Last-instar larval and eonymph mortality was assumed to depend on mortality caused by food shortage and on mean May to September temperature in the previous and current years. The effect of temperature on larval mortality in the model is an explication of the effect of host-plant quality, dependent on weather. It is known that pine tree weakening caused by water deficiency is usually associated with high temperature and favors sawfly development (Schwenke 1964, Kharlashina 1984).

Reactivation of diapausing sawfly eonymphs depends on temperature in a dose-effect manner. The temperature increases the reactivation rate in the second flight period of the current year and the first flight period in the next year (Sharov and Safonkin 1982). The reactivation rate in the first flight period is considerably reduced after an outbreak. In the model it depends on sawfly larvae density in the previous year.

The model appeared to be adequate at the qualitative level. It "predicted" five out of six sawfly outbreaks in the Rostov region from 1956 to 1983 (Sharov 1986b). It is important that this model not only predicts pest outbreaks (they can be predicted by a simple regression model as well), but that it also describes mechanisms of a population alteration. It shows that its basic assumptions are sufficient for simulation of the high rate of sawfly density increase at the beginning of an outbreak.

Role of Processes and Factors in Population Dynamics

The role of six ecological processes in the dynamics of the common pine sawfly population was examined: 1) egg mortality caused by parasitoids, 2) eonymphs mortality caused by parasitoids, 3) larval mortality caused by food shortage, 4) sawfly reactivation in the first flight period, 5) sawfly reactivation in the second flight period, and 6) larval mortality caused by diseases.

In the period of stability the coefficients of m- and v-stability of the sawfly population appeared to be MS = 0.70 ± 0.12, VS = 0.30 ± 0.19. Population m- and v-stability are linked mainly with the interaction of the sawfly with the parasitoids (Table 1). Parasitoids of eggs and eonymphs give an approximately equal contribution to the coefficient of m-stability in the sawfly life system ($\text{ß}_1 = 0.51$, $\text{ß}_2 = 0.41$). Eonymph parasitoids give the greater contribution to the coefficient of v-stability of the host $\text{ß}_2 = 0.68$) than egg parasitoids ($\text{ß}_1 = 0.20$). Interaction of mortality processes associated with two groups of parasitoids destabilizes the sawfly population dynamics ($\text{ß}_{12} = -0.59$).

The model predicts the high rate of sawfly density increase after drought. In a dry year the late-instar larval density in the second wave of development becomes 101 ± 36 m^{-2} as compared with 34 ± 11 m^{-2} in the period of stability. In the next year it increases to 995 ± 368 m^{-2}. The reduction in larval mortality caused by diseases after drought when host plants are weakened is most important in population density increase ($\text{ß}_6 = 0.55$) (Table 1). Mass reactivation of sawflies in the first flight period is also important ($\text{ß}_4 = 0.35$).

The sum of regression coefficients (5) for process interactions (2.32) is much greater than that for individual processes (1.05). Thus, process interactions but not individual ones play an important role in the increase of sawfly density at the beginning of an outbreak. The most important are interactions of temperature-dependent processes (No. 4-6) with that of egg mortality caused by parasitoids ($\text{ß}_{16} = 0.46$, $\text{ß}_{15} = 0.37$, $\text{ß}_{14} = 0.32$).

The period of density increase is naturally followed by the period of collapse. According to the simulation, in the first year after the outbreak, sawfly larval density becomes approximately only one-third as large as in the period of stability. The larval mortality caused by food shortage plays the dominant role in the fall of population density ($\text{ß}_3 = 1.61$). The sum of regression coefficients for process interactions (2.02) is greater than that for individual ones (1.92). This indicates the importance of process interactions in the sawfly density increase. The interaction of larval mortality caused by food shortage with that of eggs caused by parasitism is particularly important ($\text{ß}_{13} = 1.75$). If food is in plenty, parasitoids cannot suppress the sawfly population ($\text{ß}_1 = -0.83$, $\text{ß}_2 = 0.69$). Eonymph parasitoids cannot decrease the host density even in conditions of food shortage (coefficient ß_{23} is non-significant).

In the period of depression, the life system of the common pine sawfly is characterized by a decrease in density of "new" eonymphs diapausing less than 1 year, increased density of "old" eonymphs with diapause period more than 1 year, elevated density of parasitoids, and decreased amount of needle as compared with the period of stability. After the change of 1) "new" eonymph density, 2) "old" eonymph density, 3) amount of needle in trees, 4) density of egg parasitoids, and 5) density of eonymph parasitoids to the value peculiar for the stability period, the coefficient of refractoriness

Table 1. Effect of ecological processes on quantitative characteristics of the common pine sawfly *Diprion pini* L. population dynamics.

ß coefficients of equation (5)*	Quantitative characteristics of population dynamics **			
	y_1 = MS	y_2 = VS	$y_3 = \ln(N_o/N_s)$	$y_4 = \ln(N_o/N_c)$
0	0	0	0	0.62 ± 0.15
1	0.51 ± 0.17	0.20 ± 020	0	-0.83 ± 0.38
2	0.41 ± 0.11	0.68 ± 0.09	0	0.68 ± 0.26
12	-0.22 ± 0.10	-0.59 ± 0.10	0	0.54 ± 0.35
3	-0.01 ± 0.01	-0.02 ± 0.01	0	1.61 ± 0.50
13	0.01 ± 0.01	0.02 ± 0.01	0	1.75 ± 0.52
23	0.01 ± 0.01	0.02 ± 0.01	0	-0.15 ± 0.20
123	-0.01 ± 0.01	-0.02 ± 0.01	0	0.51 ± 0.52
4	0	0	0.35 ± 0.12	0.45 ± 0.15
14	0	0.01 ± 0.01	0.32 ± 0.11	0.12 ± 0.16
24	0	0	0.05 ± 0.03	-0.34 ± 0.15
124	0	0	0.05 ± 0.03	-0.28 ± 0.16
34	0.01 ± 0.01	0.02 ± 0.01	0	-0.36 ± 0.11
134	-0.01 ± 0.01	-0.02 ± 0.01	0	-0.35 ± 0.19
234	-0.01 ± 0.01	-0.02 ± 0.01	0	0.26 ± 0.12
1234	0.01 ± 0.01	0.02 ± 0.01	0	0.33 ± 0.26
5	0	0	0.15 ± 0.09	0
15	0	0	0.37 ± 0.27	0
45	0	0	0.13 ± 0.04	0
145	0	0	0.17 ± 0.12	0
6	0	0	0.55 ± 0.15	0
16	0	0	0.46 ± 0.15	0
46	0	0	0.24 ± 0.07	0
146	0	0	0.13 ± 0.12	0
56	0	0	0.20 ± 0.05	0
156	0	0	0.29 ± 0.16	0
456	0	0	-0.05 ± 0.02	0
1456	0	0	-0.22 ± 0.07	0
Sum of the coefficients	0	0	0.18 ± 0.14	0
Total	0.70 ± 0.12	0.30 ± 0.19	3.37 ± 0.45	4.56 ± 1.08

* Numbers of ecological processes: 1) egg mortality due to parasitoids, 2) eonymph mortality due to parasitoids, 3) larval mortality due to food shortage, 4) sawfly reactivation in the first flight period, 5) sawfly reactivation in the second flight period, and 6) larval mortality due to diseases.

** MS and VS are coefficients of m- and v-stability of the sawfly population in the period of stability; N_s, N_o and N_c are population densities of sawfly larvae per 1 m^2 in the second wave of development in the period of stability, outbreak and collapse, correspondingly.

appeared to be 1) 8.0 ± 3.4, 2) 8.5 ± 2.6, 3) 6.8 ± 4.2, 4) 6.8 ± 2.0, 5) 1.2 ± 1.6, correspondingly. In the control where no factor was deliberately changed, the coefficient of refractoriness was equal to 7.5 ± 3.5. Thus the refractoriness of the sawfly life system in the period of depression is associated with the elevated density of eonymph parasitoids. The other factors including density of egg parasitoids and amount of needles in the trees has no refractory effect.

According to the simulation, the exclusion of each group of parasitoids from the life system of the host leads to an increase of the mean log-transformed sawfly density (Table 2). Egg parasitoids suppress the mean host density to a greater extent than parasitoids of eonymphs. The standard deviation of log-transformed sawfly density decreased significantly after the exclusion of egg parasitoids. This fact indicates the destabilizing role of the parasitoids in population dynamics of their host.

DISCUSSION

Mechanisms of common pine sawfly population dynamics in the Rostov region are similar to those in western Europe (Dusaussoy and Geri 1966, Eichhorn 1977, 1982, Geri and Goussard 1984). Nevertheless there are some differences. The primary one is connected with the mechanisms of reactivation of overwintered sawflies. There are three flight periods of the common pine sawfly in western Europe instead of just two as in the Rostov region. The additional flight period takes place in July and is often the most intensive one.

In France outbreaks of mass reproduction of the sawfly have been recorded at time intervals of 17 to 28 years (Geri and Goussard 1984), less often as compared with the Rostov region where the average time interval between outbreaks is 4 years (Kharlashina 1984). This outbreak pattern is common in all geographical regions. The provoking event is apparently drought that weakens a host plant and thus increases sawfly survival. The reactivation rate of the pest also increases, particularly in the first flight period in the year following drought. As a result, the seasonal cycle of the pest becomes mainly bivoltine instead of monovoltine in the stability period. Consequently, the population growth rate increases. The parasitization rate of the sawfly decreases, which might be interpreted as the escape from parasitoids. In the period of a population decline the parasitization rate increases greatly up to 100 percent (Urban 1962, Eichhorn 1982, Kristek and Petruska 1982). Mortality caused by diseases and proportion of diapausing sawflies increase as well. In some cases lowered fertility has been observed (Urban 1962, Eichhorn 1982, Geri et al. 1990). After the outbreak the rate of parasitism decreases gradually. In the Rostov region we have observed all these effects except the lowered sawfly fertility at the end of an outbreak (Sharov 1982, 1986b, 1987).

But enumeration of peculiarities of different outbreak periods does not explain a population alteration. It is necessary to prove that a given set of phenomena considered is enough for adequate outbreak simulation, and to evaluate quantitatively the role of each ecological process in a population dynamics. It has not been done before.

Known mechanisms of common pine sawfly population dynamics do not allow us to explain its fast population growth at the beginning of an outbreak. According to Kharlashina (1984), larval mortality caused by disease, host tree resistance, and other factors comprises not more than 30 percent of the total mortality. If the mortality level from drought-induced host plant weakening were three times lower, the sawfly density would be 1.29 times higher in 1 year. Taking into account transformation of the seasonal cycle from monovoltine to bivoltine, the pest density might be $1.29^2 = 1.65$ times as high. Such a density alteration is too small to escape parasitoids. When considering the effect of parasitism, one can explain a two- to threefold increase in sawfly density, but natural population density rises two orders of magnitude during an outbreak.

Table 2. Consequences of parasitoid exclusion from the life system of the common pine sawfly (based on data simulation)

Presence of egg parasitoids	Presence of eonymph parasitoids	Mean log-transformed sawfly larvae density in the second wave of development	Standard deviation of log-transformed sawfly larvae density in the second wave of development
Yes	Yes	3.85 ± 0.20	1.53 ± 0.24
Yes	No	4.62 ± 0.27	1.36 ± 0.34
No	Yes	5.66 ± 0.39	0.46 ± 0.12
No	No	5.94 ± 0.36	0.40 ± 0.05

There are no explanations for the increased rate of parasitism during population collapse. Elevated parasitoid performance can be associated with their increased density. But in this explanation the greater population growth rate of the sawflies compared to that of parasitoids has not been taken into account. Thus the parasitism rate can only grow if some other factors inhibit the growth of the host population.

Analysis of the role of an ecological process in the alteration of a sawfly population helps explain the phenomenon. Previous attempts to explain the pattern of sawfly population dynamics failed because the interaction of ecological processes were taken into account. We have revealed the dominant role of the process interactions in the course of a sawfly outbreak. Simulation modelling is the only correct method for the description of process interactions. Thus an explanation of population dynamics can be obtained only by this method.

Some mechanisms previously not taken into account were included in our model. For example, we found that the rate of eonymph reactivation in the second flight period increased with temperature (Sharov and Safonkin 1982). The model showed this as an important mechanism of the sawfly density increase after drought.

Table 1 indicates escape of the sawfly population from parasitoids at the beginning of an outbreak as an interaction of temperature dependent processes (No. 4-6) with an egg mortality caused by parasitoids. In the collapse period parasitoids do not play any important role, but their interaction with larval mortality caused by food shortage is important. This interaction is interpreted as follows: sawflies increase their density until food exhaustion, and then parasitoids have the time to outnumber their host and to suppress the host population. Unlike eonymph parasitoids, egg parasitoids are more important in host suppression because their interaction with the sawfly occurs in an earlier phase of the life cycle. When the number of host eggs is sufficiently reduced by egg parasitoids, some hosts are available for eonymph parasitoids.

In the depression period, repeated drought does not provoke an extra outbreak because the increased density of eonymph parasitoids controls the population number of their host. Approximately 3 years after an outbreak the parasitism rate of the sawfly eonymph decreases. The next drought, in turn, will cause a new outbreak of the pest. After an outbreak, the density of egg parasitoids decreases faster compared to parasitoids of the eonymphs. This is due to the absence of a prolonged diapause in egg parasitoids. Thus they are not able to support refractoriness of the sawfly life system.

In the period of stability, the sawfly population is regulated by parasitoids. Both groups of parasitoids prevent the mean density alteration of the host, however only the eonymph parasitoids stabilize host density fluctuations. These regulation mechanisms are rather weak and cannot maintain population density at the equilibrium level during drought. Consequently another outbreak will begin.

In general, an outbreak pattern of sawfly population dynamics is determined primarily by egg parasitoids. On the one hand, they are not able to maintain a low host density under unstable weather conditions; on the other hand, they prevent continuation of a high pest density during an outbreak. Eonymph parasitoids maintain the refractoriness of a sawfly life system after an outbreak and play a certain role in the "escape effect" during host density increase.

These conclusions are supported by the simulation experiment with parasitoid exclusion. Sawfly outbreaks do not occur without egg parasitoids, however, the mean sawfly density increases. Thus egg parasitoids suppress and destabilize the host population. Similar parasitoid effects on host insect population dynamics was reported earlier for *Prieria sinica* Moore (Shiotsu and Tsubaki 1986) and for *Epinotia tedella* Gl. (Munster-Swendesen 1985).

Thus the proposed method for explanation of population dynamics pattern allows us to describe quantitatively the role of factors and processes in the common pine sawfly life system. The process interaction was shown to play the dominant role in the course of an outbreak of the pest. This fact is evident through the "entirety" of the life system and shows the necessity of the system's approach to life system analysis.

SUMMARY

The role of ecological factors and processes in the population dynamics of the common pine sawfly, *Diprion pini* L., was examined using a simulation model. Consequences of fixation of density- and temperature-dependent process rates were determined. Results were processed by methods of multi-factor analysis. In the absence of drought the sawfly density is low and fluctuates within the steady state. Density regulation described by coefficients of m- and v-stability is associated with host-parasitoid interactions. Parasitoids developing in eggs and those in eonymphs prevent the change of the mean host density level (m-stability), but only parasitoids of eonymphs stabilize host density fluctuations (v-stability). Sawfly outbreaks are initiated by droughts which weaken the host plant and interrupt eonymph diapause. Both increase and decrease of sawfly density during the outbreak are caused by process interactions rather than individual processes. In the postoutbreak period, repeated drought cannot initiate a new outbreak because of high eonymph-parasitoid density. In general, the outbreak character of sawfly population dynamics is associated with the presence of egg parasitoids that suppress but destabilize the host density. The role of each ecological process is determined not only by its own properties but by the whole life system including the population and its effective environment. The role of processes in population dynamics should be analyzed using simulation models that can describe adequately the interaction of these processes in the life system.

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BIOECOLOGY OF THE CONIFER SWIFT MOTH, KORSCHELTELLUS GRACILIS, A ROOT FEEDER ASSOCIATED WITH SPRUCE-FIR DECLINE

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INTRODUCTION

During the past two decades, the decline of red spruce, *Picea rubens* Sargent, and balsam fir, *Abies balsamea* (L.), at high elevations (900-1200 m) in eastern North America has evoked concern about the effects of anthropogenic deposition upon terrestrial ecosystems. In many high-elevation forests across New England, as many as 50 percent of the standing red spruce are dead (Hertel et al. 1987). Wood cores indicate that growth has been severely curtailed since the 1960s (Hornbeck and Smith 1985). Although acid rain is most commonly invoked as the principal causal agent of this decline, there is yet little hard evidence to support this claim (Johnson and Siccama 1983, Pitelka and Raynol 1989). A wide array of anthropogenic pollutants in combination with natural stress factors are probably involved. Above-ground portions of declining trees appear relatively pest free, and so do the roots except for observations of a few soil-inhabiting arthropods. The most prevalent among those few was a subterranean lepidopteran polyphage, *Korscheltellus gracilis* Grote, found to be extremely abundant in these declining forests (Tobi et al. 1989, Wagner et al. 1987). A member of the Hepialidae family, *K. gracilis* is relatively unknown both in habit and distribution. In North America, documented knowledge about the biology or feeding habits of Hepialidae is limited to cursory reports on *Sthenopis argenteomaculatus* Harris as a borer in maple, oak, chestnut, and alder (Felt 1906). *Sthenopis quadriguttatus* Grote bores into the roots of aspen, cottonwood, and willow (Furniss and Carolin 1977, Gross and Syme 1981). Only one species, *Hepialus mustelinus* Packard, has been reported as a borer in spruce (Felt 1906, Packard 1895). In Australia the Hepialidae are among the major pests feeding on pasture grasses (Tindale 1933), and as stem borers of living trees (Tindale 1953), and tree roots (Tindale 1964).

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Adults of *K. gracilis* occur from June through early August and are active for 20 to 40 minutes during evening and dawn twilight. Inactive during the day, the cryptically marked adults rest on tree trunks or foliage. Eggs, scattered by females while in flight, hatch in 2 to 4 weeks. The whitish, unornamented larvae pass through two winters, attaining lengths of 35 to 45 mm before pupating in the upper layer of forest litter. At all locations where we studied this insect, abundance and marked scarcity of adults alternated from year to year, thereby suggesting a 2-year cycle.

Our studies represent an attempt to clarify the relationship of *K. gracilis* to its hosts, explain its apparent abundance in high-elevation forests, and increase information about its bioecology.

EXPERIMENTAL APPROACH

Densities and distribution of *K. gracilis* were determined in high-elevation forests in Vermont, New York, and New Hampshire, and at a sea level site of red spruce in Saulnierville, Nova Scotia. Quantitative estimates of larval and pupal densities were based upon examination of a series of 0.25 m^2 soil pits at elevations of 500, 700, 900, 1,100, and 1,300 m on Whiteface Mountain in New York and Mt. Moosilauke in New Hampshire. Two plots consisting of five subplots each were used to count fall and spring larval densities at each location-exposure. The relative abundance of adults was estimated by using two interception traps (1/4-m^2 sheets of clear plastic coated with Tanglefoot) placed 50 cm off the ground. On each mountain, plot transects were deployed at the point of maximal exposure to cloud base impact and on the lee side.

We measured feeding preference and seedling damage trials in the laboratory using field-collected mid-instar larvae 2 to 3 cm in length (Grehen et al. in press). Survival and weight gain on the predominant food sources available to this polyphage at high elevations and bordering lower elevation sites were evaluated to clarify relative suitability. In addition, three groups of 20, 2-year-old red spruce seedlings were inoculated with 0, 1, or 3 mid-instar larvae in the field at elevations of 700, 900, and 1,100 m. Seedlings were planted with their roots enclosed in saran screening so as to confine inoculated larvae within soil around the roots. This not only prevented larval escape, but also prevented other *K. gracilis* larvae or organisms from attacking the roots of the seedlings.

Periodically, larvae were collected from all sites, brought to the laboratory, and reared individually on carrots to enable us to rear out natural enemies.

RESULTS AND DISCUSSION

Densities of larval and adult *K. gracilis* were consistently highest at 900 and 1,100 m, and lowest below and above these elevations (Fig. 1). Mixed hardwood predominates below 700 m, whereas the proportion of spruce-fir increases from 700 to 1,100 m, and red spruce declines as balsam fir increases up to 1,300 m. There are few if any trees above 1,300 m. The abundance of *K. gracilis* corresponds roughly with that of red spruce, together with maximal tree decline and cloud-based impact. In the fall of 1987, larval densities were extremely high at Whiteface Mountain, New York, and Mt. Moosilauke, New Hampshire; estimated densities at 900 m were 5.6 and 14.8 larvae/m^2, respectively. At these two sites, however, larval densities declined over winter by 51 percent and 72 percent, respectively (Fig. 2).

The Hepialidae are extremely polyphagous and *K. gracilis* is no exception. Field observations verified larval feeding upon woody and nonwoody roots of red spruce and balsam fir. Seedling inoculation experiments (Fig. 3) demonstrated that larvae significantly affect root area and root weight at all elevations studied. Interestingly, the roots of uninfested seedlings had greater area and higher weight as elevation increased. Dieback of seedlings was most pronounced at 700 m with larval densities of three larvae/seedling.

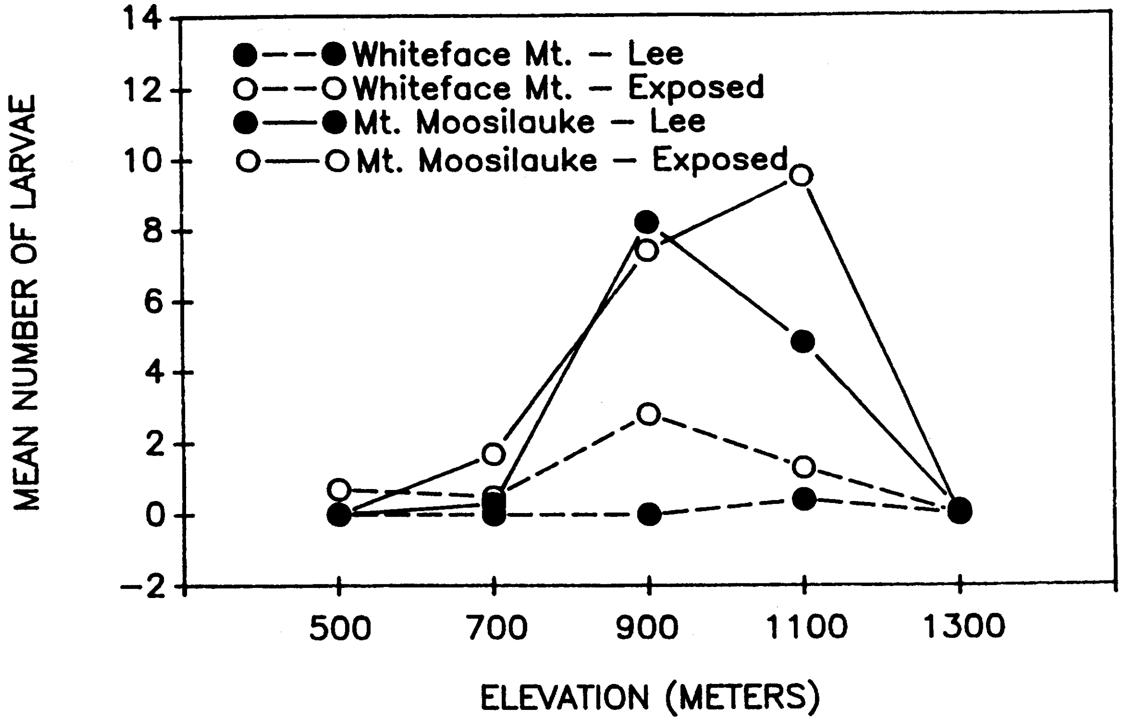

Figure 1. Fall distribution of the conifer swift moth, *Korscheltellus gracilis*, by elevation and location.

With naturally occurring densities of *K. gracilis* often averaging 10/m^2, it is very probable that larvae significantly reduce both spruce and fir regeneration.

In laboratory rearings on 10 potential food sources found in the high-elevation forests, *K. gracilis* accepted most of those offered (Table 1). Only in rotten wood did larvae fail to survive. The other food sources with which survival was greater than 50 percent were those commonly found in high-elevation forests. Sugar maple commonly occurs in mixed stands below 700 m; whereas white birch occurs in forests up to 1,200 m and mountain ash is common up to 900 m, but their proportion is low between 700 and 1,200 m. It is interesting to note that red spruce and balsam fir were once common at lower elevations, but are now more restricted to the higher elevations. Densities of *K. gracilis* are highest at elevations where spruce and fir dominate, and its survival is best on these hosts. Its poor performance on deciduous species may influence *K. gracilis* distribution and indicate that it is a weak polyphage.

It is generally accepted that larval weight gain over time (expressed as weight change from initial) is a reasonable indicator of host suitability. In our studies, carrot yielded not only highest survival but also weight gain, probably because it contains high protein and low toxic chemical levels. Another tuberous species, *Dryopteris* fern, a common component of high-elevation spruce/fir stands, showed relatively low percentages of survival and weight gain. Larvae commonly tunnel into the roots of fern in the field, but our data suggest that it is only marginally suitable. Weight gain on spruce and fir was equivalent to relative growth rates of 0.03 mg/mg/day. These growth rates are low for lepidoptera, but not unusual since tree roots are low in nitrogen (Slansky and Scriber 1985).

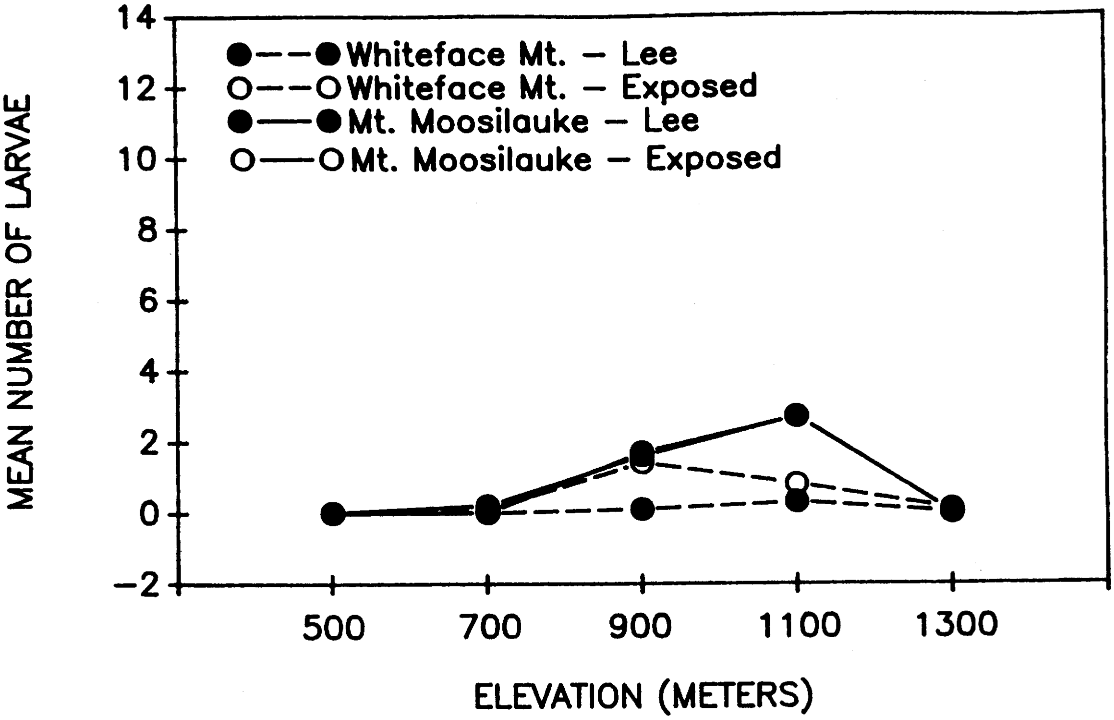

Figure 2. Spring distribution of the conifer swift moth, *Korscheltellus gracilis*, by elevation and location.

Table 1. Average survival and weight gain for the conifer swift moth reared on ten hosts

Host	Percent survival	Percent weight gain
Carrot	85.00	817.6
Moss	70.00	302.4
Fir	61.11	79.6
Hairy moss	60.00	277.0
Red spruce	55.56	93.2
Ash	44.44	1.4
Birch	33.33	105.1
Fern	33.33	32.8
Sugar maple	17.65	60.8
Rotten wood	0.00	----

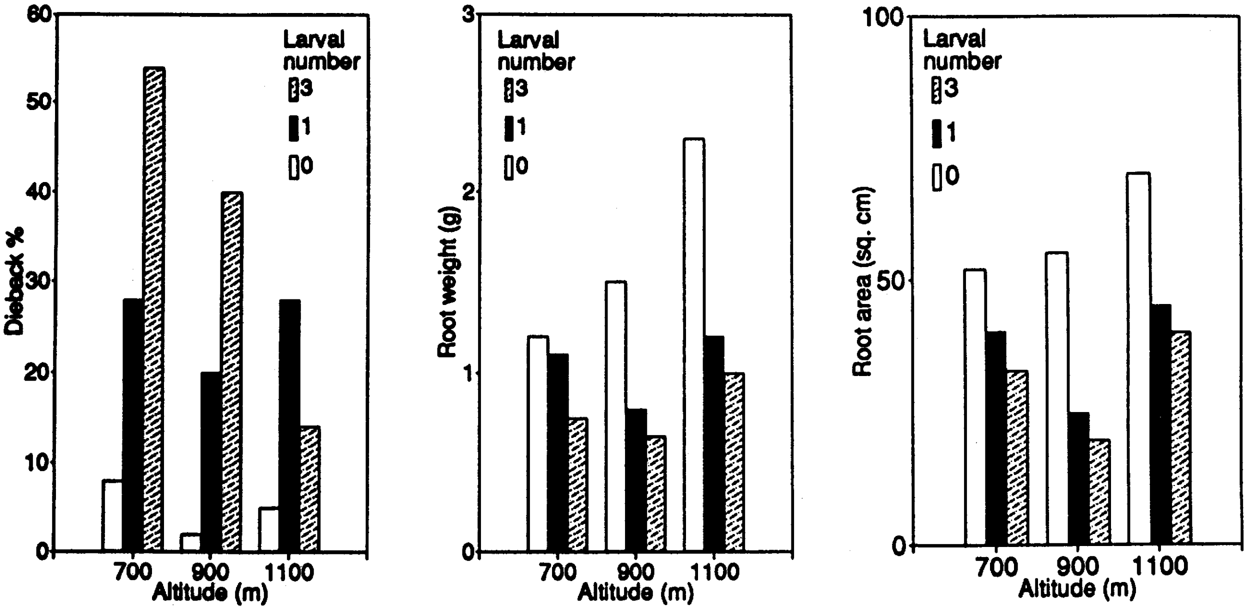

Figure 3. Response of red spruce seedlings to different densities of *Korscheltellus gracilis* larvae at different altitudes on Mt. Mansfield, VT.

The impact of *K. gracilis* feeding on roots of mature trees is less clear. We have observed larval root damage on numerous spruces and firs. In one case, a 50-year-old balsam fir contained more than 30 feeding scars. The larvae feed through the bark, but do not penetrate deeply into the xylem, creating elongate lesions along the axes of second to fourth order roots, fascicles of orange-brown frass and wood chips accumulating on either side of the wound. Such feeding sites provide entry courts for pathogens or nematodes. In fact, a wood-staining fungus has been found in association with *K. gracilis* feeding wounds in Vermont (Dale Bergdahl, pers. comm.).

The spruce-fir decline at high elevations in eastern North America is a complex process involving several factors. The fact that *K. gracilis* larvae occur at high densities in declining forests suggests that they may reduce tree regeneration and produce large numbers of feeding wounds on mature trees and thus may be one of those factors. Trees weakened by air pollution may subsequently be attacked by *K. gracilis*, or pollution-induced changes in the chemistry of the soil environment may permit unusual increases in the population of the insect, which then damages healthy trees.

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THE RECONSTRUCTION OF LYMANTRIA DISPAR OUTBREAKS BY DENDROCHRONOLOGICAL METHODS IN THE SOUTH URALS

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INTRODUCTION

Interest in investigating the influence of extreme ecological factors on the radial growth of oak (*Quercus robur* L.) is bound up with oak dieback in the South Urals during the last decade. Factors contributing to this problem in the study area are hard winter frosts, late spring frosts, and *Lymantria dispar* L. outbreaks. To distinguish the influence of these factors on radial growth, I used a methodological approach involving the analysis of radial increment, anatomical structure of xylem, histograms of ring indexes, and comparative analysis of radial growth in different plots (Kucherov 1987, 1988). By means of dendrochronological analysis, I was able to determine which specific features of radial increment were influenced by different factors (Kucherov 1988).

RADIAL INCREMENT RESPONSE TO DEFOLIATION

I found that maximal reduction of radial increment occurred following pest outbreaks during which the level of defoliation reached more than 70 percent. When defoliation did not exceed 50 percent, reduction of radial growth was not observed. The character of radial increment, further, depended on the degree of leaf regeneration after defoliation. When secondary leaves did not form, maximal decrease in radial increment took place in the year following defoliation (an after-effect). On the other hand, when secondary leaves did form, the after-effect was negligible or absent. The period of radial growth reduction, depending on the level of canopy recovery, was 1 to 2 years. Long periods of mean radial increment reduction were observed only in suppressed trees. Some of these trees (4 percent after the outbreak in 1985) were drying up. The late spring frosts, which also damaged the leaves, caused less radial increment reduction than gypsy moth defoliation.

The radial increment patterns I identified allowed for reconstruction of growth limiting determinant events since 1848. It was established that 13 outbreaks have taken place between 1848 and 1989. Intervals between the subsequent outbreaks were as follows: 11, 10, 12, 13, 12, 14, 11, 12, 6, 12, 11, and 9 years (the mean being 11 years). I discovered that in the last 50 years a significant increase in outbreak intensity had occurred relative to the preceding 90 years.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

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IMPACT OF A SPRING DEFOLIATOR ON COMMON OAK

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INTRODUCTION

We have investigated the population dynamics of some common phyllophagous insects in oak stands of the forest-steppe zone and their impact on common oak (*Quercus robur* L.). Considerable attention has also been paid to mathematical modeling of the studied processes. All field data represent samples taken from the Tellerman oak grove in the Voronezh region, where repeated observations have been made from 1969 up to the present. Our particular concern is the green oak leaf roller (*Tortrix viridana* L.), which propagates in 70 to 100-year-old oak stands in the floodplain of the region.

Fig. 1 shows characteristics of the weather conditions from 1969 to 1988 as well as results of field observations and mathematical modeling of the oak leaf roller's population density and the defoliation of oak crowns. More detailed description of methods and discussion of results are given in Rubtsov (1983) and Rubtsov and Rubtsova (1984). Last year's data showed that in all oak forests in the region significant number of eggs died during the summer to autumn period. That alters our conception of the egg stage of the oak leaf roller as its most favorable stage, subject only to high mortality during severe and prolonged frosts.

DEFOLIATION IMPACTS

Our investigations show a close relation between degree of defoliation of a stand and the ratio of late wood/early wood. For example, after 20 percent defoliation, this ratio is about 3:5, whereas after 80 percent defoliation, it is only about 1:4.

We have studied the defoliation of oaks damaged by spring phyllophagous insects since 1984. Larval feeding on oak foliage varies with weather conditions but usually lasts 18 to 24 days. Foliage is destroyed both in buds and on growing shoots. Depending on different combinations of environmental conditions, trees features, and insect populations, the defoliations have different effects, causing substantial variability in refoliation processes.

We divided all shoots that regrew after defoliation into replacement shoots (from reserve and dormant buds) and secondary shoots (from new buds). In most of the cases, the crowns of defoliated oaks have both kinds of shoots. According to our data, the greater the degree of defoliation and the faster it is reached, the earlier a tree begins to refoliate and the greater the proportion of replacement shoots among the regrowth. As larvae began feeding in the upper parts of the crowns, defoliation of the upper two-thirds of the crowns was 80 to 100 percent and that of the lowest one-third only 30 to

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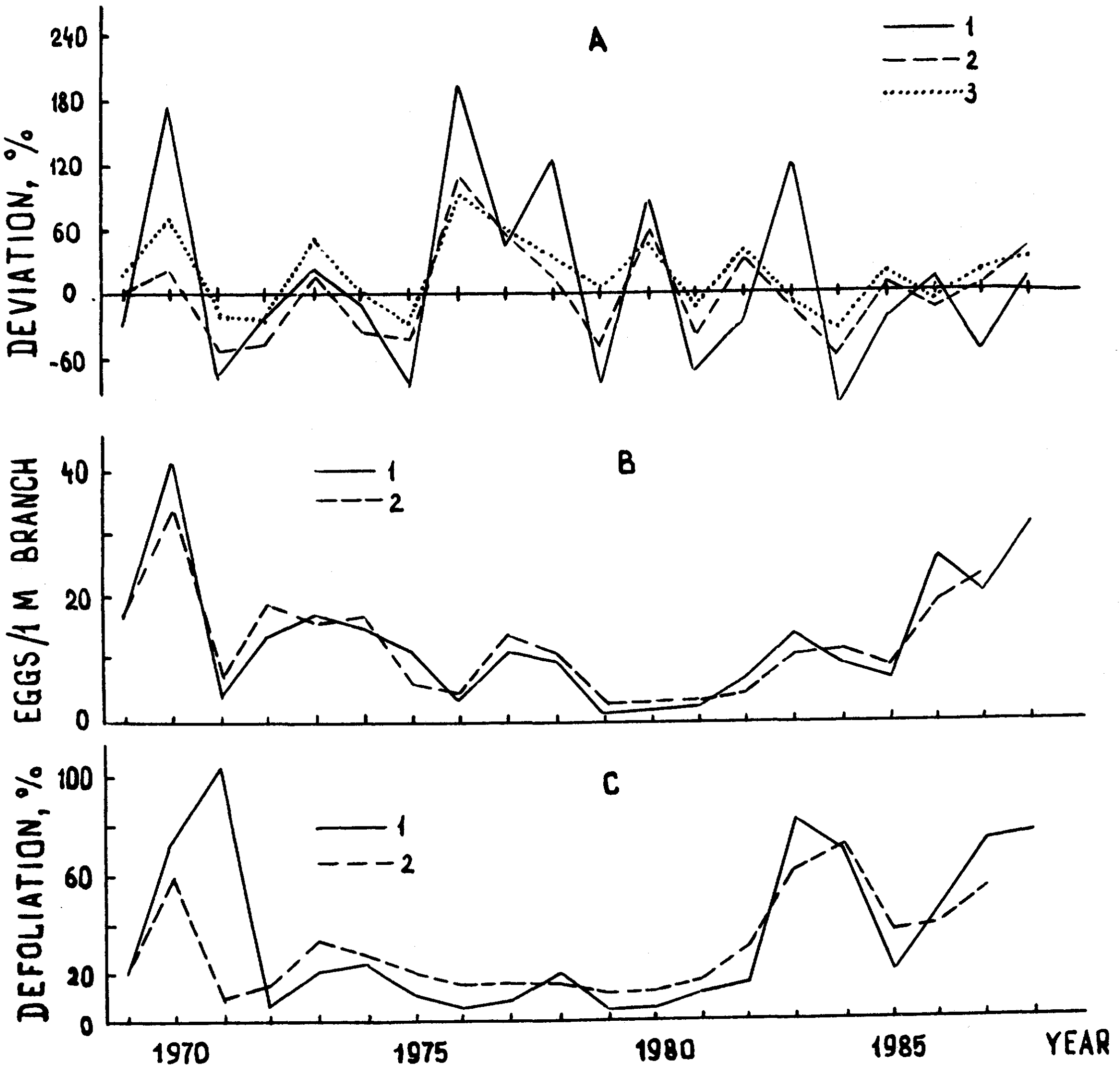

Figure 1. Weather conditions, oak leaf roller population density, and defoliation of oaks in the Tellerman oak forest from 1964 to 1988.
A) hydro-thermal coefficient (HTC) deviations from the average values of many years: 1) HTC of May, 2) HTC of growing season (May to September), 3) annual HTC; B) oak leaf roller population density: 1) field data, 2) calculated data; C) oak stands defoliation: 1) field data, 2) calculated data.

80 percent. In the latter case, secondary shoots were predominant. The greater the degree of foliage survival, moreover, the larger the share of secondary shoots among the regrowth. Since secondary shoots start growing later than replacement ones and have the lower growth rate, we can surmise that trees with a predominance of secondary shoots sustain a longer period of reduced foliage area.

Our 4-year observations show that trees with different degrees of defoliation have different numbers of reserve and dormant buds per 1 m of twigs at the end of summer. These findings are discussed at greater length by Utkina and Rubtsov (1989). Fig. 2 shows the average decrease in nongrowing buds for trees of slight and severe defoliation respectively. One can see that with slight defoliation (about 30 percent), the density of such buds is quite stable, whereas with severe defoliation

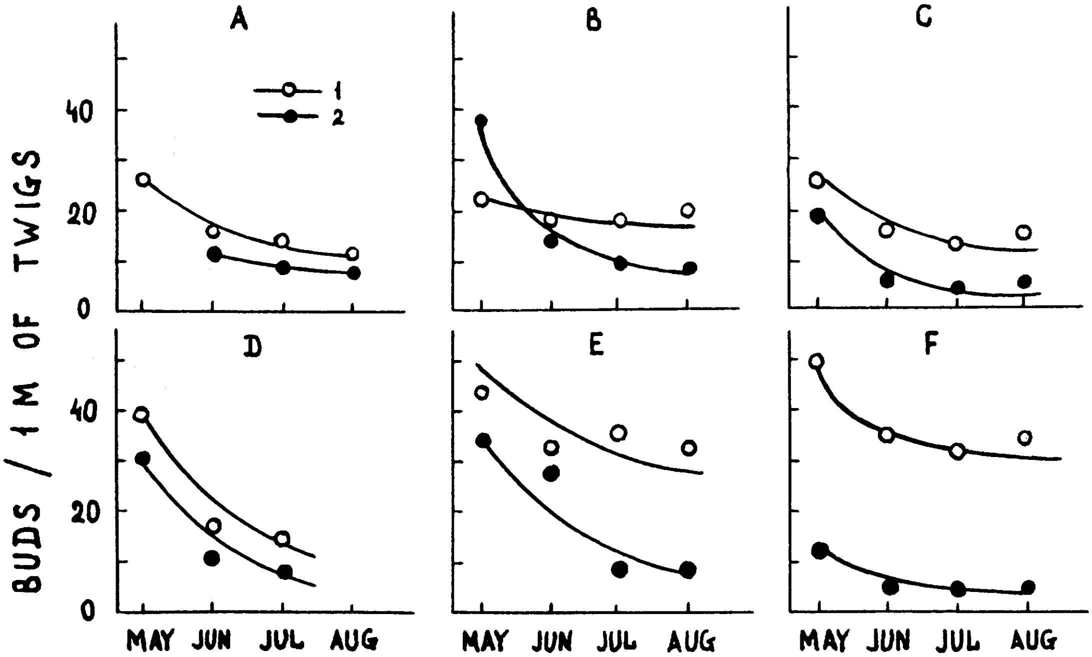

Figure 2. Numbers of nongrowing (reserved and dormant) buds in oak trees with 30 to 50 percent defoliation (1) and 75 to 100 percent defoliation (2). A), B), C), and D) 85-year-old stand from 1986 to 1989; E) and F) 105-year-old stand from 1987 to 1988.

(75 to 100 percent) the density of nongrowing buds declines from year to year. This is related to the fact that reserve buds open after defoliation, while some of them would be able to fill up the pool of dormant buds. Moreover, some share of the nongrowing reserve buds dry out in summer and fall. Fig. 3 shows the share of dead reserve buds to be largely independent of degree of defoliation. Comparison of foliage weight and area per 1 m of twigs in oak trees sustaining different degrees of defoliation suggests that, in general, refoliation is completed in defoliated crowns by the end of growing season.

One of the chief difficulties of mathematical modeling, especially of simulation modeling, is the weak data sets. In addition to such real deficiencies, moreover, there are methodological problems: inadequate structure and volume of data because of discrepancies between the final aim of the investigation, model structure and organization, and the system of field data sampling.

ACKNOWLEDGMENTS

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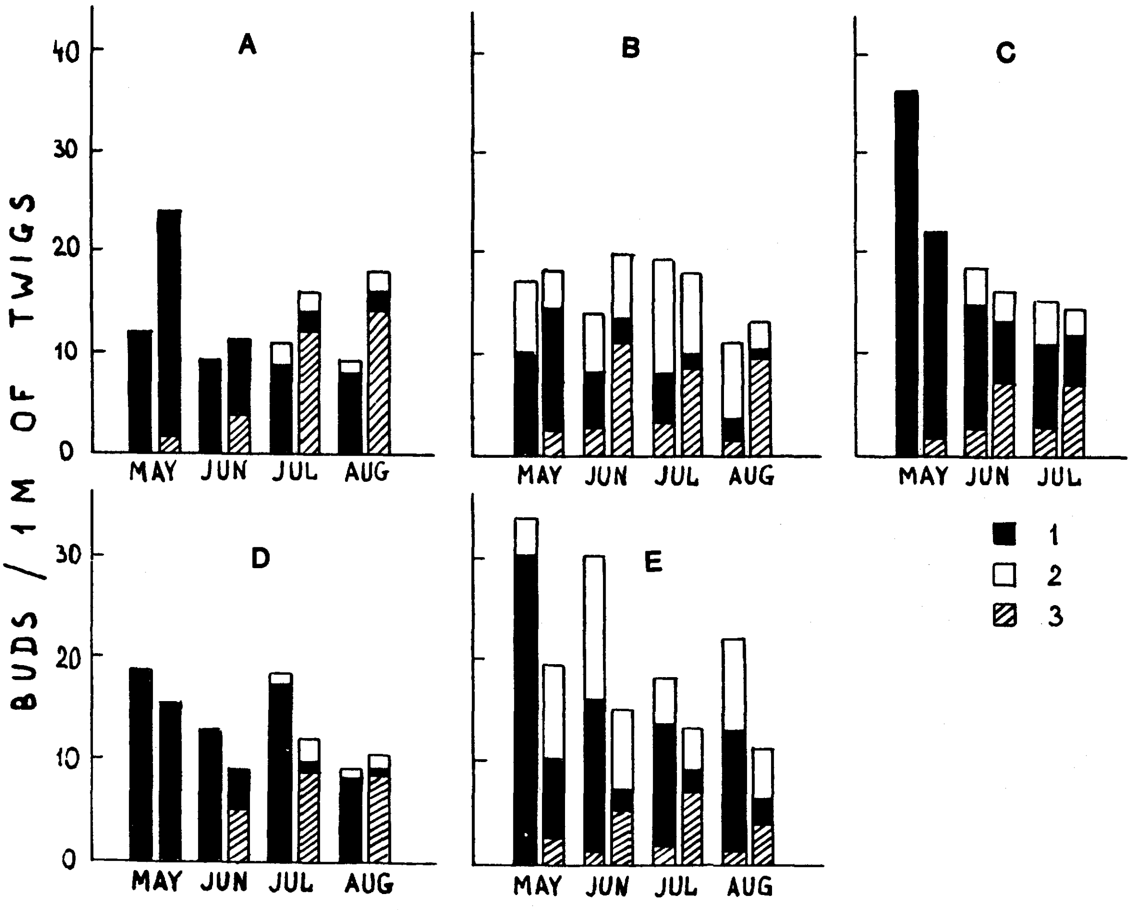

Figure 3. Numbers of reserved buds: in oak trees with 30 to 50 percent defoliation (left columns) and 75 to 100 percent (right columns). 1) alive, nongrowing; 2) dead; 3) buds grown after defoliation. A), B), and C) 85-year-old stand from 1987 to 1989; D) and E) 105-year-old stand in 1987-1988.

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TOLERANCE TO INSECT DEFOLIATION: BIOCENOTIC ASPECTS

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INTRODUCTION

Woody plant resistance to insect damage is of great importance in forest protection, and tree tolerance is an important element of this resistance.

The compensating mechanisms responsible for tolerance are nonspecific as a rule and develop after damage has been caused by phytophagous animals or other unfavorable effects. Beyond that, plant tolerance depends on duration, repetition, and phenological periods of the damage effects, and on environmental conditions. We have studied of radial increment patterns in trees as a measure of their physiological state.

This approach may be tested in areas infested by various dendrophagous species and is especially useful if the outbreak areas are vast, similar dynamics prevail in different forest site conditions, and the damage inflicted generally does not cause tree mortality. In these respects, the areas infested by *Zeiraphera griseana* Hbn., *Dasychira abietis* Schiff., *Pygaera anastomosis* L., and *Leucoma salicis* L. represent potentially significant conditions for estimation of the defoliation tolerance of larch, pine, and aspen trees, respectively, in Eastern Siberia.

TREE GROWTH RESPONSES TO DEFOLIATION

Fig. 1 shows the dynamics of radial increment of *Larix sibirica* in two biotopes that contrast in heat and water supply. The first curve shows the decrease in the increment caused by *Zeiraphera griseana* Hbn. defoliation in central larch taiga forests. Tree damage in 1953 and 1971 resulted in increment decline for the next 5 to 7 years. The second curve shows that *Zeiraphera griseana* outbreaks were more frequent in larch forests in the forest-steppe zone: in 1930, 1943, 1949, 1953, 1959, 1963, 1967, 1971, 1975, 1981, and 1987 (Fig. 1, curve 2). However, the increment decline following each defoliation was recorded over only 1 to 2 years. The same stand was also damaged by *Erannis jacobsoni* Djak. in 1964 and 1971. The consequences of that insect defoliation were registered over 5 years. This comparative geobotanical approach appears to be useful for mapping differential forest tolerance to phyllophagous insects.

The practical importance of such maps is evident given the importance of wood increment decrease as an indicator of the economic significance of phytophage outbreaks and the efficiency of the

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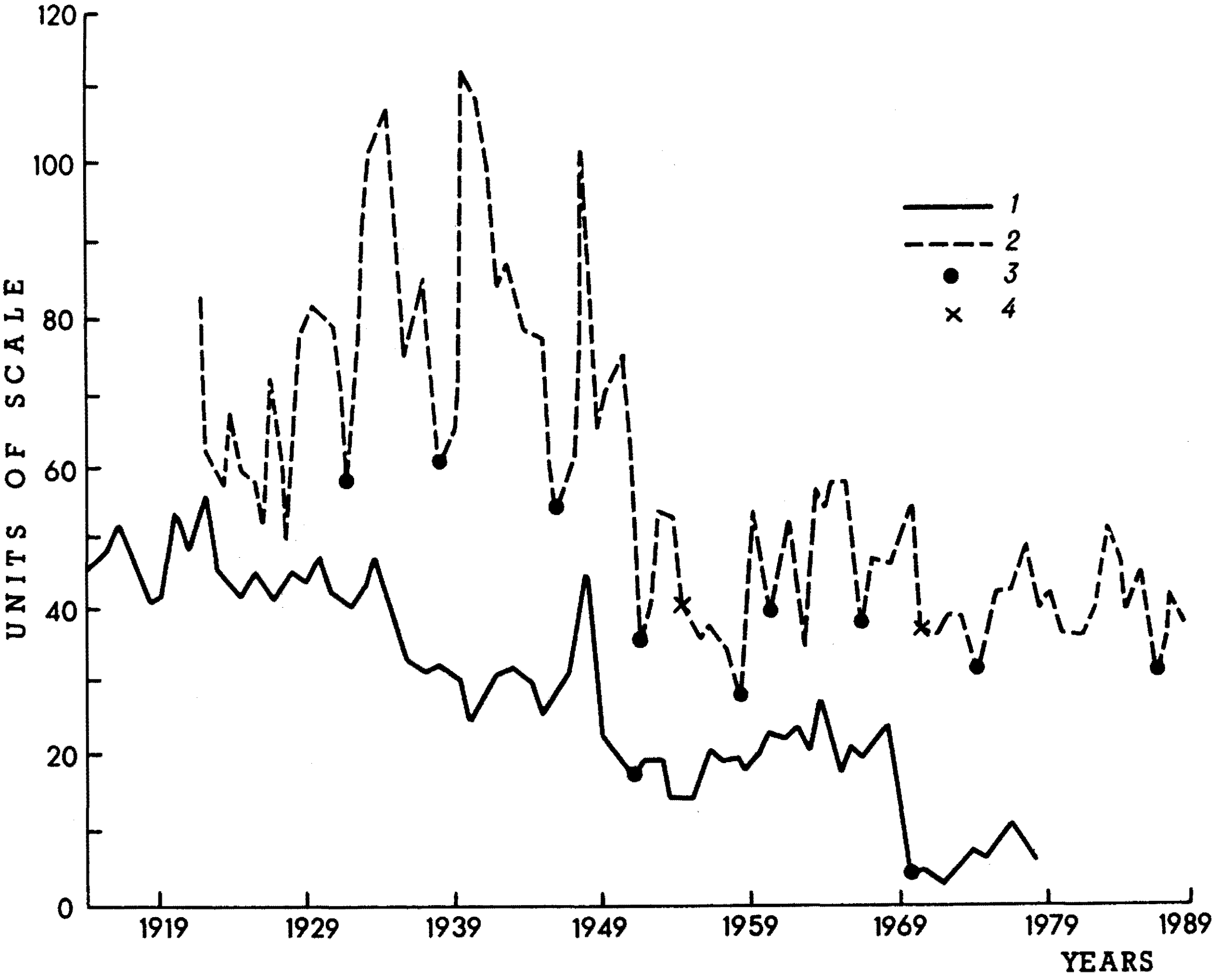

Figure 1. Fragment of dendrograms of *Larix sibirica* from different biotopes; 1. larch forests in the forest-steppe zone; 2. larch forests in the central taiga zone among herbs; 3. years of defoliation by larch bud moth; 4. years of defoliation by *Erannis jacobsoni* Djak.

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proposed forest protection measures. In addition, tolerance is directly related to the possibility of further tree damage by insects. The depression of physiological processes caused by defoliation results in temporary (passive) immunization of trees to a number of pests. Knowledge about the length of the immunization period--readily acquired through study of radial increment in damaged trees--would also contribute to better planning of forest protection measures.

Moreover, identification of the areas having high outbreak frequency is necessary for organization of forest pathological monitoring. Dendrochronological data may be used also for retrospective analysis of insect outbreaks.

INSECT-PLANT INTERACTIONS IN ANTHROPOGENICALLY TRANSFORMED ECOSYSTEMS

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INTRODUCTION

Structural and functional changes in forests due to anthropogenic factors have a considerable impact on the interaction of phytophagous insects with the phytocenosis. Many features of these processes have yet to be investigated in the deciduous forest conditions of the forest-steppe zone.

We investigated birch forests disturbed by anthropogenic factors in the middle and southern Urals. Anthropogenic transformation stages were determined using geobotanical analyses of grass (Polyakova 1983), physiological and chemical analyses of soil, and analyses of forest stand structures and the dynamics of radial increment growth. The principal subject of study was *Lymantria dispar* populations over the course of a population cycle.

INSECT POPULATION LEVELS

Analysis of the forest plots inside and outside outbreak centers showed that both suffered equally from pervasive anthropogenic impacts. The mean level of degradation was extremely high. No undisturbed forest plots were found.

The level of anthropogenic impact determines to a large extent the spatial distribution of *Lymantria dispar* outbreak centers. Thus egg density and caterpillar distribution correlate closely with the different stages of anthropogenic transformation: in the most disturbed forests (the fifth stage) a high population density and complete defoliation were caused by caterpillars. Pests attacked the least disturbed forest plots at the first stage as well, but population density and degree of defoliation were minimal there. We found a consistent difference in insect populations (mean weight of gypsy moth pupae, and adults, the sex ratio of moth) inhabiting the birch forests, at the first to second and the fourth to fifth stages of degradation. As degradation increased, we observed a concomitant increase in insect development rate.

The extent of anthropogenic transformation level also effected the activity of parasites and pathogens in gypsy moth populations. The natural mortality of late-instar larvae due to nuclear polyhedrosis was 42 percent higher in forest plots at the fourth stage than in the third stage; tachinid and ichneumonid parasitism was four times higher. In low-density birch stands significantly disturbed by anthropogenic factors, gypsy moth larvae tend to occur mainly on trunks and branches and to disperse by wind in the second instar, thus reducing the population density.

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FOREST RESPONSES TO DEFOLIATION

The forest reaction to defoliation is largely determined by the mean level of its anthropogenic transformation: at the same degree of defoliation the forest stand reaction correlates with the stages of anthropogenic dynamics. In weakly disturbed forest stands (at the first and second stages), *Lymantria dispar* does not cause complete defoliation and no structural transformation is evident except for a 10 percent growth loss, which may be caused by the dispersal of larvae to more degraded forest plots. At the third and later stages of the anthropogenic dynamic, forest reaction includes two substantially different developments: rapid death (within a year of defoliation) and slow death (over several subsequent years). Duration of the second response increases significantly in the most degraded forest plots. At third to fifth stages, total forest stand mortality in the gypsy moth outbreak centers in the Middle and Southern Urals was 10 to 20 percent and 0 to 10 percent at third stage, 20 to 40 percent and 10 to 20 percent at the fourth stage, and 40 to 80 percent and 20 to 50 percent respectively, at the fifth stage. In some forest plots, total mortality reached 100 percent of the forest stand, and the area of these forests increased substantially in the 2 or 3 years after the outbreak. Intensive bogging and 40 to 60 percent mortality of forest stand were observed after defoliation. Thus the most significant result of severe degradation is protraction of the defoliation after-effect and, as a further result, continued structural transformation of biogeocenoses. Among other reasons, this may be explained by a drastic drop in forest resistance, causing the increase in the biogeocenosis relaxation time.

Inside the outbreak centers there were plots which were infested with a tree bacterial disease caused by *Erwinia multivorum*. Analysis of the concurrence of these two processes shows an additive effect taking place. The most important after-effect of the outbreak is the consistent level of tree diseases in the forest stand just following the outbreak. Another important outbreak after-effect is the intensive attack by xylophagous insects on trees weakened by defoliation, the result of which is accelerated tree mortality.

In sum, the level of anthropogenic transformation of birch forests in the forest-steppe zone determines to a large extent the population dynamics of gypsy moth populations and the kind of phytocenosis reaction. That is why the monitoring of disturbed deciduous forest ecosystems stratified into different anthropogenic transformation stages may be a strategically important means of improving forest protection. It may also be used as a method of predicting forest resistance and the dynamics of anthropogenic ecosystems.

DOES THE PLANT DEFEND ITSELF AGAINST LEAF-FEEDING INSECTS?

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Trees do not actively respond to herbivore grazing, they react to the deterioration in the balance of their roots and crowns functions, which comes when transpiration powers fall off. Such inherent reactions of plants originated as abilities to restore photosynthesis.

THE LARCH BUDMOTH SYSTEM

For example, every 9 years the larch budmoth, *Zeiraphera diniana* Gn., depletes the subalpine, larch-cembran pine forests (Baltensweiler and Fischlin 1988). The heaviest defoliations occur at altitudes of 1600-2100 m, last 2.93 ± 0.21 years, and recur at intervals of 8.47 ± 0.27 years. At lower altitudes defoliation occurs half as often and rather irregularly. Close scrutiny has shown that larch trees defoliated more than 50 percent refoliate in a manner similar to trees that have suffered from frost. In the spring following defoliation, needles are shorter than normal with increased raw fiber and decreased protein content. From 2 to 7 years after the outbreak, the needles recover their average quality, and the bud moth populations begin to grow along with the parasites which follow them. In the growth phase of the population cycle, the bud moth females lay 116 ± 19.1 eggs. Total generation mortality is approximately 90 percent and that gives rise to a 10-fold increase from one generation to the next. In the decline phase, the females lay 12.5 ± 19.1 eggs, larval parasitism increases 10-fold and the total mortality rises to 99.98 percent. Dendrochronological data observed in fossil larch dating from Roman times and in the beams of 15th century farm houses show that larch is adapted to defoliation and therefore the bud moth here is not a pest. The causes of bud moth density oscillations depend on weather, feeding, competition for food, predators, parasites, and pathogens.

THE GREEN OAK LEAFROLLER SYSTEM

The analysis of *Tortrix viridana* outbreaks in oak forests (Rafes 1989) is another example of this phenomenon. The devouring of foliage causes a hyperfunction of chloroplasts which restores the assimilation capacity to a small degree and only at the beginning of a serious grazing cycle. During hyperfunction and further formation of secondary leaves, the tree produces increased quantities of phenols and other antibiotics which accumulate in the leaves (Fagerstrom et al. 1987, Haukioja et al. 1985). The depletion of leaves diminishes the transpiration power of a crown and the water content of trees is reduced. During the period of crown depletion a great deal of the gnawed leaves, larval excrement, and entomophages fall to the floor; all of them stimulate the extraordinary activity of saprotrophs. A chemical analysis of soil at this time demonstrates an elevated content of nitrogen, phosphorous, and potassium. After the tortrix larvae pupate, the secondary foliage grows, but amounts to no more than 75 percent of the primary foliage. That is why the autumn leaf fall is only somewhat below the ordinary level. As a result of imperfect compensation, the growth in tree stem diameter

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drops off significantly. Throughout an outbreak, the enriching of soil with NPK favors to some degree the stand condition. But at the same time the accumulation of phenols and other antibiotics in foliage has adverse effects. They poison the tortrix larvae, its parasites, the soil, its inhabitants, and affect the roots of plants. Investigations in England (Carlisle et al. 1966) have demonstrated that an outbreak of *T. viridana* can bring about the serious change in the soil.

TAKING THE SYSTEM PERSPECTIVE

An insect outbreak is a symptom of forest ecosystem dysfunction. The quantitative relations of pests, their parasites, predators, and saprotrophs are disturbed, and their behavior becomes uncommon. Ecosystem function is suppressed as a whole and incapable of autoregulation. If it is sufficiently resilient it can be restored, but this is the matter of time. If it is not resilient, this ecosystem shall be changed.

At the introduction to the workshop "State and Change of Forest Ecosystems," Andersson (1984) considered trends of the problem: most attention has been devoted to the ecological importance of photosynthesis and the flow of organic matter in the food chains of biophages. But, nutrient formation and soil processes are understood imperfectly. In the monitoring of forest ecosystems, especially for the prognosis of pest outbreaks, chemical analysis of the dominant plant foliage and of the soils should be done for the physiological studies of phytophages and their host plants.

Ecosystem is the space-time unity in which all of motions are relative, i.e. interdependent. Mathematicians modeling ecosystems are forced to make a simplified schematic pattern of the interactions, but ecologist are obliged to reveal and to explain the causes of all phenomena occurring therein.

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THE ROLE OF PHENOTYPE STRUCTURE IN THE POPULATION DYNAMICS OF GYPSY MOTH IN THE LOWER DNIEPER REGION

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INTRODUCTION

One of the characteristic features of the gypsy moth population in the Lower Dnieper area is its variable larval coloring. Phenotype frequency has been recorded over the years in separate micropopulations at different density levels. The data show the population to consist mainly of gray larvae in all life stages, and their abundance varying from 85 to 99.6 percent. Larvae with a black stripe along the back (black type) range from 0.4 to 15 percent of the population. Depending on the phase of population gradation, the phenotype concentrations in a population can vary. At high and low density levels, black stripe larvae are very rare and make up only 0.4 to 1 percent of the population, while at the onset of population growth, their relative quantity rises up to 15 percent.

Thus at the commencement of population growth, when individuals are typically the most viable and fecund, relatively large growth is recorded for the black phenotypes. Such a dynamic ratio of phenotypes in a population supports Dobrzhansky's (1970) assertion that genotype value is inversely proportional to its abundance in a population.

Hence the question arises of adaptive selective value of black stripe genotype. The data of Kolybin and Zelinskaya (1969) and Kolybin (1976) as well as our own show that these black types from the areas of different population density differ according to a number of ecological and physiological indices. In particular, their higher fecundity, egg weight, and survival rate promotes fast population growth.

GENETIC BASES OF LARVAL COLORING

We tested the genetic bases of these differences between morphs by crossing different phenotype specimens in several generations to obtain data on inheritance patterns of larvae coloration and other biological characteristics of broods. The results show that in crossings of gray females and black males, or black females and gray males, yield two types of larvae--gray and black striped specimens in a 1:1 ratio. On the other hand, in crossings of black females and black males also yield two types of larvae --gray and black striped, but in a 1:3 ratio. Crossings of gray females and gray males does not yield only gray larvae. The test showed larvae coloring to be simply inherited: gray phenotype larvae being recessive homozygotes and the black phenotype being determined by the dominant "black" gene.

Analysis of the phenotype ratios in a population and its changes depending on level of population density suggests that in the gypsy moth population we investigated, balanced polymorphism

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occurs. Essentially, it functions to maintain the most favorable ratio of homo- and heterozygotes in the given habitats. It is an adaptive reaction of a population to its environmental conditions evidenced in phenotype structure. I should note that a balanced phenotype ratio, inclined toward a predominance of gray larvae (homozygotes by coloring), is maintained due to the higher viability of homozygotes in certain sets of ecological conditions. Deviations in phenotype ratio occur under conditions deviating from the optimal ones.

ATTRIBUTES OF PROGENY FROM DIFFERENT CROSSES

Analysis of biological attributes of a phenotype crossing over a number of generations showed that in crossings of two gray types, fecundity of the next generation decreases for each, and the average weight of an egg increases in a second generation and decreases in the next ones. When we compared egg clusters obtained in crossing of gray female homozygotes with black male heterozygotes, the fecundity of the progeny turned out to be about two times higher than that of a pairing of heterozygotes ($P = 0.01$), but close to the fecundity index of a pairing of two homozygotes ($P < 0.5$). The fecundity index varies depending on the combination of parental pairs by phenotype feature, while average egg weight index has a different mode of variability. In all variant crossings of heterozygote females average egg weight in the progeny was more than two times higher than that of the homozygotes' progeny ($P > 0.001$).

Of considerable significance is the fact that even in crossings of brothers and sisters, the fecundity indices and egg weight values correlate with phenotypes of the parents in the crossing.

Comparison of the fecundity indices in all progeny of phenotype crossings--a maximum of 544 eggs and a minimum of 115 eggs--showed that the substantial variability of this index depended on parental phenotypes. The coefficient of variation in fecundity is very high, amounting to 61.4 percent. On the other hand, that of the average egg weight is only 13.29 percent.

Data on progeny variability from different parental crossing are of special interest. Beginning with the third generation the specimens of gray coloring turned out to be the most viable. The viability of gray and black specimens in the laboratory experiment was compared with the phenotypes ratio at different stages of population dynamics in nature. These data showed population heterogeneity to increase owing to a greater probability of sexual encounter between different phenotypes. This may lead to increase in both viability and fecundity and, consequently, to greater population density.

In subsequent generations, when population density increases, the probability of sexual encounter between hetero- or homozygotes decreases owing to the greater frequency of homozygotes. However, the achieved potential for viability increases owing to phenotype hybridization and promotes both population growth and outbreak. Population abundance decreases with the overcoming of high heterogeneity.

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NOVEL ASPECTS OF HOST TREE RESISTANCE TO LEAFMINERS

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INTRODUCTION

At least 10,000 species of leafminers in four orders of insects (Lepidoptera, Diptera, Coleoptera, and Hymenoptera) are found worldwide. The common feature of all leafminers is that larvae feed within leaves for at least some larval stages. Larvae of facultative mining species feed internally but also externally as free-feeders, usually in later larval instars. Larvae of obligate mining species feed exclusively, and may also pupate, within leaves (Hering 1951, Powell 1980). Despite wide interspecific variation in life histories, leafminers are generally more closely associated with their feeding substrates than are free-feeding insects (Mattson et al. 1988). This "intimacy" (sensu Mattson et al. 1988) is the primary factor in directing their evolution and influencing population dynamics.

For leafminers, as distinct from most free-feeding insects, selection of feeding substrates is determined solely by female oviposition choice, at least for obligate leafminers. Eggs may be cemented to the surface or embedded in the leaf, so adult females determine feeding sites not only among plants but also within leaves. For facultative leafminers, female oviposition choice determines larval feeding sites for at least some larval instars, and female choice generally plays a much larger role in larval feeding sites than it does for most external feeding insects. Confinement to a single leaf means that larvae cannot behaviorally escape deteriorating abiotic or biotic conditions associated with their substrates as vagile insect larvae can, though a few species can mine more than one leaf by exiting the mine or mining through the petiole to adjacent leaves. The individual leaf is the arena where the fates of larvae are decided.

Because of this tight link between oviposition and larval feeding sites and survival, one expects strong selection on female oviposition choice. Since many free-feeding larvae are mobile, however, oviposition choice may be less critical. Furthermore, since most adult lepidopteran leafminers do not feed, selection of suitable leaves should be driven by survival and fecundity of offspring, not by feeding preferences of adults as with many free-feeding insects.

The leafminers differ from other endophagous insects, such as the stem and twig borers and gallformers, in several important ways. A leaf usually has less biomass than either a stem or a twig. Structurally, most leaves are essentially two-dimensional with little depth, while stems or twigs provide three-dimensional substrates. The two-dimensional nature of the leaf constrains the size and shape of larvae more than borers. Leafminers are the smallest of all the microlepidopterans and many are compressed dorso-ventrally. The lack of depth in leaves increases the likelihood of inter- and intraspecific interactions and may facilitate attack by natural enemies. Leaves are generally more photosynthetically active and composed of different cell types than twigs or stems. Some galling insects

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are also confined to feeding on single leaves, but by virtue of their isolating properties, galling insects are less likely to interact directly with other galling insects. Gall tissues also differ phytochemically from the leaves in which they are formed (Zucker 1982). Thus leafminers may be more intimately associated with their host leaves than are gallformers.

I contend that this close association between leafminers and the leaf substrate causes phenological and morphological traits of plants to override other factors in governing host plant resistance. The biology and ecology of a lepidopteran leafminer, *Cameraria* sp. nov. Davis (Lepidoptera: Gracillariidae, *agrifoliella* group), are presented to elucidate that argument.

HOST PLANT RESISTANCE

Strictly speaking, plant resistance consists of the intrinsic (inherited) traits of a plant which prevent herbivore damage (Williams et al. 1988). Many extrinsic factors, however, such as abiotic conditions, interactions with natural enemies and other herbivores (including microbes), and the association of the host plant with other plants, influence the susceptibility of host plants to insect herbivores. Here, resistance is considered in the broad sense, i.e. what factors generally influence abundances, and thus population dynamics, of leafminers on their host plants.

Temporal and Spatial Patterns of Abundances of *Cameraria* on Emory Oak

Cameraria sp. nov. Davis is a dominant, univoltine leafminer on *Quercus emoryi* (Fagaceae) in some localities in central Arizona. Adults emerge from puparia inside leaves as they abscise in April. Adults mate and females oviposit on newly expanded leaves in late April to early May. Eggs hatch a few days after oviposition and larvae immediately form upper-surface, blotch mines. Larvae complete three to four instars by August to September, apparently undergo a larval diapause in winter months (although larvae can be observed feeding on warmer winter days), then rapidly complete the last four to five instars in March and April, and pupate in leaves to complete the yearly cycle. Successful larvae consume most of the upper-surface leaf area of the relatively small Emory oak leaves (Bultman and Faeth 1986a).

I have monitored the temporal patterns of abundances of *Cameraria* on eight Emory oak trees at a locality in central Arizona (Oak Flat, Pinal Co.) noted for unusually high densities. Other leafmining species typically remain at very low densities (≈ 1 mine/100 leaves) on Emory (Faeth 1986) and other oaks (Faeth and Simberloff 1981). Several spatio-temporal patterns emerge. Resistant trees in one season tend to be resistant in the next (Fig. 1a, 1b) and whereas overall abundances vary among trees and years, the pattern of tree resistance remains the same, as does the pattern of higher densities within trees on interior, shaded leaves (Fig. 2).

Patterns of spatial distribution at finer scales have also been observed. Within trees, *Cameraria* is highly clumped among leaves (Faeth 1990). Fewer unmined leaves and more leaves with more than two mines occur than would be expected by chance. The leafminer occupies larger leaves more frequently than small ones. Within leaves, multiple mines are clumped on the basal half of individual leaves (Faeth 1990).

Two related questions emerge: what factors determine the pattern of among-tree distribution, and how are the consequences of within-tree and within-leaf clumping of *Cameraria* related to this pattern? Both of these questions are fundamental to concepts of plant resistance. The first examines the initial colonization or habitat selection of trees and leaves, which is a function of female oviposition choice. The second question focuses on the fate of the population after colonization and thus on future colonization by leafmining survivors.

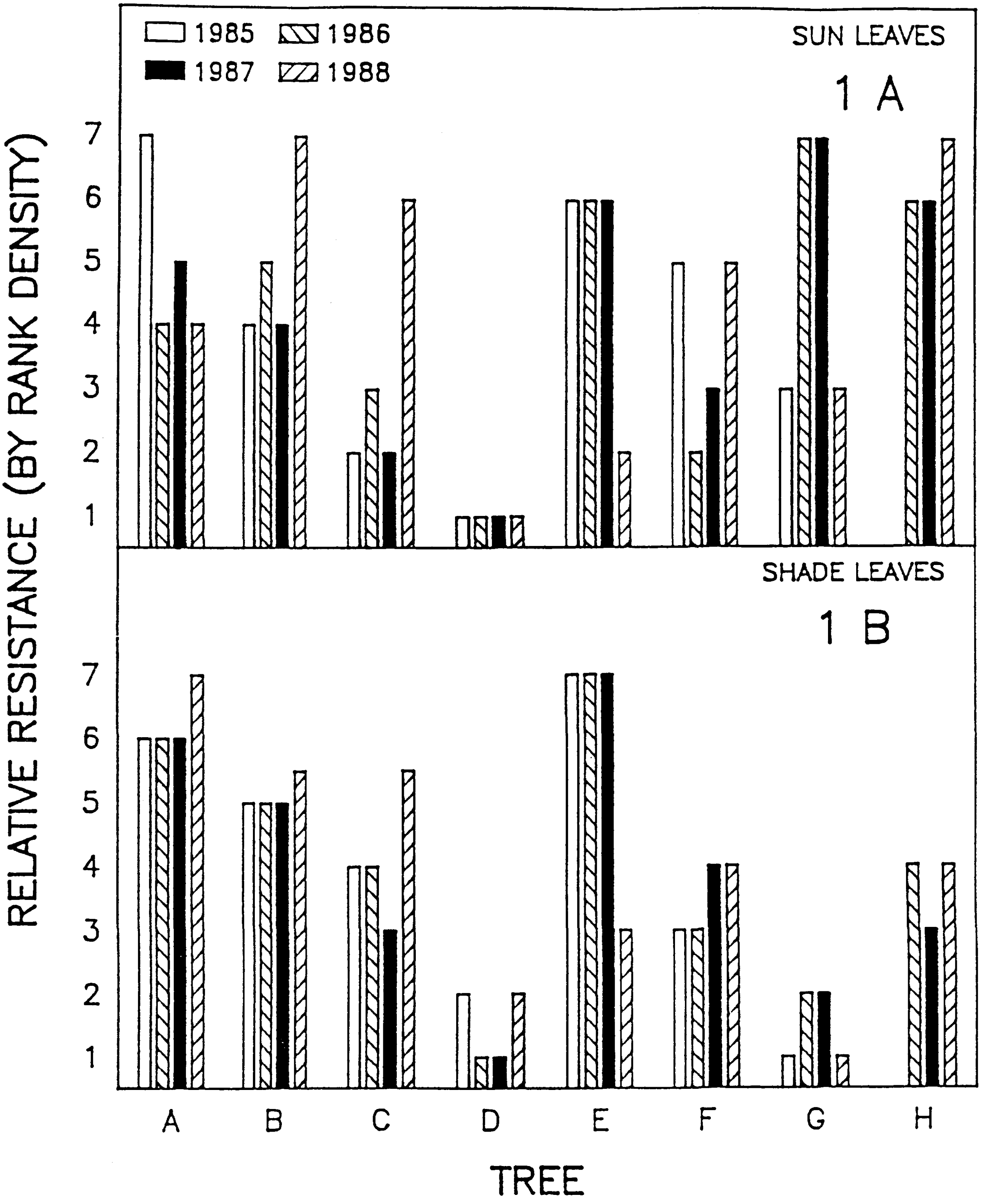

Figure 1. Relative resistance of sunny (1A) and shaded (1B) regions within eight study trees to *Cameraria* infestation over four growing seasons. Resistance is defined as rank by mean density. Ranks of sun and shade leaves in one season were tested for independence in the following season by Kendall's nonparametric test for independence and are as follows: Sun, 1985-86, $p > 0.20$; 1986-87, $p < 0.001$; 1987-88, $p > 0.40$; Shade, 1985-86, $p < 0.001$; 1986-87, $p < 0.001$; 1987-88, $p = 0.05$. Densities of Tree H were not recorded in 1985.

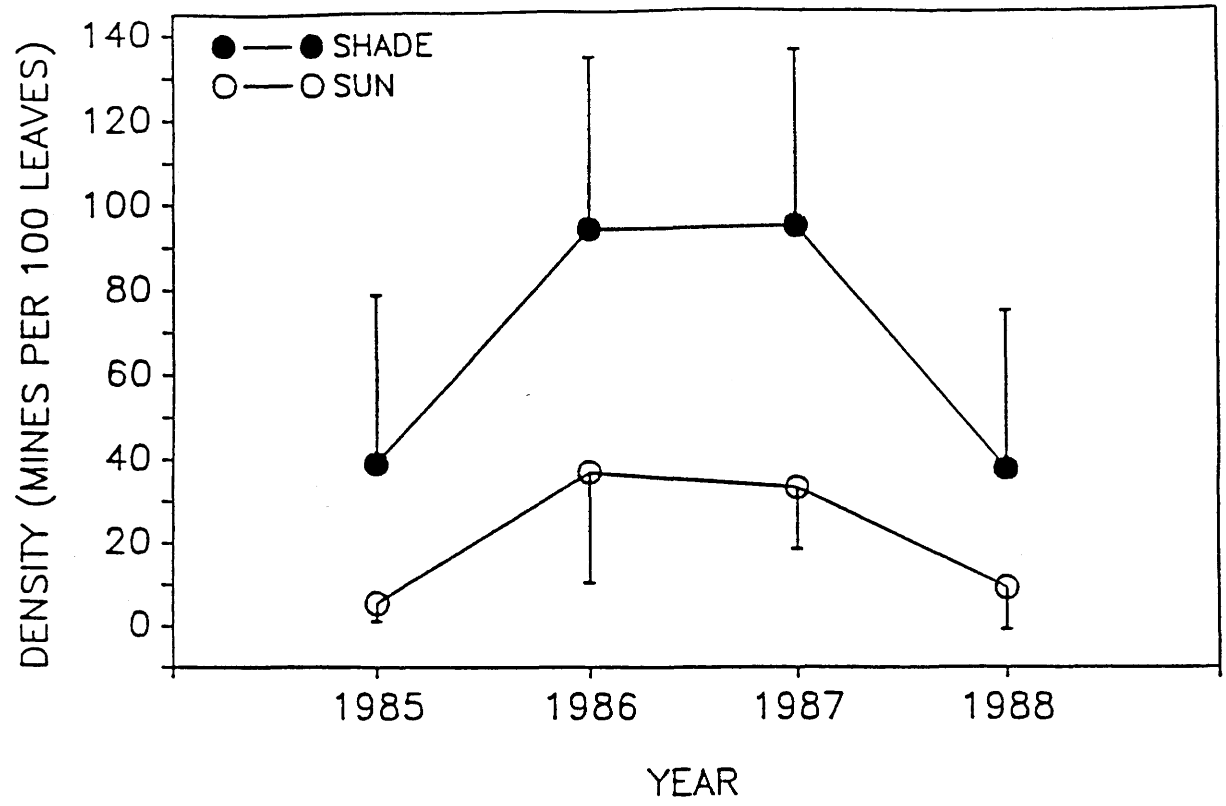

Figure 2. Mean densities of *Cameraria* (± SE) in sun and shade leaves from 1985 to 1988. Densities in shade leaves are significantly greater than sun leaves in each year, except 1985 (paired t-test, 1985, $t = 2.23$, $df = 6$, $0.10 > p > 0.05$; 1986, $t = 4.92$, $df = 7$, $p < 0.01$; 1987, $t = 4.53$, $df = 7$, $p < 0.01$; 1988, $t = 2.40$, $df = 7$, $p < 0.05$).

Oviposition Choice

The operation of selection on adult females via survival of offspring has apparently resulted in behavioral and physiological mechanisms by which they discriminate suitable leaves for oviposition, at least in some leafminers. McNeil and Quiring (1983) reported an oviposition deterring pheromone in the dipteran alfalfa blotch miner, and others have suggested that lepidopteran leafminers can detect the presence of conspecific eggs (Simberloff and Stiling 1988, Auerbach and Simberloff 1989). In all of these studies, co-occurrence with conspecifics on a leaf resulted in increased mortality. Godfray (1986) showed that observed clutch size (three per leaf) of the leafmining fly, *Pegomyza nigrotarsis*, produced greatest larval survival, suggesting that natural selection has optimized clutch size. In addition to the presence of conspecifics, adult leafminers select leaves based on phenological or morphological traits such as 1) leaf size (Bultman and Faeth 1986a, 1986d, Godfray 1986, Faeth 1990), 2) propensity of leaves to abscise (Bultman and Faeth 1986c, Stiling et al. 1987, Simberloff and Stiling 1988), 3) previous leaf damage (Faeth 1986), and 4) age of leaves (Quiring and McNeil 1987).

Budbreak phenology can also influence oviposition and, consequently, densities. Some leafmining species embed eggs only on new, supple leaves, perhaps because the ovipositor cannot penetrate mature, toughened leaves. Auerbach and Simberloff (1985) showed that atypical production of new, secondary leaves on *Quercus nigra* resulted in increased densities of two leafmining species that are restricted to oviposit and feed on new foliage. Opler (1974) suggested that late-season generations of the leafminer *Neurobathra bohartiella*, a new leaf specialist, were dependent on early-season defoliations by a dioptid moth that resulted in secondary flushing of new leaves.

It is interesting to note that all of the above features associated with habitat selection are pheromonal, phenological, or morphological, and not phytochemical. Phenological and morphological features of leaves and detection of the presence of co-occurring leafminers may be more important than phytochemistry in determining habitat selection by females. Possible reasons for the absence of correlation of habitat selection and larval survival with phytochemistry are discussed below.

Population Dynamics

Once the feeding substrate has been more or less fixed via oviposition, do factors which influence survival of larval leafminers differ from those which affect free-feeding insects?

Abiotic Factors

Feeding within leaves may ameliorate certain abiotic factors known to affect free-feeding folivorous insects. Because of insulation provided by the leaf, larvae may be less susceptible to external temperature fluctuations. Some species of leafminers continue to feed on evergreen host plants during the winter months in temperate zones despite sub-freezing external temperatures that kill externally-feeding larvae. In some cases, the translucent mine may act as a miniature greenhouse, since dome-shaped blotch mines may magnify sunlight (Hering 1951).

In warmer climates, leafminers continue to feed when external temperatures rise above lethal limits for most externally-feeding insects, perhaps due to the mine's insulation and cooling provided by evapo-transpiration from stomata. Leafmining larvae are less susceptible to desiccation since the environs of the mine provide higher relative humidity than ambient air (Hering 1951). *Cameraria*'s unusually long larval development time (11 months) in Arizona, which includes both extremely warm and sub-freezing temperatures, may be possible due to the amelioration of harsh ambient temperatures. Opler (1974) proposed that leafminers feed longer on evergreen oaks than deciduous ones because of poorer leaf quality. I suggest that these long development times are not caused by phytochemistry, but rather that internal feeding negates many of the climatic hazards of feeding externally. In addition, prolonged development in the case of *Cameraria* appears to reduce attack by predators. The larvae escape ant predation (see discussion of natural enemies below) by remaining small during the summer months when ant activity is greatest and rapidly growing in late winter to early spring when ant activity is low (Faeth, unpubl. data).

Host Plant Factors

Phytochemistry. One might hypothesize that phytochemistry is a crucial factor in survival of leafminers because of their confinement to individual leaves. Variation in phytochemistry is a prevalent explanation for non-random distribution of free-feeding insects (Denno and McClure 1983, Kareiva 1983, Spencer 1988). However, studies of leafminers have usually shown that phytochemistry is either not related to leafminer abundances or shows an inverse relation to that predicted (Feeny 1970, Faeth et al. 1981a, Faeth 1985, Stiling et al. 1982, Bultman and Faeth 1988, Rooney 1989). Similarly, in a detailed study of nutritional (protein) and allelochemical (tannin) variation among and within trees, the distribution of *Cameraria* among or within trees was not correlated with any phytochemical parameters

(Faeth 1990). Moreover, survival of *Cameraria* larvae was not related to phytochemical parameters of individual leaves (Faeth 1990).

The general failure of phytochemistry to explain host plant resistance to leafminers may be accounted for in several ways. First, leafminers, like other endophagous insects, are more specialized on host plants (narrower host ranges) than insects that feed externally (Hering 1951, Powell 1980, D. Tonkyn, pers. comm.) and therefore may be better physiologically and behaviorally adapted to the chemistry of their host plants. However, performance of specialized insects is not necessarily better on their host plants than that of generalists (Bernays and Graham 1988). Second, specialized feeding within leaves by leafminers may circumvent poor quality tissues. Some larvae feed only on selected tissue layers that may be more nutritious and contain lower amounts of fiber and secondary compounds (Needham et al. 1928, Hering 1951). However, some leafminers feed primarily on tissue layers that contain secondary compounds (e.g. palisade layers), and others mine fully through all depths of the leaf such that ingestion of some tissues with secondary compounds is certain. Third, other phenological and morphological features of leaves may override differences in chemistry. This explanation seems most likely. Although phytochemical cues may play some role in the location of adult females of appropriate host plants and leaves within host plants, phytochemical effects on offspring may be less important than phenological and morphological ones. Furthermore, effects of morphology and phenology may interact with effects of competition and natural enemies.

Phenology and morphology. The link between oviposition choice and offspring survival is most evident when host plant phenology and morphology are considered. Endophagism increases risks of larval death from early leaf abscission via desiccation (Askew and Shaw 1979a, Faeth et al. 1981b, Williams and Whitham 1986, Stiling et al. 1987, but see Kahn and Cornell 1983, Pritchard and James 1984), and adults of some species may select leaves within trees based on propensity to abscise (Bultman and Faeth 1986c, Stiling et al. 1987, Simberloff and Stiling 1988). The effect of leaf abscission varies greatly depending on length and seasonality of larval development, leaf area required by larvae, normal leaf duration (i.e. deciduous versus evergreen), and external climatic conditions (early abscission in hot and dry locales may exacerbate desiccation) (Bultman and Faeth 1986c).

Variation in budbreak phenology can directly affect abundances of leafminers via availability of leaves for oviposition, but variable budbreak can also indirectly affect larval mortality. Variation in budbreak leads to differences in ages of leaves which can affect survival, often in complex ways. For example, West (1985) forced oviposition on young, spring leaves by a leafminer that normally oviposits on mature leaves and found that survival on young leaves declined due to interactions with chewing folivores that prefer new leaves. Quiring and McNeil (1987) showed that the dipteran leafminer, *Agromyza frontella*, preferentially searched and oviposited on new leaflets of alfalfa, but apparently because these leaves were less likely to be occupied by conspecifics. A late-season *Cameraria* sp. nov. (*guttifinitella* group), which normally mines mature leaves of Emory oak, will oviposit on new, secondary foliage. Survival is higher in new foliage than mature foliage because these leaves are less likely to abscise than mature leaves (Faeth 1987).

Leaf size can strongly affect larval survival and fecundity, particularly for leafminers that require relatively large areas of leaves for successful development (Bultman and Faeth 1986d). Bultman and Faeth (1986a) showed that four species of leafminers on Emory oak chose leaves for oviposition according to leaf area required for larval development (i.e. leafminers requiring small areas chose small leaves and those requiring large areas chose large leaves). However, leaf size was correlated with survival only for *Cameraria* sp., which requires large leaf areas.

Natural Enemies

Hering (1951) proposed that feeding within mines kept leafminers protected from natural enemies. Powell (1980) implied that endophagous lepidopterans have not evolved characteristics that permit exposed feeding (distastefulness, urticating hairs and glands, aposematism) because endophagism provides protection from natural enemies. Among-guild comparisons are difficult, but apparently natural enemies of leafminers are neither less diverse nor is attack on them less intense than that on free-feeding insects. Invariably, detailed studies of leafminers reveal a wide array of parasitoid species attacking each leafminer species (Askew and Shaw 1974, 1979a, 1979b, Green 1979, Hawkins 1988, Faeth sub. man.). Moreover, natural enemies (parasitoids and predators) typically account for a large fraction, if not the majority, of the mortality of leafmining larvae and pupae (Askew and Shaw 1979a). Many parasitoid species specialize on certain leafmining species by using cues associated with the mine or frass (Hawkins 1988) or even acoustic signals of mining larvae (Sugimoto et al. 1988). At present, then, there is no evidence to suggest that leafminers are more protected from natural enemies than are other herbivorous insects.

At least in some cases, however, the opposite may be true. Gross and Price (1988) found that an obligate gelechiid leafminer on horsenettle is more vulnerable to macroparasite attack than a congeneric facultative leafminer on groundcherry that can depart the mine and move freely over the leaf surface. The horsenettle trichome morphology apparently has selected for mine architectures, which exclude free-feeding and, in turn, increase parasitism. Because of humid and perhaps warmer conditions within the mine, leafminers may also be more susceptible to infection by microbial parasites or pathogens such as fungi and bacteria (Faeth and Bultman 1986).

Natural enemies of *Cameraria* include more than 20 species of Hymenoptera, mostly in the families Encyrtidae, Eulophidae, and Braconidae. Predators are mostly adult parasitoids, which feed on larvae, and the arboreal ant *Pseudomyrmex apache*. Typically, rates of natural enemy attack are from 15 to 40 percent. Natural enemy attack varies among trees and within trees, probably as a function of leafminer densities and local distribution of natural enemies (Faeth 1980), although not necessarily in a density-dependent fashion (Heads and Lawton 1983, Stiling 1987).

Natural enemy attack may also be a complex function of interaction with other herbivores and the ensuing phytochemical and morphological changes they cause. Faeth (1986), for example, showed that leafminers feeding in leaves previously damaged either artificially or by herbivores had significantly increased rates of parasitism. Subsequent experiments indicated that both phytochemical (Faeth and Bultman 1986) and structural (Faeth, unpubl. data) changes induced by herbivory can increase the rate of natural enemy attack.

Competition

Confinement within leaves increases the probability of inter- and intra-guild interactions relative to other folivorous insects. The vagility of free-feeding insects permits behavioral avoidance of both direct (interference competition or cannibalism) and indirect competition as well as amensalistic interactions (exploitation competition, induced defenses, competition via natural enemies). Such is not the case for leafminers. Competition has been shown to occur for hymenopteran leafminers on birch trees (Tuomi et al. 1981), for dipteran leafminers on citrus (Murai 1974), alfalfa (Quiring and McNeil (1984), *Spartina* (Stiling et al. 1984), and American holly (Potter 1985), and for lepidopteran leafminers on oak (Bultman and Faeth 1986b, Auerbach and Simberloff 1989). Cannibalism or killing of co-occurring conspecifics (Condrashoff 1964, Murai 1974, Quiring and McNeil 1984, Auerbach and Simberloff 1989, Faeth 1990) is probably more common among leafminers than free-feeding folivores at comparable densities because of restriction within leaves.

The sedentary nature of leafminers also increases susceptibility to amensalistic interactions with nonleafmining insects. Punctures or tears in mines via feeding by leafchewing or sucking insects can result in desiccation and death of most larval leafminers. Insect damage to nonmined areas of the leaf can increase the propensity of the leaf to abscise (Faeth et al. 1981b, Faeth 1986), change the phytochemistry of the leaf (Faeth 1986), attract natural enemies (Faeth and Bultman 1986, Faeth unpubl.), and increase the likelihood of leaf infection by endophytic or epiphytic fungi (K. Hammon, pers. comm.). Interactions with free-feeding insects are generally unilateral, since mining damage is usually minimal and can be avoided by mobile insects (but see Hartley and Lawton 1987).

Morphological and phenological variation may influence the intensity of intraspecific competition. Competition among leafmining larvae should be a function of relative leaf size as well as density and dispersion of the leafmining larvae. A field study is described to illustrate the complex interactions of variation in leaf size with density, dispersion, and competition among *Cameraria*.

EMORY OAK RESISTANCE TO *CAMERARIA*

Methods

To test the hypothesis that leaf size influences *Cameraria* colonization, dispersion, and subsequent survival via intraspecific interactions, 12 branches of *Q. emoryi* (two branches per six trees) were enclosed with fine mesh screening before budbreak in 1986. Twenty pupae were added to each enclosure on 24 April 1986, about a week after budbreak. Emerging adults were allowed to mate and oviposit on leaves within enclosures. Enclosures were removed at the first appearance of larval mines to allow access of natural enemies and to minimize any cage effects. All mined leaves were marked with a small dot of latex paint so that any abscised leaves could be identified (abscised leaves were collected from beneath trees bimonthly during the study period). Enclosures were again placed on the branches in late March 1987 to capture leaves during the peak of leaf abscission. Pupation and most natural enemy attack occur before this time. Leaves were collected from within enclosures on 3 and 24 April 1987; all leaves had abscised from the branches by the latter date.

Collected leaves were returned to the laboratory and each was examined for the presence and number of mines to determine densities and distribution. Distribution on each branch was tested against a random (Poisson) and, if significantly different, against a clumped (negative binomial) distribution. Densities were plotted against k of the negative binomial to determine the relationship of density and degree of clumping. Sizes of mined and unmined leaves were determined by weighing a random sample of dried leaves in each category from each branch.

Survival (presence of an emergence hole or protruding pupal case) or mortality of each leafminer was ascertained by dissecting each mine. Specific categories of mortality were not ascertained for dead leafminers. Thus I examined intraspecific competition in the broad sense, i.e. how co-occurrence affects overall mortality, be it from cannibalism, depletion of food resources, increased leaf abscission, or changes in rates of natural enemy attack. The question of interest in this study is how leaf size and densities interact to affect survival and thus population dynamics and tree resistance. Other studies in this system have examined specific categories of mortality in detail (Bultman and Faeth 1986b, 1988, Faeth and Bultman 1986, Faeth 1990).

To test for density-dependent effects at the spatial level of the branch, survival of all leafminers, of leafminers occurring alone, of those co-occurring with one conspecific, and of those co-occurring with two or more conspecifics were regressed separately against mean branch densities.

Because of leafminers' confinement within leaves, tests of density-dependent mortality of leafminers may be more appropriate at finer spatial scales (i.e. within leaves of varying sizes with varying numbers of co-occurring leafminers). Log linear analysis was therefore used to determine relationships between the response variable, survival (S), and leaf size (L), number of mines per leaf (M), and aggregation within branches (K), estimated by k of the negative binomial. Plots of k versus branch densities showed that branches fell into two categories: low and high degree of clumping (Fig. 3). Leaf sizes were divided into three categories: small (0-30 mg dry mass), medium (31-60 mg) and large (> 60 mg) leaves. Categories of mines per leaf were one, two, and > two per leaf. The

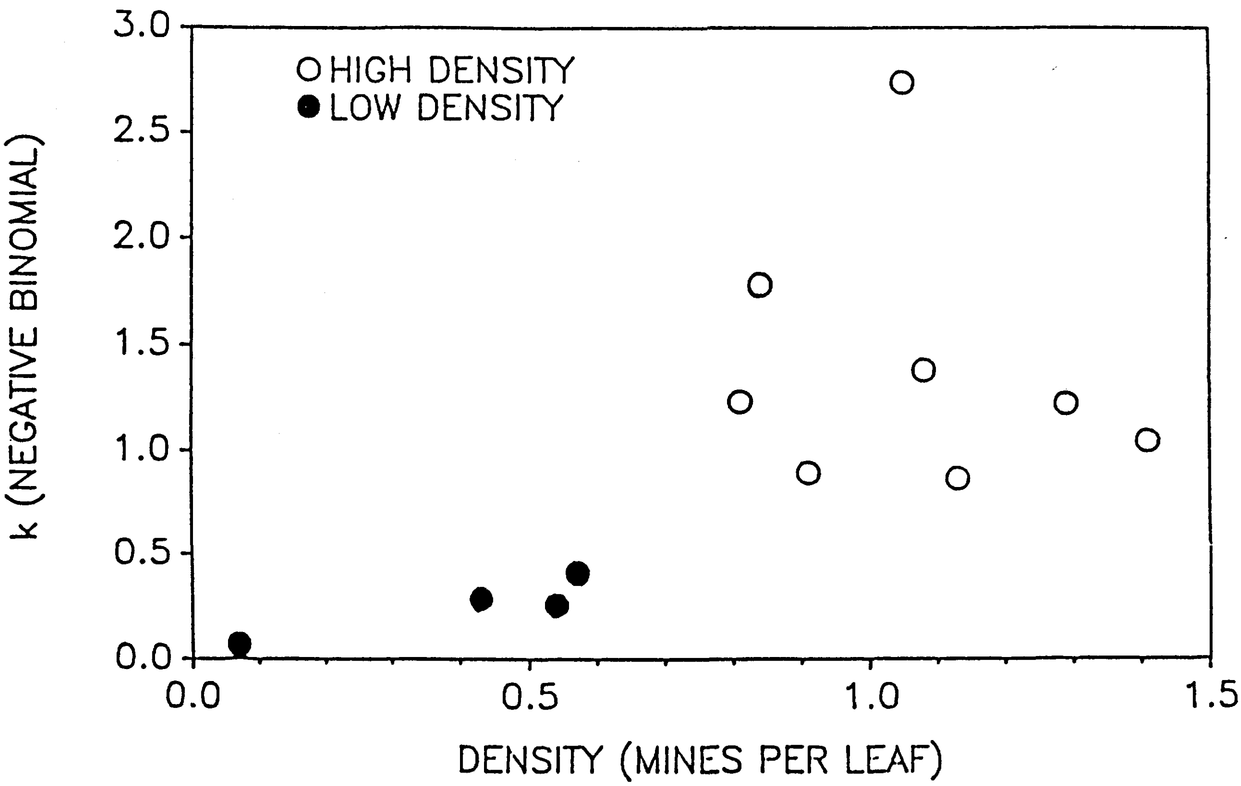

Figure 3. Relationship of density of *Cameraria* and k of the negative binomial.

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response variable, survival, was simply whether each leafminer in each multi-way classification had either survived or died.

Log linear analysis is a powerful method of examining relationships among categorical variables (Jenkins 1975, Vepsäläinen et al. 1988), but it is subject to certain statistical and biological assumptions. I followed the methods of Jenkins (1975) by beginning with the most complex model (all four three-way interactions) and then testing progressively simpler models (dropping complex interaction terms) until the simplest model was found where the log-likelihood ratio was no longer significant at $p \leq .05$. This method assumes that the simplest model is the most biologically relevant one (Jenkins 1975). Data was partitioned in a biologically reasonable fashion based upon previous studies and knowledge of the system. Data was combined from all branches so that cells within the multi-way table were sufficiently large (Vepsäläinen et al. 1988).

Results

Dispersion

Dispersion of leafminers on all branches was significantly different from a random Poisson distribution (Table 1). Generally, more leaves were unmined and more leaves had multiple mines than would be expected by chance. On nine of the 12 branches, dispersions were not significantly different from that expected by a negative binomial (clumped) distribution (Table 1). Leafminers were also more aggregated (smaller k) at lower densities than higher ones (Fig. 3).

Table 1. Spatial distribution of *Cameraria* among leaves within individual branches compared to a random (Poisson) and an aggregated (negative binomial) distribution. Common letters denote branches from the same tree. Chi square tests of significance are based upon deviation of observed from expected. Observed classes with < 5 observations are lumped with previous categories. Number of classes ranged from three (0, 1, > 1 mines per leaf) to seven (0, 1, 2, 3, 4, 5, > 5 mines per leaf).

Branch Chi square	Poisson	p[@] Chi square	Negative binomial	p[@]
1A	82.5	***	0.2	NS
2A	249.8	***	12.1	*
1B	161.4	***	4.7	NS
2B	258.8	***	6.0	NS
1C	65.4	***	8.8	NS
2C	183.3	***	20.8	**
1D	155.0	***	7.0	NS
2D	49.7	***	4.0	NS
1E	39.2	***	1.9	NS
2E	96.8	***	13.4	*
1F	41.1	***	1.2	NS
2F	279.8	***	7.9	NS

[@] NS, not significantly different; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Leaf size

For all branches, mined leaves were significantly larger than unmined ones (Table 2).

Mortality

Mortality was shown to be inversely related to density at the spatial scale of branches whether one considers overall mortality (Fig. 4a) or mortality of leafminers occurring alone (Fig. 4b), with one conspecific (Fig. 4c), or with more than two conspecifics (Fig. 4d).

At the finer spatial scale of individual leaves, the simplest log linear relating survival (S) to clumping (K), leaf size (L), and mines per leaf (M) is: (LK)(LM)(SK)(SM). Inclusion of three-way interactions did not improve the model, nor did inclusion of the two other possible two-way interactions, (SL) and (KM). This model suggests that degree of branch clumping and number of mines per leaf are related to leaf size ((LK) and (LM) terms). Generally, more single mines and fewer multiple mines occurred on small leaves as compared to medium or large leaves (Fig. 5). Survival was a function of degree of clumping both at the level of the branch (SK term) (Fig. 6) and at the level of individual leaves (SM term) (Fig. 6). Under conditions of high branch clumping, survival was lower for leafminers occurring alone or with other conspecifics (Fig. 6). Finally, branch clumping was shown to

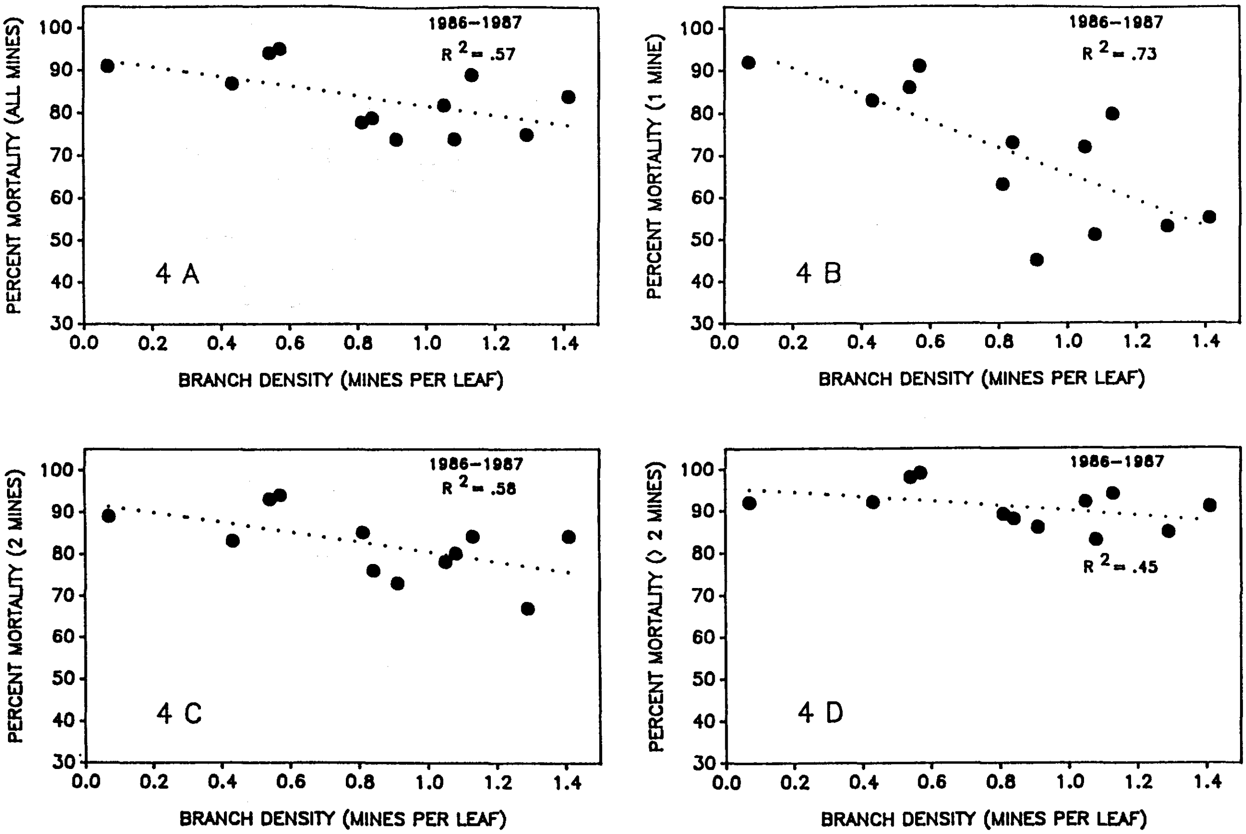

Figure 4. Regressions of mean branch density and mortality for all leafminers pooled (4A), those occupying leaves alone (4B), with one conspecific (4C), or with more than one conspecific (4D). All slopes of regressions are significantly different from zero ($p < 0.05$).

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be a function of available leaf sizes (LK term), and more clumping occurs when mean leaf sizes of branches are small (Fig. 7). Of interest is that the term (SL) is not in the model. Survival was not a function of leaf size (Fig. 8), although adults apparently oviposit more frequently on larger leaves (Table 2).

DISCUSSION

Contrary to expectations, mortality of *Cameraria* sp. nov. appears to be inversely density-dependent, at least at the spatial scale of branches (Fig. 4a-4d). This relationship is most pronounced for leafminers occurring alone (Fig. 4b). Given this result alone, one might conclude that intraspecific competition is not an important process in the population dynamics of this leafminer. Others (Strong et al. 1984, Lawton and MacGarvin 1986) have concluded on the basis of evidence from insect life tables that population dynamics of phytophagous insect populations are generally not driven by competition.

However, consideration of mortality only at the level of branches may obscure the complex interactions underlying the dynamics of *Cameraria*. The more appropriate scale may be that of the leaf because, after all, that is where ultimate oviposition choice and larval-larval interactions occur. When

Table 2. Mean size in mg (± SE) of all (mined and unmined leaves) and mined leaves. Sample sizes of each category for each branch are in parentheses.

Branch	Mean size of all leaves Mean ± SE (N)	Mean size of mined leaves Mean ± SE (N)
1A	26.24 ± 11.28 (50)	36.24 ± 10.18*** (41)
2A	27.46 ± 12.26 (50)	40.95 ± 13.26*** (99)
1B	32.75 ± 16.01 (50)	44.61 ± 16.47*** (99)
2B	34.00 ± 16.71 (50)	48.98 ± 18.97*** (122)
1C	38.69 ± 19.49 (50)	45.90 ± 16.10** (125)
2C	42.71 ± 19.49 (50)	51.20 ± 17.56** (172)
1D	48.63 ± 20.39 (50)	58.85 ± 19.30** (77)
2D	38.98 ± 18.57 (50)	49.72 ± 14.01*** (132)
1E	40.57 ± 19.64 (50)	52.44 ± 18.00*** (151)
2E	38.17 ± 21.71 (50)	55.29 ± 19.88*** (147)
1F	38.97 ± 19.21 (50)	48.69 ± 19.81** (126)
2F	37.68 ± 16.48 (50)	48.76 ± 15.17*** (170)

** Significantly different mean size of mined leaves compared to mean size of all leaves by Student's t test at $p < 0.01$

*** Significantly different mean size of mined leaves compared to mean size of all leaves by Student's t test at $p < 0.001$

one considers mortality at the level of leaves, a different picture emerges. Survival is a function of number of mines per leaf. Most of this increase in mortality (and decrease in pupal mass, and thus fecundity, of survivors) with mine number is attributable to cannibalism, and, secondarily, to premature leaf abscission (Faeth 1990). Translated into the spatial scale of branches, survival becomes a function of how clumped larvae are, with greater clumping leading to decreased survival (Fig. 6). Clearly, *Cameraria* mortality is density-dependent, but only when one examines the proper spatial scale.

I propose that Emory oak resistance to *Cameraria* is based in part on variation in leaf sizes, which influences the two components of tree resistance, colonization by ovipositing females and survival of larval offspring. At the level of the branch, clumping appears to be a function of available leaf sizes (LK term) (Fig. 7), with mean leaf size of the branches explaining a significant ($R^2 = 0.43$) proportion of the variation in k, an index of clumping. At the scale of individual leaves, number of mines per leaf is also related to leaf size (LM term). Rejection of small-sized leaves for oviposition (Table 2) is the likely mechanism for clumping within branches and among leaves (Faeth 1990). Rejection of small leaves may be selected through survival of offspring. A larva requires relatively large areas of Emory oak leaves successfully to complete development. Of the 1,915 mined leaves examined in this study, no leafminer survived in leaves of less than 20 mg dry mass. A critical lower size limit thus exists below which survival of even single leafminers does not occur. Thus branches or

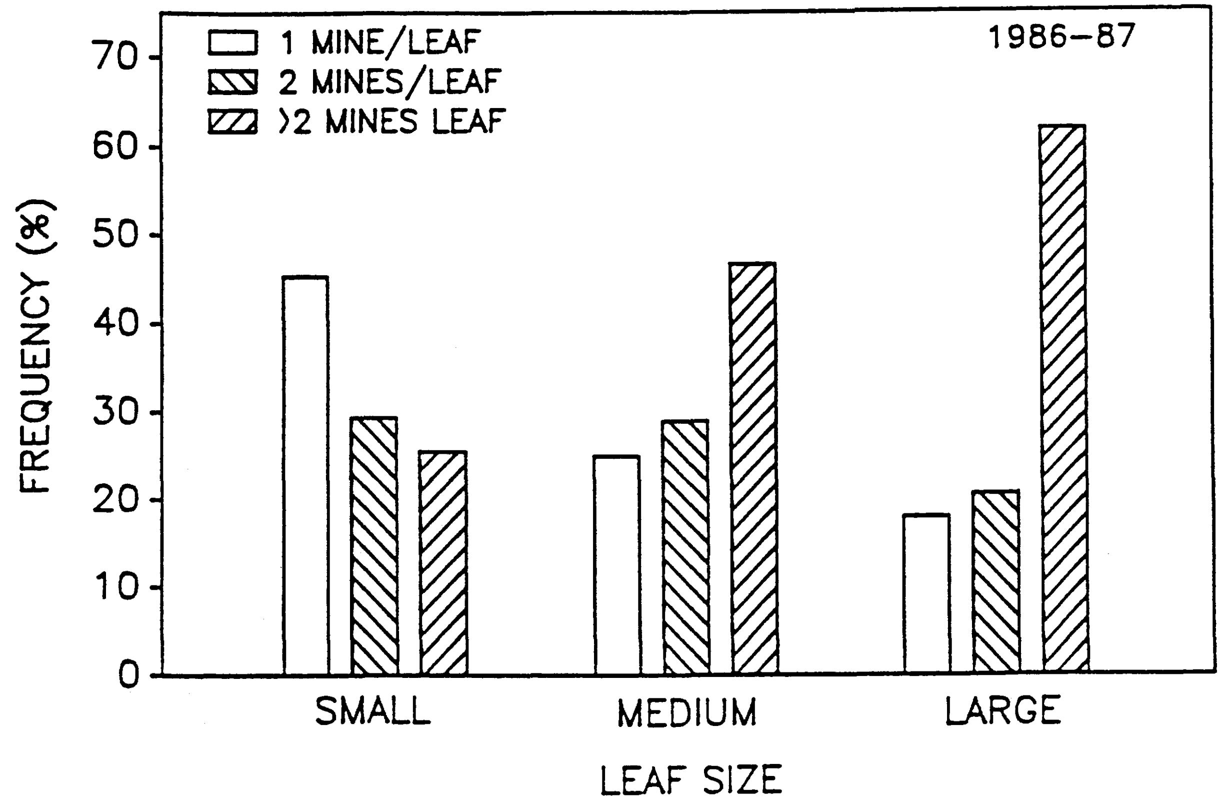

Figure 5. Percent of leafminers occurring on small-, medium- and large-sized leaves by number of mines per leaf.

trees with smaller mean leaf sizes may be more resistant at oviposition because fewer eggs are laid and those that are tend to be highly clumped on the reduced pool of suitably sized leaves. The high degree of clumping suggests that these females do not have an oviposition deterring pheromone as do some other leafminers (McNeil and Quiring 1983, Simberloff and Stiling 1988, Auerbach and Simberloff 1989), although this is yet to be determined.

Increased clumping clearly results in increased larval mortality, the second component of tree resistance. Co-occurrence exacerbates cannibalism, exploitation competition, and premature leaf abscission. Leafminers in highly clumped branches have lower survival when occupying multiply or singly-mined leaves (Fig. 4a-4d). When survival in individual leaves was examined, only 25 of the 1,617 multiply-mined leaves in this study had two larvae that survived simultaneously, and none had more than two. The consequences of confinement and co-occurrence in terms of intraspecific competition are thus severe. Colonization in the next growing season may be reduced and resistance thus reinforced if colonization occurs primarily in situ. Since pupation and emergence occur in leaves that have fallen beneath relatively isolated oak trees at the study site, this prediction may hold. Experiments are underway to test this hypothesis.

In 1987 we tested leaf size as a predictor of resistance independently by correlating leafminer densities with mean leaf size on eight Emory oak trees. Mean leaf size is a good predictor of density and explains a significant proportion of the variation in densities ($R^2 = 0.41$) (Fig. 9). Considering the multifarious factors that can influence host plant resistance to insects, it is noteworthy that a single parameter, mean leaf size, can predict a large part of oak tree resistance to leafminers.

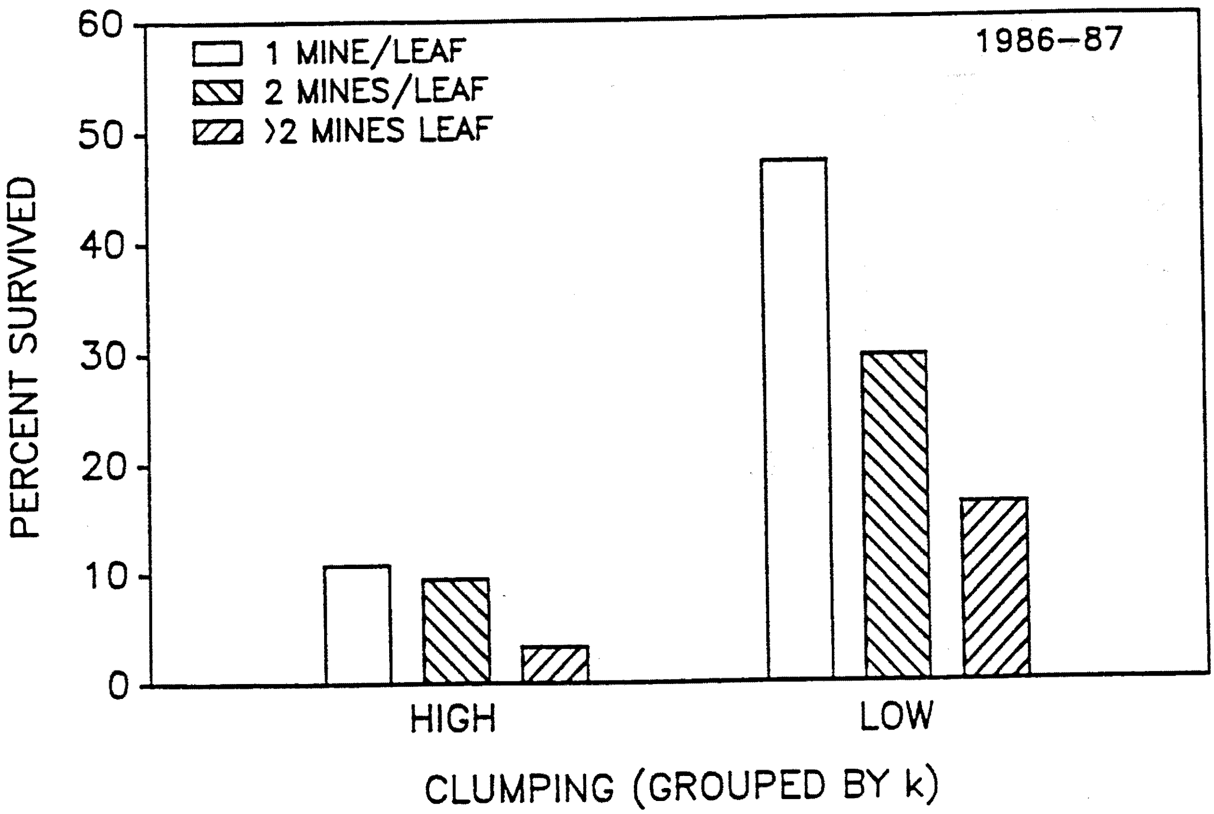

Figure 6. Survival of leafminers occurring alone, and with one or more conspecifics on branches grouped by high (n = 4) or low (n = 12) degree of branch clumping as indicated by k of the negative binomial.

Certainly, leaf size does not explain all the variation in tree resistance to leafminers. Two other phenological factors, variation in premature leaf abscission and timing of budbreak, can also influence colonization and survival. For example, Bultman and Faeth (1986c) showed that leaf abscission rates are greater in sun leaves compared than leaves and can explain some variation in both distribution and mortality. Others (Askew and Shaw 1979a, Faeth et al. 1981b, Potter 1985, Stiling et al. 1987, Simberloff and Stiling 1988, Auerbach and Simberloff 1989) have shown that premature leaf abscission is an important factor in leafminer survival. Higher rates of premature leaf abscission for sun leaves (Bultman and Faeth 1986c) may explain why leaf size accounts for less variation in *Cameraria* densities on sunny than shaded leaves (Fig. 9) (sun leaves $R^2 = 0.27$, shade leaves $R^2 = 0.51$).

Variable budbreak probably influences initial colonization also, since colonization is closely synchronized with budbreak. For example, unusually warm weather in the spring of 1988 caused early budbreak accompanied by emergence of leafmining adults. A late frost then occurred, many new leaves were destroyed, and further budbreak ceased on some trees until after adults had disappeared. These events may explain some reversals in tree resistance in 1988. Tree C, for example, exhibited delayed budbreak, and resistance greatly increased in 1988 as compared to previous years (Fig. 1). Obviously, both variable budbreak and abscission may act to intensify intraspecific interactions if the pool of suitable leaves for oviposition is enlarged and increased clumping ensues.

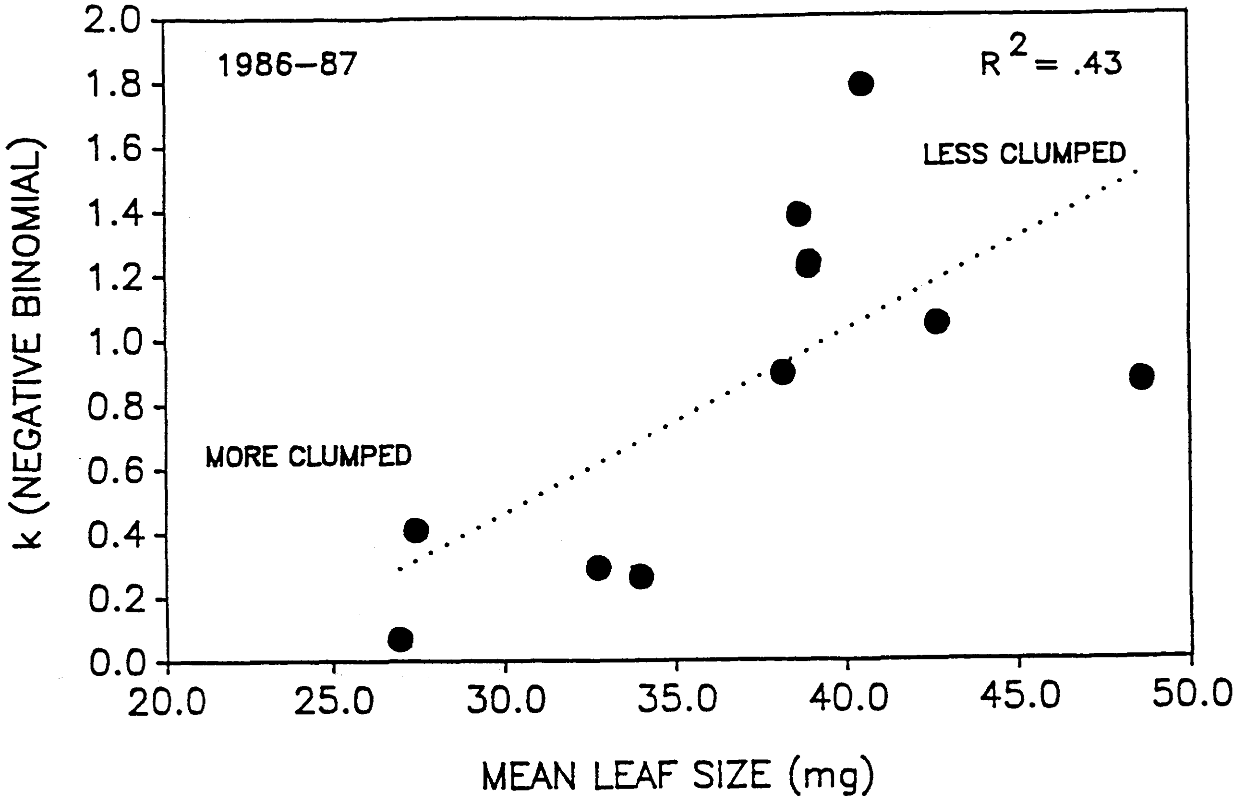

Figure 7. Relationship of clumping (k) and mean leaf size of individual branches. Slope of the regression is significantly different from zero ($p < 0.05$).

It is important to note that neither foliar nutrition nor allelochemical variation, long the bastion for explaining resistance of host plants to phytophagous insects, appears to determine Emory oak resistance to *Cameraria* (Faeth 1990). This is not to say that phytochemistry is not important in adult selection of, or larval survival in, leaves. Leaf size, for example, probably co-varies with some phytochemical parameter used by ovipositing females. It does seem, however, that variable phenology overrides variable phytochemistry in the dynamics of this leafminer.

It is premature to suggest that host plant resistance to other species of leafminers is driven mainly by phenological factors and their effects via competition. Leaf size, for example, may have little effect on leafmining species that require relatively small leaf areas for development or remain at low densities such that co-occurrence on leaves is rare. The latter situation is typical for most leafmining species, as it is for other guilds of phytophagous insects (Schultz 1983, Barbosa and Schultz 1987). A multitude of biotic and abiotic factors may be responsible for keeping populations of most phytophagous insects at low levels. I suggest, however, that the "ceiling" (sensu Strong 1986) on population densities of *Cameraria* and possibly other species in the leafmining guild is set by the interaction of phenological and morphological factors and competition. For example, in 1987, 50 pupae were introduced into the same branch enclosures (2.5x the number introduced in 1986) in an effort to boost densities and thus interactions. Yet leafminer abundances were not different from those in 1986 (1986 $x = 0.844$ (± 0.37) mines/leaf, 1987 $x = 0.986$ (± 0.73) mines/leaf, paired $t = 1.04$, $df = 11$, and $p > 0.20$). Branches and trees may thus be saturated in this system, although many leaves were not mined because they were either 1) of unsuitable size, 2) likely to abscise, or

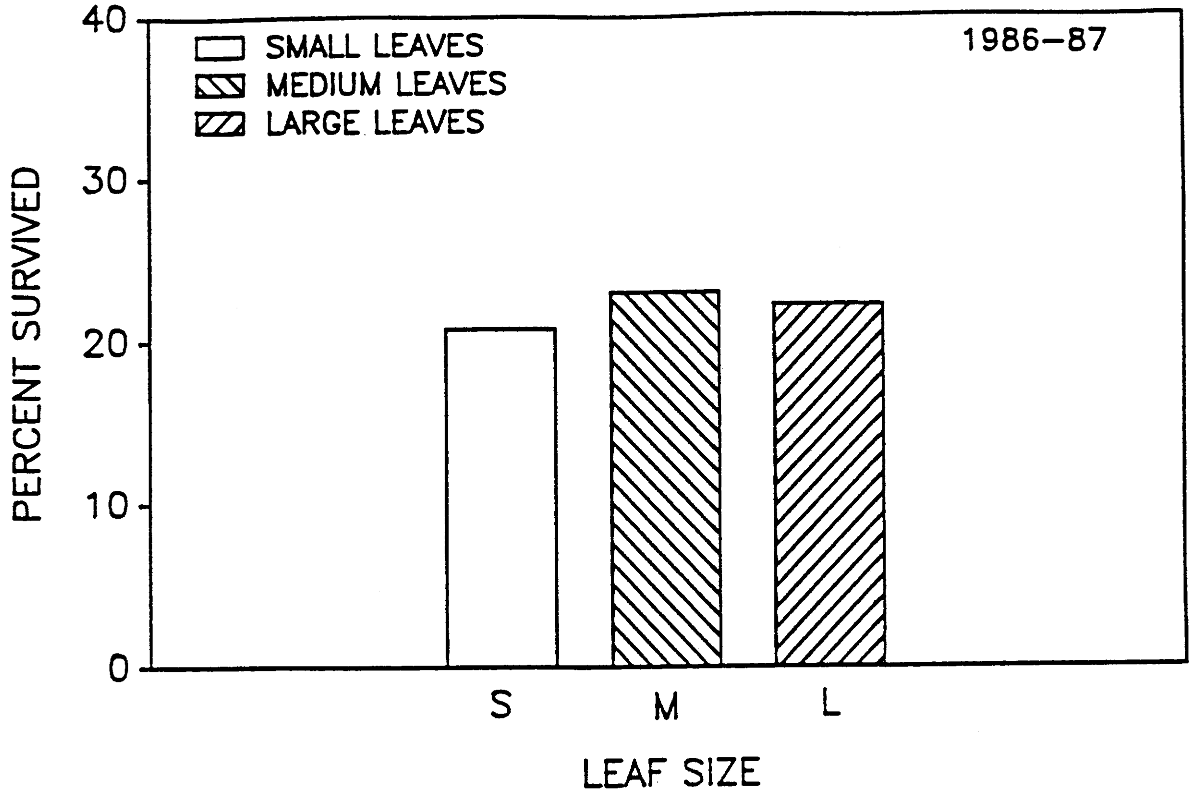

Figure 8. Percent of leafminers surviving on small-, medium-, and large-sized leaves. Data from leaves with varying numbers of mines per leaf were pooled. The interaction of leaf size and survival is not a significant term in the log linear model.

3) unavailable for oviposition due to variable budbreak or time and energy constraints on female search. Saturation is further indicated in that leaf size per se, is not related to survival (Fig. 8). The risks of co-occurring with other conspecifics on larger leaves may be balanced by risks of mining alone on smaller leaves when densities are saturated.

The "ceiling" on *Cameraria* populations may be much lower than expectations based upon simple density estimates, especially if one considers the relationship between density and mortality at the wrong spatial scale. Variation in phenology and morphology and search constraints on females may restrict the pool of high quality leaves such that competition occurs at relatively low densities.

SUMMARY

Leafminers are endophagous insects that spend all or part of their larval feeding stages confined within leaves. Oviposition thus determines larval feeding sites among and within host trees and leaves. Host tree resistance to leafminers may be a function of initial colonization via female ovipositional preferences and the way in which these preferences translate into survival of offspring. For leafminers, ovipositional choice and offspring survival may be more closely linked to variation in tree and leaf phenology and morphology than they are for free-feeding insects.

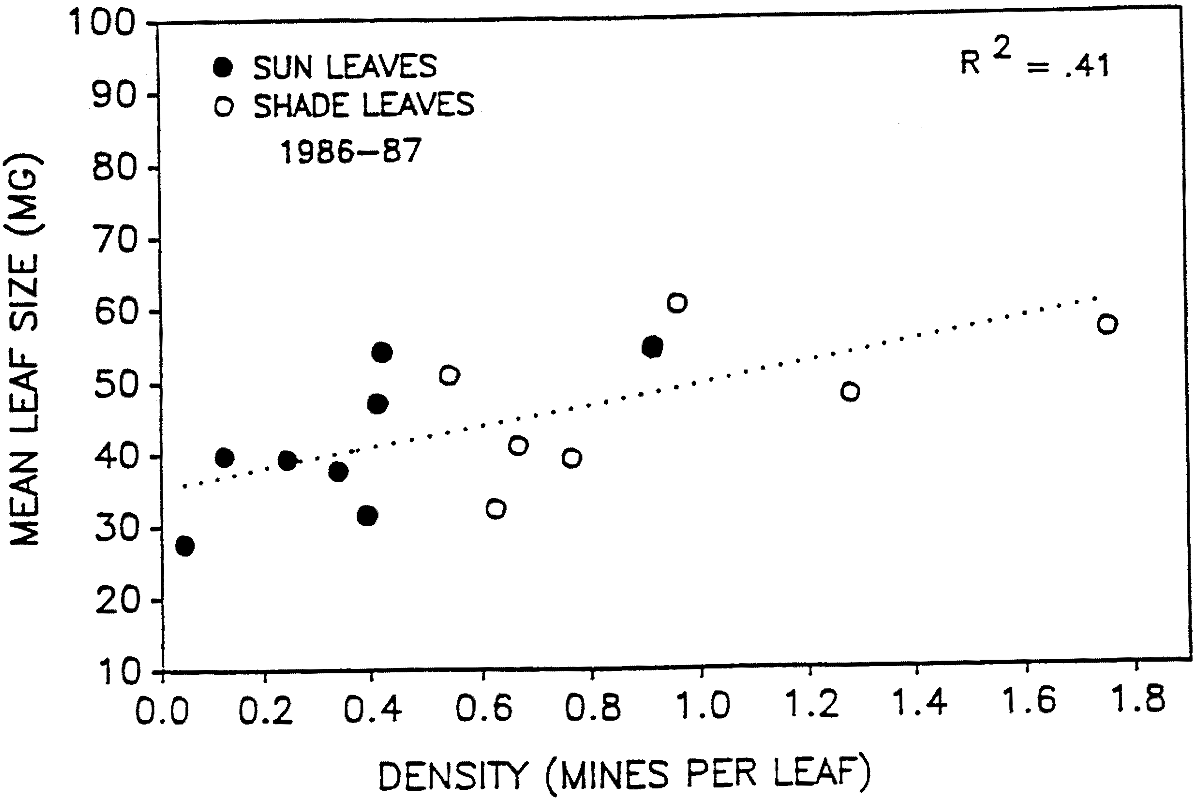

Figure 9. Regression of mean size against density of *Cameraria* on sun and shade leaves from eight Emory oak trees. Slope of the overall regression (sun and shade data combined) is significantly different from zero ($p < 0.05$).

To illustrate these arguments, patterns of abundances and distribution of a dominant leafminer, *Cameraria* sp. nov., on *Quercus emoryi* are described. These patterns appear to be determined mostly by variation in leaf sizes among and within trees, which in turn causes variation in intensity of intraspecific competition among ovipositing females and their larval offspring.

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THE WITHIN-TREE DISTRIBUTION OF CATERPILLAR MINES

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INTRODUCTION

Lepidoptera is a relatively young order and one of the largest and most diverse in the Insecta. The first paleontological vestiges of moths were found among lower Jurassic deposits, but the most intensive lepidopterous evolution (mainly in suborder Ditrysia = Papilionina) took place in the mid-Cretaceous Period, coterminous with the expansion of angiosperm plants. The flowering plants were a highly determinant factor in the development of the environment, their influence on moth speciation extending beyond provision of food for caterpillars and adults. The greatly increasing heterogeneity of plants in space and time became a base for many potential ecological niches, many of which were afterwards occupied by lepidopterous species. Paleontological data indicate that the mining mode of life was already formed in the first stages of lepidopterous evolution (Kozlov 1988). In recent time, mining caterpillars can be found in nearly all large groups of Lepidoptera. The mining moths are the most specialized ecological group, characterized by important morphological and physiological adaptations at larval stages. They interact very closely with their host plants. Applicability of the term "parasitism" to the mining moths is now under discussion: some authors consider all insects feeding on living plants to be parasites; others question the value of so broad a use of the term. Dogel (1962) wrote, "The parasites are organisms which use other living beings as environment and source of food and make their hosts responsible (partly or completely) for regulation of their interactions with external space." In line with this definition, we consider mining insects true parasites on their host plants.

In this paper, we consider the question how mining caterpillar distribution on host plants reflects topical aspects of the coevolution of insects and plants.

The Heterogeneity of Different Plant Parts and Their Influence on Herbivorous Insects

Leaves on annual shoots differ in morphological, anatomical, and biochemical aspects. This phenomenon is called heterophylly (Serebryakov 1962). Important changes in leaf anatomical structure on annual shoots were described for the first time in Zalensky's (1904) classic work on more than 40 plant species. Apical leaves of all studied plant species are more xeromorphic than basal ones: they have more ribs per surface unit, smaller epidermal cells, smaller mesophyllic cell diameters, thicker epidermal cell membranes, and more developed mechanical tissues.

Krenke (1940) attributed heterophylly to the ontogenetic origin of leaves from structures of different ages. He established the cyclic character of metameric variability: the complete cycle can be described by the unimodal convex curve. This curve reflects changes in morphological and anatomical

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BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

characteristics (leaf size, for example) and physiological processes, but serves only as theoretical background for the primary changes occurring with age. The majority of physiological processes, taking place during the ontogeny of each organ and plant as a whole, follow the unimodal curve; the length of its parts and the maximal point are different for various processes (Gupalo 1975, Klyachko and Kulaeva 1975).

Analyzing the annual shoot structure of *Liriodendron tulipifera*, Vasiliev and Goltsova (1979, 1980) distinguished six characteristic groups by the type of curve describing their changes. They stressed that the variability of external leaf characteristics is more pronounced than that of internal ones. The diversity of organ characteristics is greater than that of tissues and cells.

The structure of a leaf depends both on its location on a shoot and the type of shoot. For example, the leaves of *Populus alba* short shoots are similar to the leaves on the base of the long ones (Pautov 1989). The peculiarities of leaves on different types of shoots are determined not by the differences in the structure of their growing apexes, but by development conditions.

Leaf structure may be affected by environmental factors as well. Zalensky (1904), for example, showed that xeromorphic features increase in leaves as one moves from the basal to the top parts of a shoot.

Initiation of different leaf elements in the bud does not take place not simultaneously. Accordingly, one can distinguish leaf parts different in age and different, therefore, in anatomical, morphological, and biochemical features. Basal and apical parts of a long leaf are known to be distinguished in the same way as basal and apical leaves on the shoot (Tshizhevskaya 1954).

Thus we may conclude that both different leaf parts and different leaves on a shoot are distinguishable by anatomical, morphological, and biochemical features, which may determine their suitability for herbivorous insects. Let us consider, then, the ability of insects to distinguish specific leaf characteristics.

One of the first reports on the ability of females to evaluate the size of host plant leaves demonstrated that egg clutch size of the lilac moth, *Caloptilia syringella* F. (Polejaev 1939), was positively correlated with leaf size. Similar results were obtained for the mining moths inhabiting oak *Quercus emoryi* (Bultman and Faeth 1986b) and for larvae of the mining fly, *Pegomyia nigritarsis* Zett., feeding on different Rumex species (Godfray 1986). The importance of this phenomenon promoting optimal food utilization is obvious, but its mechanisms are still unknown. Leaf preference of attelabid beetles, on the other hand, is determined by length of the leaf margin which the female runs along (Sakurai 1988a, 1988b).

The ability of the papilionid butterfly, *Battus philenor* L., to distinguish leaf shape has also been described. Females of this species prefer to lay eggs either on the wide-leaved *Aristolochia reticulata* or on the narrow-leaved *A. serpentaria*, depending on their individual experience. The leading role of vision in this process is confirmed by the fact that these females also visit nonhost plants with either wide or narrow leaves (Rausher and Papaj 1983, Papaj 1986).

The female orientation to the color of the host plant leaf has been described for the fly, *Pegomyia hyoscyami* Panz., which lays its eggs on the dark, oldest leaves of beets. Leaf color in autumn is the chief criterion in choice of host trees by migrating female aphids *Periphyllus californiensis* Shinji: the majority of females prefer yellow-orange leaves, some of them prefer red, and all ignore yellow-green and green leaves. The species of the host plant, *Acer amoenum* or *A. palmatum*, is not a factor in the choice (Furuta 1986).

The shape and color of leaves are usually distinguished by the insects remotely. Any additional information about plant chemistry and its surface structure is received by touch. Host plant selection and orientation on leaf surface depend considerably on composition of the cuticular wax components. These components determine, for example, host plant selection by the aphid *Acyrthosiphon pisum* Harr., stimulate egg laying by the fly *Pegomyiabetae* Curt., and increase the number of feeding probes by the weevil *Sitona lineatus* L. (Klingauf et al. 1978). The cuticular wax composition also influences host plant selection by the aphid *Tuberculoides annulatus* Hart. (Kennedy 1986a), but for this species microrelief of leaf surface is of greater importance. *T. annulatus* inhabits the rough leaves of *Quercus robur*, and does not like the smooth leaves of *Q. ilex*. Tarsi of the aphid *Myzocallis schreberi*, by contrast, can be easily fixed on smooth surfaces with the help of a drawing empodium (Kennedy 1986b). The tarsal morphology of the cicadid *Empoasca fabae* is adapted for fixation on smooth leaf surfaces, which is why this species avoids haired varieties of soya (Lee et al. 1986). Thus host plant preference is often determined by insect tarsus morphology.

Hairs on the leaf surface inhibit insect movements and can prevent feeding or egg laying. Although female *Diaphania nitidalis* and *D. hyalinata* moths are not able to distinguish extracts from hairy and hairless leaves of the cucumber *Cucumis sativus* in experimental conditions, they lay more eggs on smooth leaves. It is thought that this preference is a function of tactile stimulation (Elsey and Wann 1982).

The physiological condition of the host plant also affects insect development. Plant weakening is sometimes known to be accompanied by a decrease in its resistance to pests. Decrease in resistance is caused, in turn, both by reduction of allelochemicals and changes in acidity and osmotic pressure of cellular liquid toward promotion of insect development (Radkevich 1980). Baranchikov (1983) divides factors of plant resistance into two groups: those based on origin--passive and active factors--and those based on direction of effect--general and specific factors. The passive factors are characteristic for a plant independent of its relations with insects, and active factors come into play as a response to damage. General resistance depresses successful development of all herbivorous species, specific resistance that of unspecialized herbivores only. During leaf ontogeny, specific resistance factors are replaced by general ones, accounting for the different food values of young, mature, and old leaves for specialized and nonspecialized consumers.

The specificity in food preference is a general adaptation of phytophagous insects to a heterogenous, "spotted" habitat formed by host plant parts. The first detailed analysis of parasite specificity was made by Dogel (1962). According to Dogel, specificity is a norm of parasite response to environmental conditions or a close connection between parasites and their hosts. Slepyan (1973) extended the concept of specificity. He classified specificity into three forms: hostal, topical, and ontogenetic. Hostal specificity is identical to that defined by Dogel. Slepyan called the preference by parasites for a certain place on or in the host body topical specificity. It is of great importance for less mobile organisms with highly localized feeding, mining moth caterpillars, for example. According to Slepyan, ontogenetic specificity is the ability of parasites to develop in host organs of a certain age and offering certain morphological and physiological conditions. Since in the vigorous plant the individual age of each serial homological part, such as leaves on the shoot, is strongly connected with its place among other metameres, topical and ontogenetic specificity are identical in the context of our work. The influence of host tree age on insect mine distribution has not been investigated.

The irregularity of mine distribution in some spring moth species is connected with the dates of leaf appearance. For example, female Eriocraniidae moths deposit their eggs in birch buds, and that is why the larval mines are usually located on the first or second leaf of a shoot. This phenomenon may be called false topical specificity.

Thus heterophylly and the heterogeneity of leaf parts, together with the ability of phytophagous insects to discriminate almost all morphological and physiological characteristics of host plants, lead to the irregularity of insect mine distribution on leaf parts, on leaves of shoots, and on the types of shoots put forth by host trees.

The objective of this paper is to describe the mine distribution of 34 moth species belonging to the families Nepticulidae, Tischeriidae, Gracillariidae, and Coleophoridae on 22 host tree species.

MATERIALS AND METHODS

Material for this work was collected from 1986 to 1989 in Leningrad, Murmansk, Moscow, Voronezh, Kiev, the Kujbishev districts, the Krasnodar and Primorje areas, and Georgia.

Mine distribution on the parts of a simple leaf was investigated according to the method elaborated by Shevtchenko (1958). The leaf was subdivided into strips of equal area perpendicular to the central leaf rib and in twice the number of strips parallel to this rib. The number of mines was calculated in every rectangle of this net; data for right and left leaf parts were compiled. Equal strip areas allow us to describe the empiric functions of mine distribution along both coordinate axes of the investigated two-dimensional space. The ratio between the mine number and the rectangle area can be used to represent the niche structure in volumetric diagrams (Fig. 1). The height of the columns is related to the number of investigated mines, but the ratio between heights is specific for every insect and its host plant. The simpler method is the calculation of mine number in leaf parts between the lateral ribs. It should be noted that diagrams of mine distribution along the central leaf rib are different for the two described methods.

The leaves on annual shoots, the leaflets of the compound leaf, and the parts of the simple leaf were numbered from the base to the top of the organ. The mine distribution on the crown of a tree is described by their ecological density: the share of mining leaves in a probe. Mine distribution on the different leaf parts was compared by Chi-square and lambda methods and Kholmogorov-Smirnoff criteria (Sachs 1972).

The niche overlap of coexisting species was calculated according to Slobodchikoff and Schultz (1980):

$$\alpha = 1 - \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{k} |p_{ij} - q_{ij}|$$

where p_{ij} and q_{ij} are the mine frequencies of coexisting species in the rectangle with i and j coordinates, and n and k are the number of vertical and horizontal strips of the sample leaf. Mine localization on compound leaves or annual shoots was described by one coordinate (the number of leaves or leaflets), and niche overlap was calculated by the modified formula:

$$\alpha = 1 - \frac{1}{2}\sum_{i=1}^{n} |p_i - q_i|$$

A degree of interaction between coexisting species was measured by D/W ratio, where D is the difference between the mean value of resource consumption and W is the mean standard deviation (Giller 1984). The ratio $D/W < I$ indicates the potentially strong competition between coexisting species. The ratio $D/W > 3$ indicates that the interaction is all but absent. The D/W criterion can be used for the dome-like function only. Calculating niche overlap for the border values of this criterion we found $\alpha > 0.70$ indicates strong competition and $\alpha < 0.26$ the absence of interaction.

Non-mined leaves with identical numbers gathered from equal annual shoots at the same height and on the same side of a tree crown were used to investigate leaf venation. The leaves were treated for lighting by sulfuric acid and alkali and colored by gentian violet and saphranin (Isakov et al. 1984). Venation density of leaf parts was calculated by measuring the number of crossings of ribs per unit of leaf length with an ocular ruler. The lighting conditions of mined and nonmined leaves were measured by luxmeter. The results were analyzed using standard statistical methods.

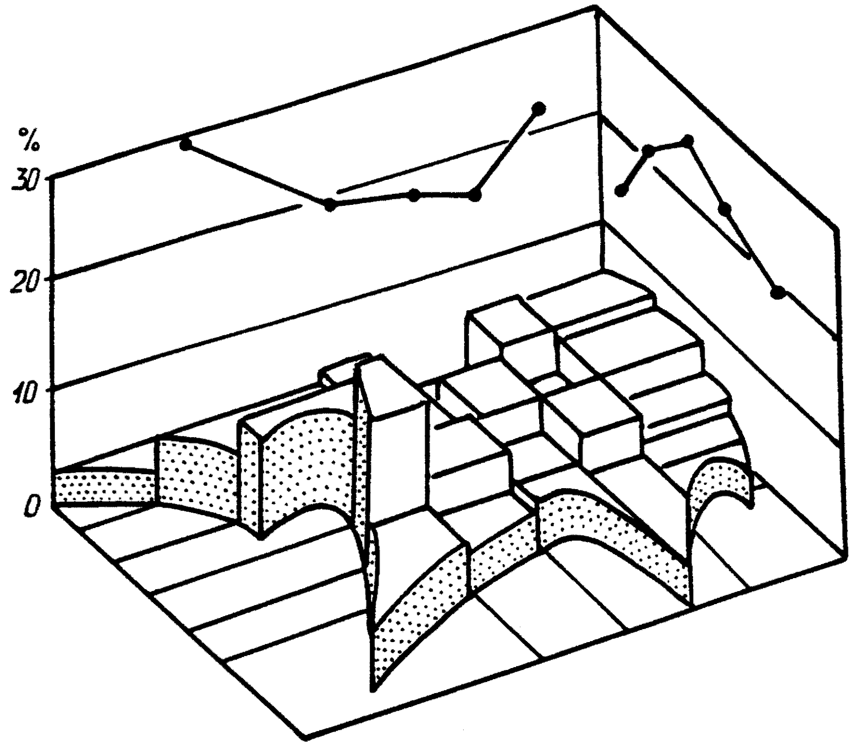

Figure 1. The scheme of leaf subdivision of the strips of equal area and volumetric diagram of niche structure: *Stigmella ultima* Pupl. on *Acer mono* (Primorye Region).

RESULTS

Types of Mine Distribution on the Host Plant

Leaf Parts and Leaflets

The distribution of mines over leaf parts was analyzed for 34 lepidopterous species on 18 host plants. Types of mine distribution over both sectors of simple leaves and over leaflets are similar. They are described by the convex curve with one maximum on 2 to 5 sectors or leaflets (Fig. 2). Two-dimensional analysis shows the pattern of mine distribution over simple leaves to depend on both insect species and host plant species. Significant distinctions in mine distribution are typical both for different moth species inhabiting the same host plant (Fig. 3) and for the single insect species feeding on different types of leaves on the same host plant. For example, the distributional pattern of *Lithocolletis issikii* Kum. mines on the large stool shoot leaves of *Tilia cordata* differs from that on ordinary leaves: $\chi^2 = 18.19$ and 17.85; the level of significance for both coordinate axes is 0.99 (Fig. 4). The mine distribution of *Lithocolletis* sp. on brachyblast and auxyblast leaves of aspen *Populus tremula* also differ significantly (Fig. 5). The distribution of *Lithocolletis issikii* Kum. mines along the midrib of the leaves of *Tilia cordata* from short and long shoots differ with the level of significance 0.999 ($\chi^2 = 24.32$ and 29.89 respectively), as do the leaves of different areas.

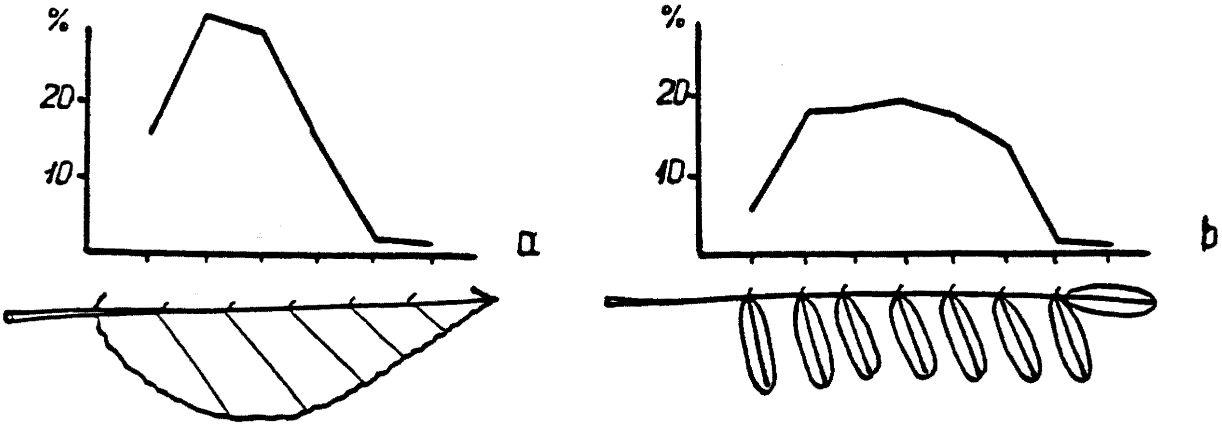

Figure 2. The mine distribution among the leaf parts of simple leaf (a) and among the leaflets of compound leaf (b): a = *Stigmella malella* Stt. on *Malus domestica* (Krasnodar); b = *St. sorbi* Stt. on *Sorbus aucuparia* (Leningrad).

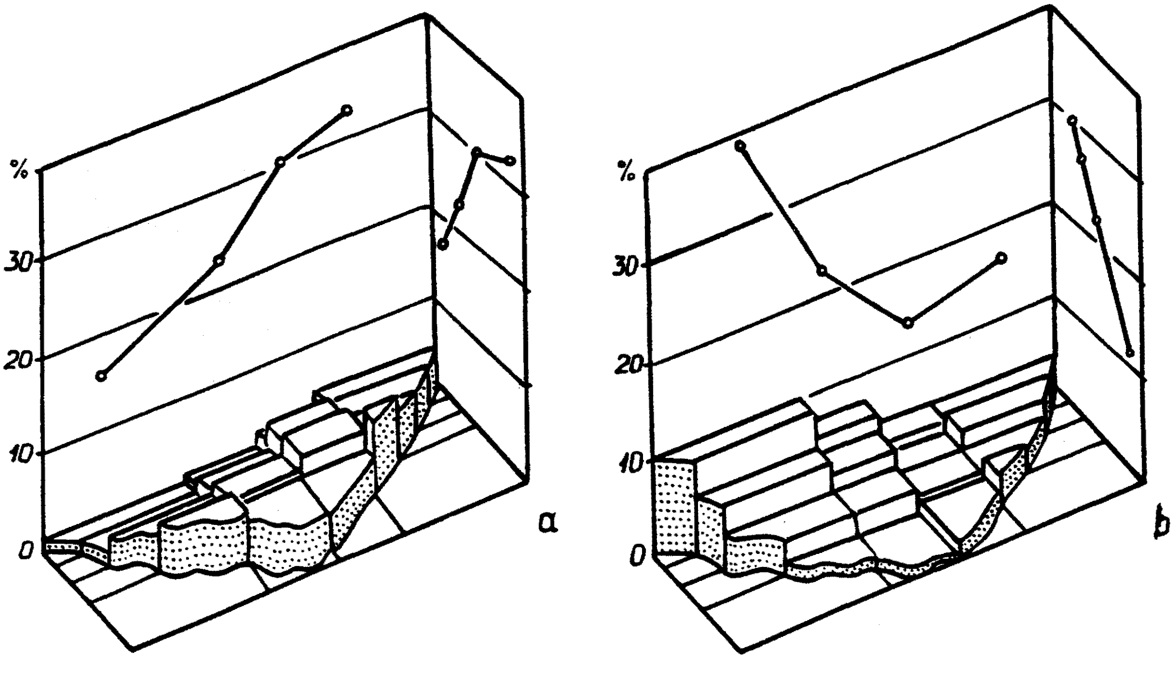

Figure 3. The mine distribution of coexisting species on leaf parts: a = *Stigmella* sp. and b = *Lithocolletis malella* Gram., both on *Mespilus germanica* (Georgia).

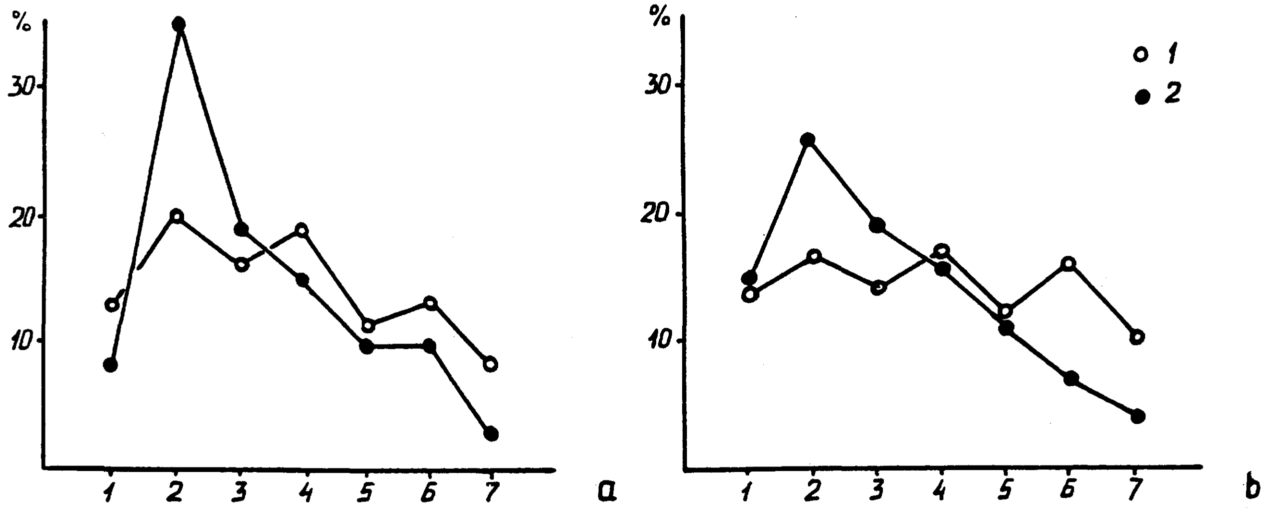

Figure 4. The mine distribution on leaf parts of two leaf types: *Lithocolletis issikii* Kum. on *Tilia cordata* (Kiev). 1 - shoot leaves, and 2 - ordinary leaves; a - parallel to central vein and b - perpendicular to it.

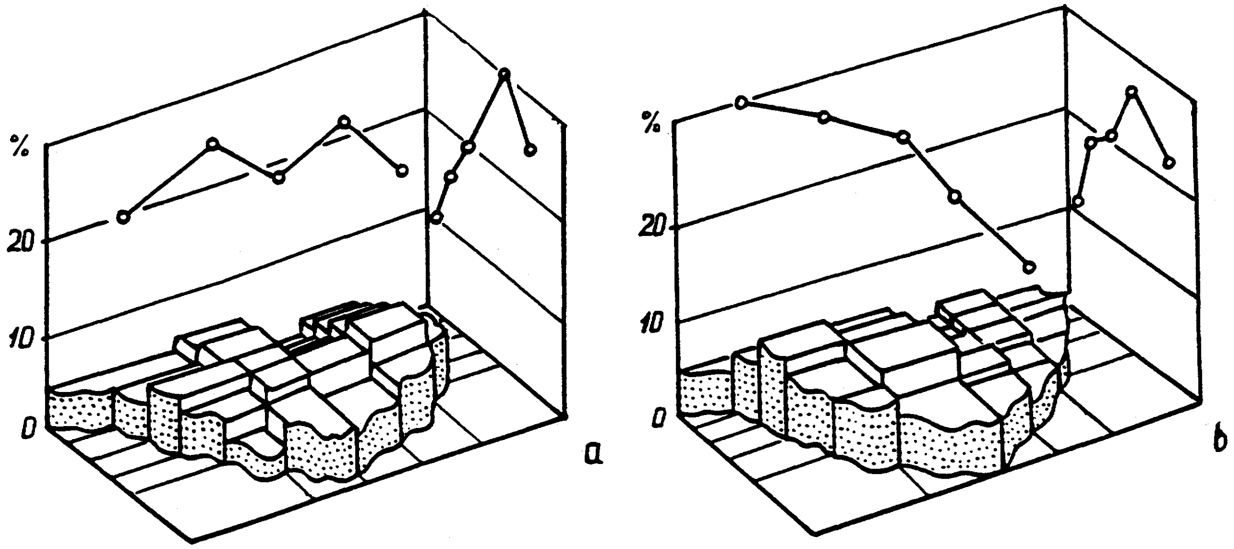

Figure 5. The mine distribution on leaf parts of leaves from two shoot types, *Lithocolletis* sp. on *Populus tremula* (Leningrad): a - auxyblasts; b - brachyblasts.

Comparison of mine distribution in four populations of *L. issikii* Kum. (from Kiev, Kuibyshev, Voronezh, and Moscow) showed geographical variability of this feature (Fig. 6); it is probably dependent on morphological and biochemical differences in leaves of host plant populations. The distribution of *Stigmella nylandriella* Tengstr. mines on leaflets of a compound rowan tree leaf differ

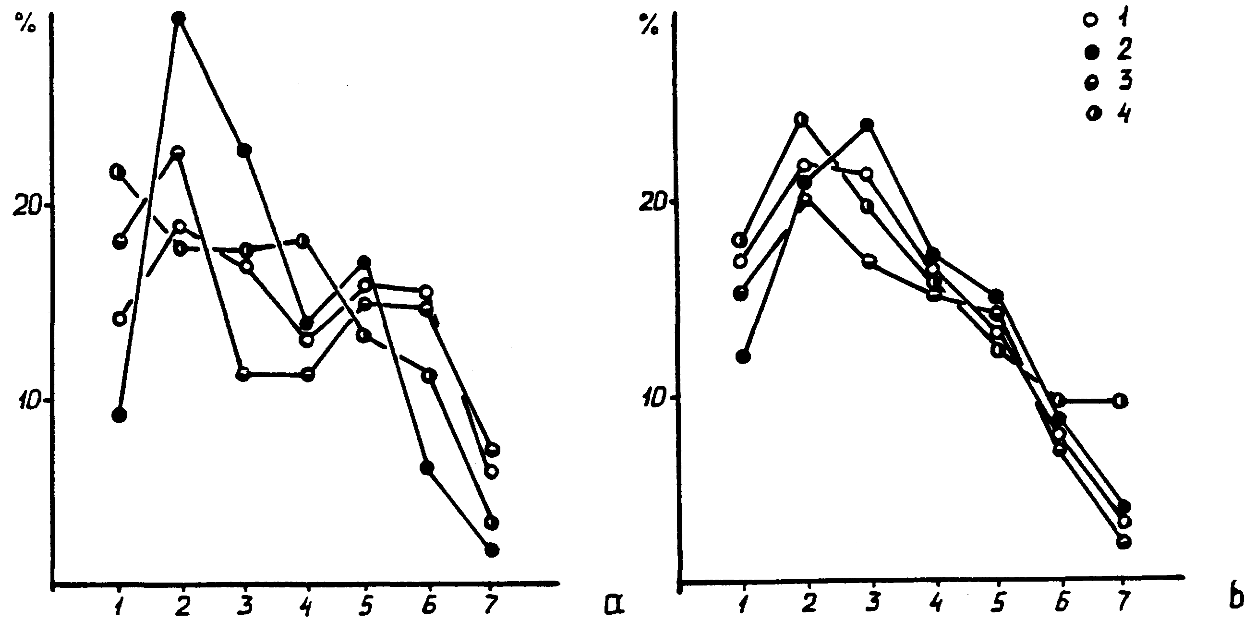

Figure 6. The mine distribution of leaf parts in various geographical regions, *Lithocolletis issikii* Kum. on *Tilia cordata*: 1 = Voronezh district, 2 = Moscow district, 3 = Kujbyshev, 4 = Kiev; a = parallel to central vein and b = perpendicular to it.

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significantly in Murmansk and Leningrad (χ^2 = 16.67 and 16.05; level of significance 0.95). That may be explained by climatic particularities of these regions or by the differences between host plants (*Sorbus aucuparia* in Leningrad and *S. gorodkovii* in Murmansk).

Annual Shoots

Mine distribution over the leaves of annual shoots was investigated for 18 lepidopterous species on 13 host plants. In most cases, this distribution is described by the convex unimodal curve or its segments (Fig. 7). The polymodal character of some empirical distributions may be explained by insufficient number of calculated mines.

Some empirical curves may approximate power, normal, or Poisson function, but the change of curve with the leaf number increase on the shoot is specific for every species, which is why their typification is nearly impossible. The mean number of injured leaves (calculated as arithmetic mean of injured leaf numbers) is the only comparable parameter of distribution. In most cases, the mean value increases with leaf number on the annual shoot. But for three species--*Stigmella sorbi* Stt., *Caloptilia syringella* F., and *Lithocolletis issikii* Kum. first generation--the maximum is observed on the shoots of the middle length.

The pattern of mine distribution on annual shoots is connected with the systematic positioning of phytophagous insect species. Accordingly, the nepticulid moths prefer first leaves of shoots (Fig. 7a), while the gracillariid moths choose leaves in the middle of shoots (Fig. 7b). On the other hand, host plant species can also be a factor in the mine distribution. For example, in Murmansk Territory, over

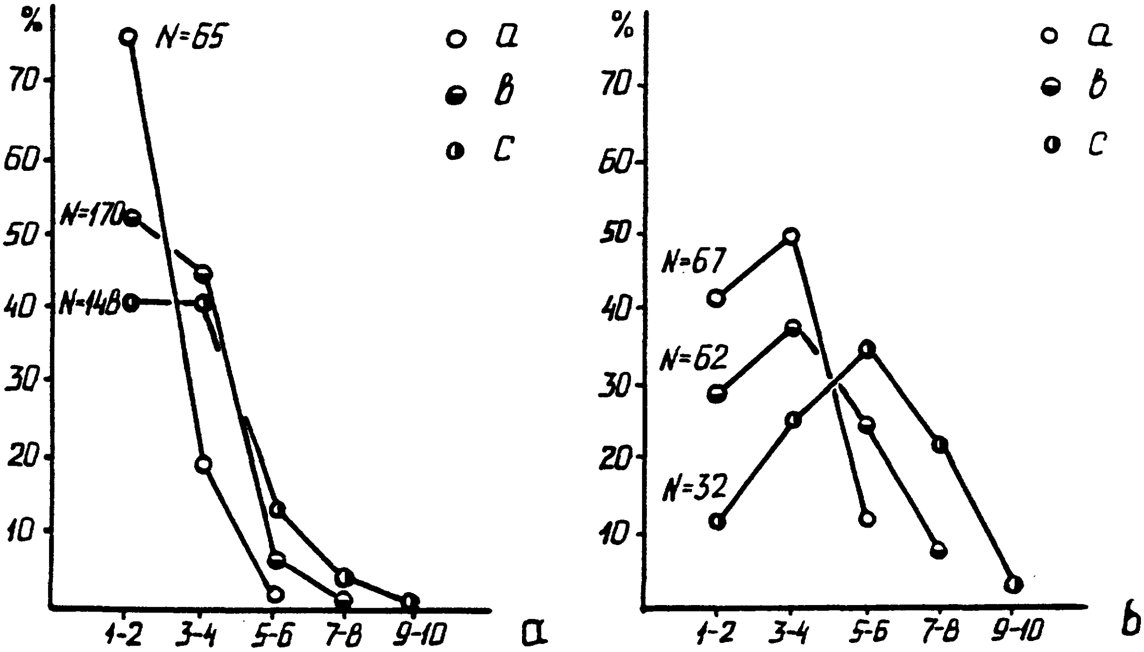

Figure 7. The mine distribution among the leaves of annual shoots of (a) *Stigmella malella* Stt. and (b) on *Malus domestica* (Krasnodar): a = shoots with 4 to 5 leaves, b = 6 to 7 leaves, and c = 8 to 9 leaves. Horizontal scale = the leaf number; N = number of investigated mines.

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90 percent of *Stigmella sorbi* Stt. mines can be found on the first or second leaf of mountain ash shoots, but on the second or third leaf of *Cotoneaster* shoots (Kozlov and Koricheva 1989).

Significant distinctions in mine distribution were discovered between three populations of *Caloptilia syringella* F. on common lilac and two populations of *Lithocolletis issikii* Kum. on small-leaf linden on shoots with five or more metameres.

In some cases, the location of mines is determined by sequence of leaf blossom. In Voronezh Territory, the seventh leaf on the shoot of small-leaf linden blossoms out after egg laying by females from the hibernated generation of *Lithocolletis issikii* Kum. and so is not damaged by caterpillars of the first generation. Maximums of curves for mine distribution of the second generation are shifted toward the top of long shoots. That is why the mine distribution on shoots with six to seven leaves differs considerably for the first and second moth generations.

Comparison of mine distributions over leaf sectors on common beech *Fagus silvatica* on shoots of different length and over leaves of different numbers on shoots of equal length, which was carried out for *Lithocolletis maestingella* Müller showed no significant distinction between them. Thus the distribution of mines on the leaf does not depend on leaf position on the shoot. For five species, we compared the frequency of mines on the shoots of different length with the frequency of occurrence of these shoots on the host plant. These frequencies differ significantly for *Lithocolletis* sp. on speckled alder, *Lithocolletis maestingella* Müller on common beech, and *Caloptilia syringella* F. on common lilac, which indicates a distinct preference for shoots with a certain number of metameres.

Crown Layers

Mine distribution over crown layers was studied for four lepidopterous species. Most *Caloptilia syringella* F. mines are concentrated on the *Syringa vulgaris* and *S. josikae* bushes in the lower and middle layers of the crown, at a height of 40 to 120 cm above ground surface, where shoots with 3 to 5 pairs of leaves are predominant. The upper layer of the crown consists of longer shoots with 7 to 12 metameres, where mines seldom occur.

The maximal ecological density of *Lithocolletis blancardella* F. and *Stigmella malella* Stt. mines on the apple has been recorded at a height of 1.5 m (the normal tree height is about 4.5 m).

Ecological density of first-generation mines of *L. maestingella* Müller on common beech trees, about 25 to 30 m high, decreases in the upper layer of the crown. This may be explained by a temperature gradient (in the spring the ground warms up more rapidly than the air). Ecological density of the second generation increases up to 25 m, then falls abruptly, probably because of the wind, which can blow the female moths away. In this case, mine distribution over both leaf sectors and annual shoots is similar in the various crown layers. This fact allows us to consider topical specificity and vertical changes in ecological density to be independent parameters jointly determining the distributional pattern of mining moths over a tree.

Factors Influencing Mine Distribution Over the Host Plants

Unlike other phyllophagous insects, mining caterpillars have no opportunity for food choice. Even nepticulid caterpillars, which make long serpentine mines, occur mainly near the place of egg laying. So, in both *Stigmella oxyacanthella* Stt. on *Crataegus caucasica* and *St. confusella* Wood. on *Betula pendula*, there are no distinctions in distribution of mines or eggs over the leaf surface ($\lambda = 0.40$ and 0.98 respectively). Thus preference of place for oviposition by the female coincides with the food preferendum of caterpillars.

Significant differences between distribution of mines with dead and living caterpillars of *L. issikii* Kum. on leaves of small-leaf linden ($\chi^2 = 12.68$, level of significance 0.95) indicate the importance of the choice of oviposition place by this species. The survival of caterpillars is likely to depend on mine location on a leaf.

Caterpillar distribution on the host plant can also be influenced by abiotic factors, among which illumination particularly important. Females of *Malacosoma californicum* pluviale Dyar are shown to prefer the sunny side of the tree (Moore et al. 1988), moths of *Stigmella malella* Stt. prefer the shady leaves (Chambon 1968). *Caloptilia syringella* F., which occurs in the lower layer of the shrub crown, is known to damage most heavily the common lilac growing in shadow (Lazareva et al. 1985). Comparison of lighting conditions of leaves with and without mines, as well as our experiments with moth females, showed that the lilac moth lays eggs on less illuminated leaves.

Biotic factors influencing mine distribution are diverse: leaf structure, density of herbivorous insect populations, and interspecific competition, among others.

Experimental study of the behavior of *Stigmella malella* Stt. females before egg laying (Chambon 1968) showed the moths of this species to prefer the prominent relief of ribs (lower side of a leaf). The degree of vascular system development and the peculiarities of leaf venation are of great importance for mining caterpillars. The investigation of leaf venation carried out on different parts of the leaf for *Tilia cordata.*, *Mespilus germanica*, *Fagus sylvatica*, and *Carpinus betulus* showed a negative correlation between mine number and rib density for four of the 11 species of mining moths inhabiting these plants (Fig. 8). The coefficient of this correlation is not high ($r = -0.14$ to -0.24), but it is statistically significant.

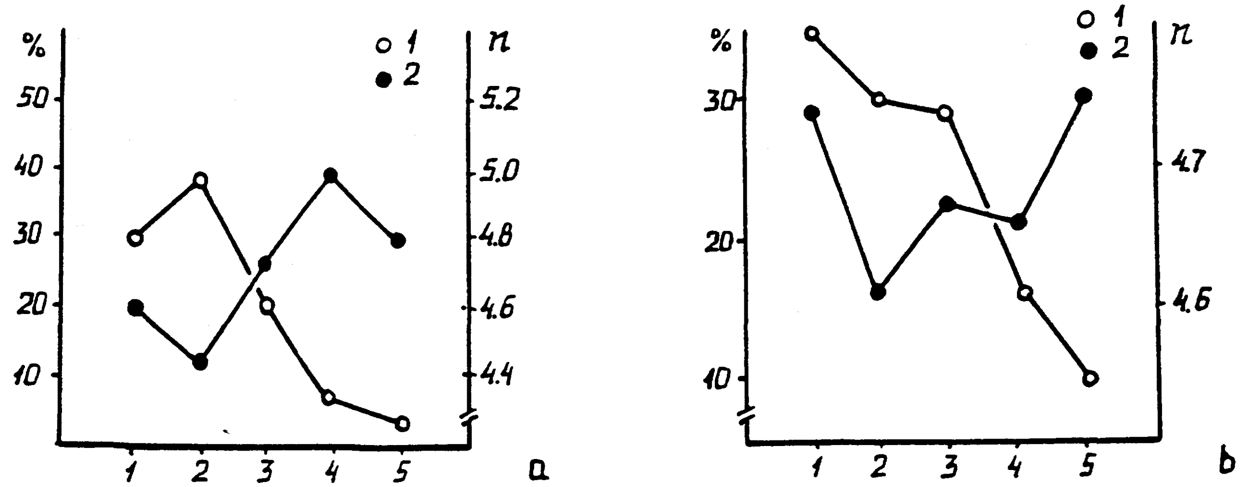

Figure 8. The connection between vein density and mine distribution among the leaf parts, *Coleophora* sp. on *Carpinus betulus* (Kiev): a = perpendicular to central vein and b = parallel to it; 1 = the mine distribution (left scale, percent) and 2 = the vein density (right scale, the number of vein crosses with 1 mm scale).

In one case (*Coleophora* sp. on *Carpinus betulus*, r = -0.12), the choice of place for mine was made not by the moth, but by the caterpillar. Last instar caterpillars of this species leave the mine, build the case, and move freely on a leaf surface. They bore a hole in the epidermis and feed on mesophyll tissues, forming a bilateral mine. A negative correlation between mine number and density of ribs has been found for *Stigmella* sp. on *Fagus silvatica* and *St. microtheriella* Stt. and *St. carpinella* Hein. on *Carpinus betulus*, taking into account only initial parts of serpentine mines (r is -0.2 and -0.16 respectively). If we consider all leaf parts with a mine, the correlation becomes insignificant. Obviously, for caterpillars of the genus *Stigmella* Schr., the low density of leaf venation is necessary at early stages of mine formation only, when larval mandibles cannot penetrate the hard cover of leaf veins. The important role of moth females in choice of place with low rib density is confirmed by their peculiar behavior (Strokov 1956) and by the presence of sensory elements on the end of their abdomen (Chambon 1968).

The pattern of mine distribution may depend on population density of herbivorous insects. For example, if the ecological density of *Stigmella nylandriella* Tengstr. in Voronezh Territory is low (about 1 mine per a compound leaf of mountain ash), the distribution of leaflet areas and mines differs significantly (λ = 2.32); if insect density increases up to 18 mines per leaf, distribution of the two becomes equal (λ = 0.48) (Kozlov and Koricheva 1989). Analogous "substrata saturation" was described for the gall midge *Miciola fagi* Hart., inhabiting beech, when its ecological density was increasing (Dajoz 1981).

If the ecological density of herbivorous insects is low, their food resources are practically unlimited. Therefore, in case of joint utilization by a few species, food preferendums may coincide. But many phytophages and miners in particular sometimes become enormously abundant, damaging up to 90 percent of leaves (Petrenko 1967, Tshagelishvili 1972). In that case, the degree of environmental resource saturation decreases and, according to the competitive exclusion principle, the coexistence of species is possible only if there are some ecological distinctions between them. Coexisting species of mining moths have a similar food source; thus repeated resource utilization is impossible if there are temporal confines between coexisting species. In that case, evidently, those dimensions of the niche which are connected with heterogeneity of host plant, i.e. the site parameters, must play the main role.

The study of mine distribution in seven moth complexes on the leaves of annual shoots and the parts of leaves indicates some interaction between coexisting species. In Kiev Territory, six species inhabiting the european hornbeam, *Carpinus betulus*, have in most cases strong coincidence in one leaf dimension and considerable discrepancy in the other. Mine distribution of *Parornix carpinella* Frey and *Coleophora* sp. differs significantly in both dimensions from the many other species, and, conversely, distribution of mines *Stigmella microtheriella* Stt. and *Lithocolletis quinnata* Geoffroy show no distinctions in either dimension. The last pair of species, in addition to four other species inhabiting european hornbeam, have a coefficient of niche overlap of more than 0.7, which suggests strong competition. Distinctions in both dimensions of a leaf are significant for pairs of species coexisting on elm, common beech, small-leaf linden, and medlar; the coefficient of niche overlap for them is less than 0.7.

For species of *Stigmella centifoliella* Z. and *Tischeria angusticolella* Zett. in Kiev Territory, there is no difference in mine distribution on leaflets of compound leaves ($\lambda = 0.86$, 0.99, and 0.51 for leaves with 3, 4, and 5 leaflets respectively); coefficients of niche overlap are more than 0.7 ($\alpha = 0.79$, 0.84, and 0.75). Among three species inhabiting mountain ash, *Sorbus aucuparia*, mine distribution over leaflets of compound leaves differs significantly only in two species; the coefficient of niche overlap is more than 0.7. However, mine distribution of these species on annual shoots overlaps considerably less ($\alpha = 0.53 - 0.65$). Distinctions between *Stigmella sorbi* Stt. and *St. nylandriella* Tengstr. gradually increase with growth of leaf number on mountain ash shoots, reaching their maximum on shoots with 7 to 8 leaves. The most considerable distinction between *Stigmella sorbi* Stt. and *Lithocolletis sorbi* Frey was recorded on shoots with 3 to 4 and 7 to 8 leaves respectively. Thus niche overlap of these species is maintained at a minimal level on all shoot types.

If we assume that mine distribution is controlled by interspecific competition, our data should satisfy several criteria (Brown and Davidson 1977, Addicott 1978). First, the potential competition between species should be factored into analysis of their niche structure. In our case, the coexistence of species under the large overlap of mine distribution functions on leaf parts of simple and compound leaves can be explained by divergence of these species along other dimensions of resources, such as mine distribution over the leaves of annual shoots in three moth species mining the mountain ash. Moreover, ecological density of the majority of studied species was rather low (about 1 mine per leaf) and preferendum coincidence may be explained by the excess of resources. However, the tendency of optimum to diverge at least along one dimension is observed in general.

The second criterion is the utilization of mutual resources by the competitors. The method of material collection (at one time on one host plant) and the detection of mines of different moth species on a leaf show that this criterion is correct for mining caterpillars.

Third, the behavior of a certain species in nature must verify intraspecific competition. Its presence in the case of mining larvae is proved by the fact that more uniform mine distribution over the leaf is observed by an increase in ecological density of the species (Kozlov and Koricheva 1989). The increase in *Lithocolletis* Hbn. (= *Cameraria* Chapm.) mortality has been shown experimentally to depend on high caterpillar density (Bultman and Faeth 1986a).

These data confirm the importance of competition in the mining moth guild, albeit indirectly. They have prompted some authors to propose the alternative hypothesis on the mechanisms of species diversity regulation in folivorous insects (Lawton and Strong 1981). They suppose that the population density of herbivorous insects is usually lower than the quantity of resources allows and that intensification of competition during outbreaks cannot play the decisive role in formation of community structure. Individual ecological reactions--to climate, host plant phenology, biochemistry, and distribution--together with isolation, migration, and the influence of predator and parasite, are of principal importance.

According to this view, the coexistence of species became possible not as a result of the mutual adaptation of potential competitors, but owing to the initial differences in their ecology.

However, there is direct evidence of interspecific competition in coexisting herbivorous insect species. For example, it has been shown for four aphid species that the growth rate of each is higher in the absence of competitors than in the presence of other species on the host plant (Addicott 1978). Besides, among folivorous insects the competition for food can be observed even at low ecological density, since plants, and in particular their vegetative organs, have low nutritional value and contain secondary metabolites. Such a situation might be typical when competitors are abundant. In nature one usually finds only a slight competition between a few species in the community. This can probably be explained by the fact that competition is too powerful a factor, one which during the evolution process either forces out one of the competing species or causes them to diverge into different niche dimensions. The study of Far-Eastern *Lithocolletis issikii* Kum., which suddenly appeared some years ago in the European part of the U.S.S.R., is of particular interest in this regard.

Irregularity of distribution of mining caterpillars is based on differences in the structure of various leaves (or their parts) and their location on host plants; it can be regarded as a result of insect-plant coevolution. Mine distribution reflects the specific oviposition behavior of females, which discriminate different features of a host plant. One of the mechanisms regulating mining moth diversity is species competition. The presence of competition is confirmed by the above-mentioned tendency toward differentiation of ecological niches of potentially competing species. The role of different factors in the formation of associated mining moth structures is a question requiring further study.

CONCLUSIONS

Mine distribution over a simple leaf and over the leaflets of a compound leaf is irregular and specific for each moth and plant species. Mine distribution of a certain species can differ if the host plant's leaves are very heterogenous, as are the leaves of auxyblasts and brachyblasts, stoll shoots leaves, and ordinary leaves, and if the leaves are of different size and located on shoots of different length.

For four moth species, the geographical variability of mine distribution on leaf parts and leaves of annual shoots is shown. In the majority of cases, the mine distribution on leaves of annual shoots can be described by a convex unimodal curve or its rising or descending part. Species of the family Nepticulidae prefer the basal leaves of a shoot independent of host plant species; the family Gracillariidae prefers leaves from the middle part of a shoot. The species of host plant can also be an influential factor in the distributional pattern of mines, however.

The mine frequency of three among five studied moth species on shoots of different length does not coincide with the frequency of these shoots on host plants. We can conclude that females choose a certain shoot type. Ecological density of mines at a certain crown layer is determined by light conditions and possibly by different distribution modes of shoots in the crown. For 4 out of 11 studied species of mining moths, a significant negative correlation between mine number and vein density on leaf parts was discovered. This correlation can become insignificant with development of a mine.

Significant distinctions in damage frequency of lilac leaves by *Caloptilia syringella* F. mines were discovered in different light conditions. The moths of this species prefer shadowed leaves. Significant distinctions in mine distribution along at least one resource dimension were discovered for coexisting species. The irregularity of mine distribution on host plants results from active choice of the ovipositional place by moth females. This choice is influenced by both biotic factors, such as veins density, herbivorous insect population density, and interspecific competition, and abiotic factors, such as light conditions.

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ADELGID AND SCALE INSECT GUILDS ON HEMLOCK AND PINE

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INTRODUCTION

Five piercing and sucking insects which were accidentally introduced from Asia during this century, together with one native species, have become very serious pests of two important forest tree species in the northeastern United States. Two armored scales, *Fiorinia externa* Ferris and *Nuculaspis tsugae* (Marlatt), and an adelgid, *Adelges tsugae* Annand, attack eastern hemlock, *Tsuga canadensis* Carriere (Fig. 1). A margarodid scale, *Matsucoccus resinosae* Bean and Godwin, and two adelgids, *Pineus boerneri* Annand and *Pineus coloradensis* (Gillette), attack red pine, *Pinus resinosa* Aiton (Fig. 2).

In Japan, their homeland, *F. externa* and *N. tsugae* are common inhabitants of two native hemlocks, *Tsuga diversifolia* Masters and *Tsuga sieboldii* Carriere. However, these scales seldom attain injurious densities in Japan. Both scales were introduced accidentally into the vicinity of New York City about 80 years ago and have since become serious pests of *T. canadensis* in several northeastern states (Fig. 3). Both scales feed together on the needles of hemlock by sucking cell fluids from the mesophyll. In the United States their densities often increase rapidly to levels which cause needles to discolor and drop prematurely and branches to die. Many ornamental and forest trees have been killed in 10 or fewer years after infestation.

Adelges tsugae is probably also native to Japan, where it is a harmless inhabitant of *T. diversifolia* and *T. sieboldii.* This adelgid was first noticed in North America 70 years ago on *Tsuga heterophylla* Sargent in British Columbia. It now occurs throughout much of that province and the northwestern United States, where its damage has been rare. In the eastern United States, *A. tsugae* was first reported 30 years ago on *T. canadensis* in Virginia. Since that time it has spread primarily northeastward and now occurs as far north as New England (Fig. 3) (McClure 1987a). Unlike the mesophyll-feeding scales, *A. tsugae* sucks sap from the phloem parenchyma of the young branches, causing rapid desiccation and drop of needles, dieback of main limbs, and death of the tree, usually within 2 years.

Another Japanese species, *M. resinosae,* now considered to be the same species as *M. matsumurae* (Kuwana) (McClure 1983a), was first discovered in Connecticut in 1946 in a dying plantation of *P. resinosa.* Historical evidence suggests that this scale was introduced into the United States on exotic pines planted at the New York World's Fair in 1939 (McClure 1983a). This scale sucks sap from the phloem parenchyma of the 3-year-old wood, which causes desiccation and dieback of branches and tree death within 2 to 5 years. In China, where it was probably also introduced (McClure 1983a), *M. resinosae* has caused extensive injury to *Pinus densiflora* Siebold, *P. thunbergiana* Franco, and *P. tabulaeformis* Carriere. In Japan injury from this scale is rare and occurs only on cultivated trees (McClure 1983a).

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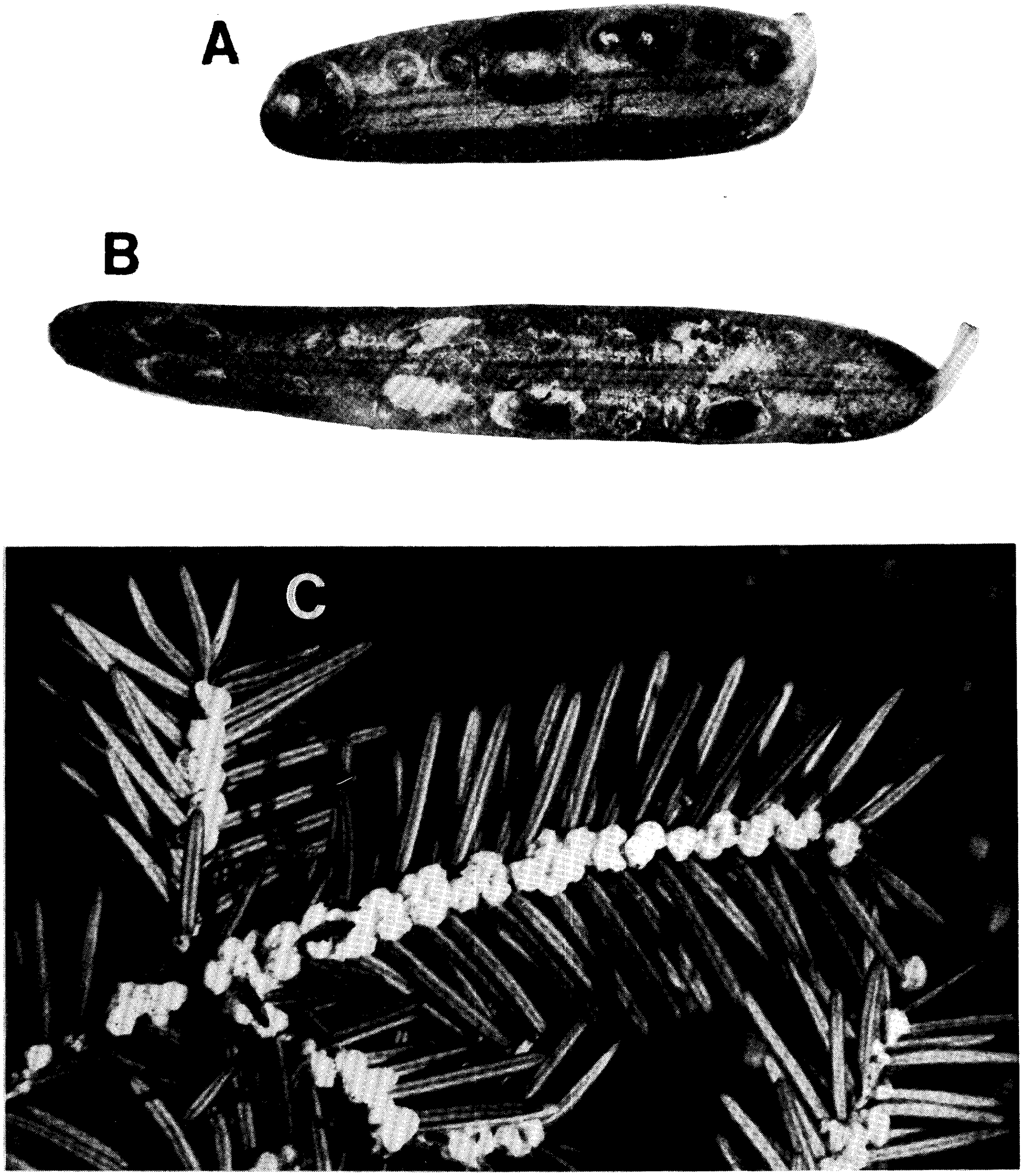

Figure 1. Guild species on *Tsuga canadensis*: nymphs and adults of the diaspidid scales, *Nuculaspis tsugae* (A) and *Fiorinia externa* (B), on the needles (10X magnification); and ovipositing adults of the adelgid, *Adelges tsugae* (C), on the branches (3X magnification).

The adelgid *P. boerneri* was probably introduced from Japan on the same pines that carried *M. resinosae* to North America (McClure 1982). This adelgid feeds primarily on the 3-year-old wood, where it sucks sap from the phloem parenchyma and causes the same type of damage as *M. resinosae*.

Unlike the scale, however, *P. boerneri* also feeds within the needle sheaths. Following their introduction 50 years ago, both *M. resinosae* and *P. boerneri* expanded their ranges northward (Fig. 3). The adelgid has spread much more quickly than the scale because *P. boerneri* completes more generations each year and because the occurrence of its wind-dispersed nymphs coincides more closely with the prevalence of winds from the southwest (McClure 1989a).

The native adelgid, *P. coloradensis*, attacks only the exposed parts of the needles of its host, where it sucks sap from mesophyll cells. Until recently the impact of this adelgid on *P. resinosa* was inconsequential (McClure 1982). However, during the past few years, trees have become increasingly less resistant to *P. coloradensis*, possibly because of a host response to stressful environmental conditions (McClure 1989c).

GUILD SPECIES INTERACTIONS WITH THEIR HOST PLANTS

Host Responses to Herbivore Attack

Adelgids and scales can induce a wide variety of defensive and pathological responses in the host plant, a discussion of which extends far beyond the scope of this report. Barbosa and Wagner (1989) devote an entire chapter to a discussion of the impact of piercing and sucking insects on trees and may be consulted for details. In general, adelgids and scales injure the host by removing sap and/or by injecting a toxic saliva during feeding. Effects on the host include reduced growth and vigor, physical destruction of host tissues, deformation of plant parts, alterations in host physiology and biochemistry, and increased susceptibility to destructive secondary agents such as unfavorable weather, disease, and other insects. Often the damage is insidious, the plant gradually losing vigor and only portions of it eventually dying. Populations of the introduced adelgids and scales, however, often multiply rapidly and kill their new host plants.

The mechanism by which the insect guilds on hemlock and pine bring about the rapid decline of their host plants has not been investigated. However, in related species of adelgids and margarodid scales which also feed on the cortical parenchyma, saliva introduced into the plant during feeding triggers an imbalance in plant growth hormones (Puritch and Petty 1971). This causes structural modification of the xylem, restriction of water uptake by the sapwood, and rapid desiccation and death of the tree.

Red Pine

The impact of feeding by *M. resinosae* and *P. boerneri* on *P. resinosa* is similar to that reported for *Matsucoccus josephi* on *Pinus halepensis* and *Pinus eldarica* (Mendel and Liphschitz 1988) and for *Adelges piceae* on *Abies balsamea* (Hain 1988). Studies comparing the growth of infested and uninfested *P. resinosa* in the greenhouse and in a field plot revealed that relatively low densities of *M. resinosae* and *P. boerneri* reduced the biomass of new growth by 72 percent and of older (1- to 3-year-old) growth by 53 percent. Branches became distorted and cracked and emitted copious quantities of resin from wounds in response to attack by these insects. The needle-feeding *P. coloradensis* caused a more insidious injury by reducing the photosynthetic capability of the tree. However, when infestations of this adelgid attain high density, as they have in recent years (McClure 1989c), the loss of needles can be substantial and lethal to the host.

The deleterious impact of *A. tsugae* on hemlock is sudden and usually lethal. Feeding by nymphs on the preferred youngest branches inhibits production of new growth from these branches during the following year. A single feeding nymph is sufficient to elicit this response in areas of the branch distal to the attack zone. Only 2 percent of the buds present per 0.5 m length of infested hemlock branch were viable the following year, and viable buds produced only 4.3 ± 0.5 mg of new

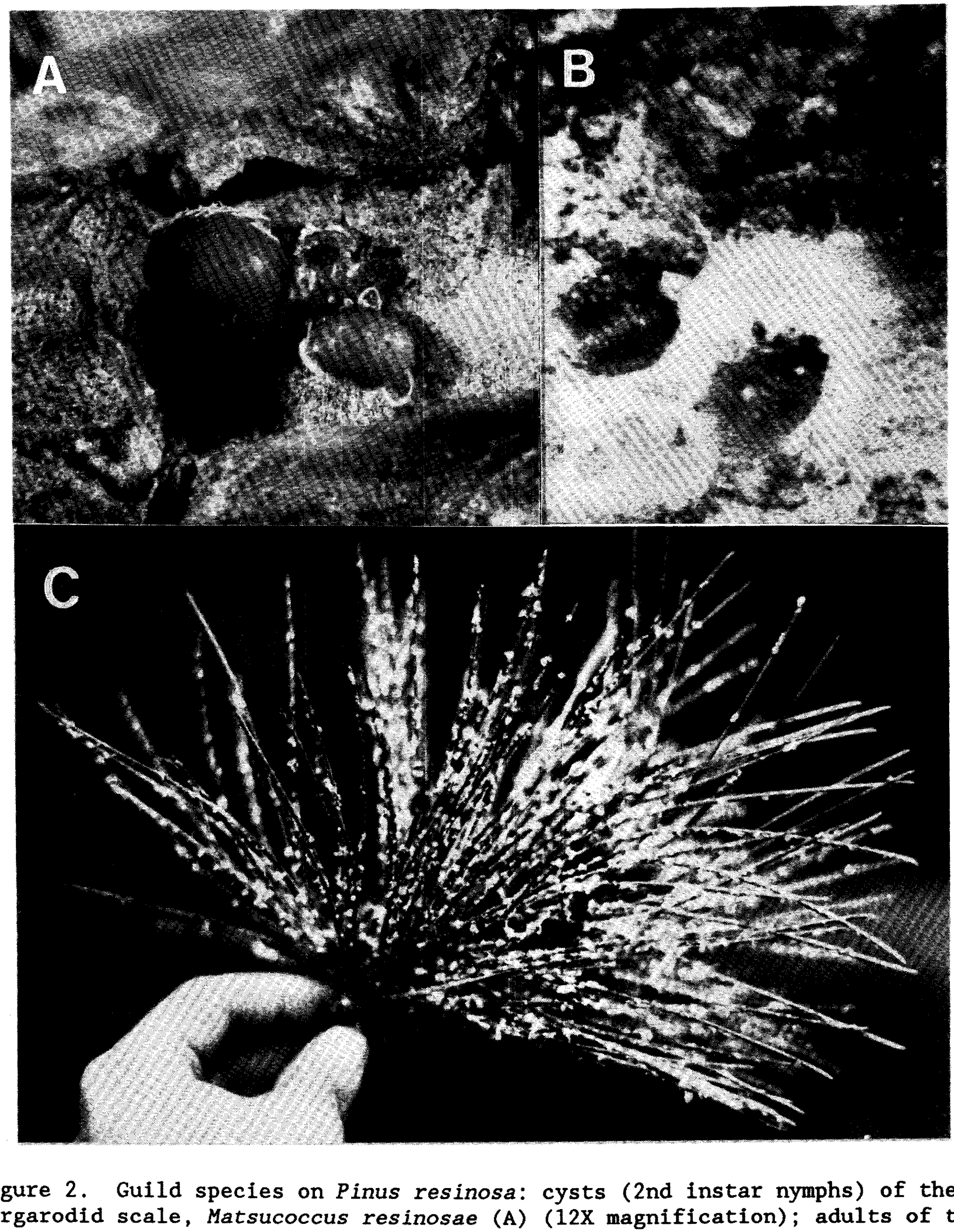

Figure 2. Guild species on *Pinus resinosa*: cysts (2nd instar nymphs) of the margarodid scale, *Matsucoccus resinosae* (A) (12X magnification); adults of the adelgid, *Pineus boerneri* (B) (20X magnification), on the branches; and nymphs and adults of the adelgid, *Pineus coloradensis* (C) (2X reduction), on the needles.

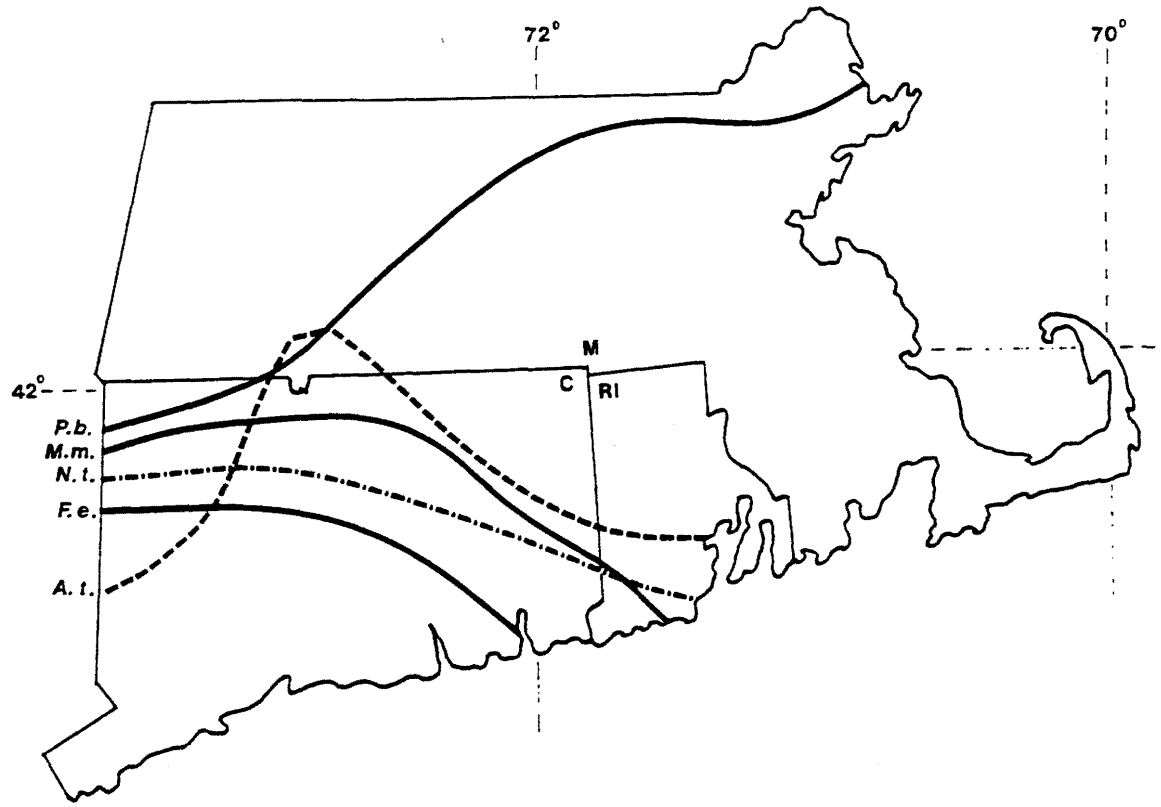

Figure 3. Current distributions (area below each line) of the introduced adelgids and scales on *T. canadensis* and *P. resinosa* in Connecticut (C), Massachusetts (M), and Rhode Island (RI). The species are *A. tsugae* (A.t.), *F. externa* (F.e.), and *N. tsugae* (N.t.) on hemlock, *M. matsumurae* (= *M. resinosae*) (M.m.) and *P. boerneri* (P.b.) on pine.

growth. Within trees this effect was quite localized; all of the buds produced on uninfested branches of infested trees were viable and produced 71.2 ± 6.7 mg of new growth the following year.

Eastern Hemlock

The impact of the mesophyll-feeding scales on hemlock is much less severe than that caused by *A. tsugae* feeding on cortical parenchyma. The main impact of *F. externa* and *N. tsugae* is the reduction in energy reserves and photosynthetic capability of the host resulting from the premature loss of existing foliage and the retardation of new foliage production. Hemlocks infested with these scales for 5 years supported only one-third the total foliar biomass and produced only half as much new growth as their uninfested counterparts. Five to 10 successive years of this photosynthetic deficiency usually kill the tree. Feeding by these scales also reduced the nutritional quality (nitrogen concentration) of current and subsequently produced foliage (McClure 1980a). We shall see that nitrogen is important to the performance of this guild on hemlock and pine.

Herbivore Responses to Host Changes

These species on hemlock and pine display strong preferences in their selection of colonization sites on the branches and needles. The preferences reflect physical and chemical attributes of these colonization sites. Hemlock and pine respond to attack by reducing the availability and suitability of these preferred colonization sites, which adversely affects the performance of these insects. For example, *M. resinosae* and *P. boerneri* preferentially colonize the 3-year-old pine branches where the fissured, flaky bark offers protection from inclement weather and natural enemies (McClure 1990). As densities of these insects increase, resinosis from wounds at the preferred feeding site engulfs and kills many of the older settled nymphs. It also forces the young mobile nymphs to colonize less suitable younger branches, where they subsequently incur significantly greater mortality from exposure to harsh weather conditions and from natural enemies (McClure 1977a, 1987b). Similarly, the needle-feeding adelgid, *P. coloradensis*, shifts its colonization sites to the branches as pines deteriorate in response to attack. Nymphs feeding on the branches incur nearly twice as much mortality as those feeding on the needles (McClure 1984).

One of the responses of hemlock to attack by these species is a significant reduction in the quantity of new growth produced. The two needle-feeding scales and the wood-feeding adelgid prefer to colonize the youngest growth (Table 1), where survival is significantly greater than on older growth (McClure 1980b) (Table 1). Therefore, as in the pine guild, the reduced availability of preferred colonization sites on hemlock following herbivore attack has a substantial deleterious impact on the performance of the hemlock guild species.

Changes in the quality of feeding sites on hemlock and pine in response to herbivory also have profound effects. For example, life table data revealed that the single most important factor leading to the collapse of *M. resinosae* populations on *P. resinosa* was a change in the magnitude of overwintering mortality incurred by nymphs (McClure 1983b). Drastic reductions in scale numbers in the winter more than offset population growth during the rest of the year and resulted in overall annual population decline. Steadily increasing overwintering mortality from year to year was due to a steadily decreasing developmental rate, which resulted from scale-induced reductions in the nutritional quality of feeding sites. The reduced developmental rate caused nymphs to overwinter at a younger age, when they were incapable of surviving even relatively mild winter conditions.

Table 1. Percent of *Fiorinia externa*, *Nuculaspis tsugae*, and *Adelges tsugae* colonizing youngest and 1-year-old growth and percent survivorship of nymphs on that growth. For each parameter, means (+ 1 SD) in each row followed by different letters differ significantly ($p < 0.05$) by ANOVA.

	Colonists (%)		Survival (%)	
Species	Young	1-yr-old	Young	1-yr-old
F. externa	91.2 ± 17.5a	8.8 ± 5.7b	87.2 ± 2.5a	82.6 ± 0.9b
N. tsugae	61.8 ± 13.8a	38.2 ± 9.2b	78.6 ± 4.7a	72.0 ± 5.2b
A. tsugae	83.4 ± 6.3a	16.6 ± 2.4b	54.2 ± 6.7a	15.4 ± 3.6b

The nutritional quality of food for piercing and sucking insects has often been linked to the quantity of organic nitrogen available to nymphs. Indeed extensive studies have demonstrated the importance of nitrogen to the performance of these species on pine and hemlock. For example, fertilization experiments revealed that nymphs of *F. externa* incurred 13 percent less mortality and each adult produced 45 percent more offspring on hemlocks whose foliar nitrogen concentrations had been elevated only 1 percent above the unfertilized controls (Table 2). The performance of *A. tsugae* was also enhanced by fertilization, as nymphs incurred 48 percent less mortality and each adult produced twice as many offspring on fertilized trees as on unfertilized ones (Table 2).

Results of greenhouse and forest experiments have shown that the nutritional quality of hemlock typically declines as the host responds to attack by these insects (McClure 1980a). Concentrations of foliar nitrogen were reduced by an average of 18 percent after only 7 weeks of feeding by *F. externa*; concentrations of nitrogen in young needles were nearly three times higher on uninfested hemlocks than on those which had been infested previously (McClure 1980a). Clearly, deterioration in both the quantity and quality of colonization sites as hemlock and pine respond to attack have a significant negative impact on the performance of these species.

SPECIES INTERACTIONS WITHIN THE GUILD

Density-Dependent Feedback

There is substantial evidence from both pine and hemlock that dense adelgid and scale populations significantly limit the success of individuals of subsequent generations. Because these species rapidly attain high population levels, density-dependent negative feedback is a common feature of their population dynamics. We have seen that density-dependent reduction in nymphal developmental rate is the most important factor in the population dynamics of *M. resinosae*. Other fitness parameters of this scale are also affected by density-dependent feedback. The relationship between scale density and scale performance was examined over a 6-year period from population increase to decline in a plantation of *P. resinosa* in Connecticut (McClure 1983b). Initially when scale density was low and injury to trees was minor, survival and developmental rate of nymphs and fecundity of adults were not correlated with density. However, as density increased and pines became significantly injured, each of these fitness parameters was negatively correlated with scale density. Even

Table 2. Effect of fertilization on foliar nitrogen concentration and subsequent survival and fecundity of *Fiorinia externa* and *Adelges tsugae*. Numbers are means (± 1 SD).[a]

		F. externa		*A. tsugae*	
Treatment	Nitrogen in needles (% dry wt)	Survival of nymphs (%)	Eggs per female (number)	Survival of nymphs (%)	Eggs per female (number)
Fertilized	5.6 ± 0.4	81.5 ± 4.6	13.3 ± 2.1	79.8 ± 16.7	98.2 ± 14.3
Unfertilized	4.3 ± 0.4	68.5 ± 7.9	9.3 ± 1.9	31.3 ± 8.6	49.8 ± 11.5

[a] Differences in fitness parameters between fertilized and unfertilized trees were all significant ($p < 0.005$) by ANOVA.

though scale density decreased sharply after the fourth year, scale performance continued to decline, indicating that the deterioration of *P. resinosa* as a host was progressive and irreversible.

Similar density-dependent feedback has been observed among the other species of this guild on pine. Survival, developmental rate, and fecundity of *P. boerneri* and *P. coloradensis* were strongly negatively associated with their population densities during a 5-year period in forests throughout New England (McClure 1984, 1989a, 1990). However, as with *M. resinosae*, the performance of these adelgids continued to decline even after their densities fell in response to host deterioration.

There is also substantial evidence for density-dependent feedback in the hemlock guild species. On heavily infested hemlocks, mortality of *F. externa* nymphs was four times greater, several more days were required to complete nymphal development, and up to 30 percent fewer eggs were produced per adult than on sparsely infested trees (McClure 1979). Further indication that density adversely affects hemlock scale reproductive rates was seen when scale populations rapidly resurged following pesticide spraying (McClure 1977b). Scales that survived on sprayed trees had significantly higher fecundity than did those on controls, probably because of improved host quality following reduced herbivore pressure.

Studies in several hemlock forests in Connecticut have revealed that the performance of *A. tsugae* is also adversely affected by density-dependent feedback. The presence of this adelgid, even in low densities, inhibits production of new growth, which in turn causes high nymphal mortality in subsequent generations. Density also has a profound impact on the performance of the current generation of *A. tsugae*. Mortality of nymphs was 15 percent higher, and adults produced only 25 percent as many eggs on heavily infested hemlocks as on sparsely infested ones (Table 3).

Even more significant to the population dynamics of this adelgid, however, was the impact of density on the production of sexuparae, the winged stage which migrates to spruce. The life cycle of *A. tsugae* includes a wingless generation which remains on hemlock and a winged generation which must feed on and complete its development on certain *Picea* spp. (McClure 1989b). Hemlock and all of the native and more prevalent exotic *Picea* spp. which occur in the northeastern United States are unsuitable hosts for the sexuparae of *A. tsugae* (McClure 1987a). Therefore, presumably, that portion of the adelgid population which develops into winged sexuparae each summer dies. As adelgid densities on hemlock increased, an increasing proportion of the nymphs developing in summer became winged sexuparae. For example, on the sparsely infested trees, only about 14 percent of the population became sexuparae, whereas on the heavily infested trees, nearly 90 percent of the population became sexuparae and dispersed from hemlock in an unsuccessful attempt to locate a suitable *Picea* host (Table 3). Clearly, this density-dependent feedback mechanism has a significant impact on the dynamics of *A. tsugae* populations on hemlock.

Interspecific Competition and Competitive Exclusion

All the exotic species discussed herein invaded New England from the southwest and now, therefore, have similar geographic distributions (Fig. 3). As a result, two or more species often occur on the same trees. However, extensive studies of both hemlock and pine have revealed that species compete intensely and that coexistence is transient. Interspecific competition leading to competitive exclusion is common in both guilds.

P. coloradensis versus *P. boerneri*

Studies in the greenhouse and in four cohabited pine stands in Connecticut revealed that *P. boerneri* established and maintained numerical dominance over *P. coloradensis* (McClure 1984). Decreasing density of *P. coloradensis* in mixed infestations has been caused by a combination of greater mortality on needles and greater colonization of bark, where chances for survival are poor. Population trends of these adelgids during a 5-year period in 15 pine forests in southern New England suggest

Table 3. Relationship between density of *Adelges tsugae* nymphs feeding on young hemlock branches and their subsequent survival, fecundity, and development. Means (± 1 SD) in each column followed by different letters differ significantly ($p < 0.001$) by ANOVA.

Number of adelgids per 5 cm	Mortality of nymphs (%)	Number of eggs per female	Sexuparae (%)
33.6 ± 3.9a	19.7 ± 6.0a	105.2 ± 21.0a	14.3 ± 1.6a
62.9 ± 7.7b	34.3 ± 8.8b	28.1 ± 11.0b	88.4 ± 9.2b

that *P. boerneri* has displaced *P. coloradensis* in all three previously cohabited pine stands and in 7 of 12 others where *P. coloradensis* initially had occurred alone and where *P. boerneri* invaded subsequently (McClure 1989c). In four of the five remaining stands in the latter category, *P. coloradensis* had been reduced to very low density. These results reaffirm the superior competitive ability of *P. boerneri* demonstrated in greenhouse experiments.

P. boerneri versus *M. resinosae*

Later experiments in the field revealed that the performance of *P. boerneri* feeding both on branches and on needles of *P. resinosa* was significantly reduced by the presence of *M. resinosae*, which fed only on branches (McClure 1990). The presence of *P. boerneri* had no significant reciprocal effect on the fitness of *M. resinosae*. Interspecific competition was a significant limiting factor for *P. boerneri* even though it fed on needles and *M. resinosae* did not. Population trends of these insects during a 7-year period in six cohabited pine stands substantiated the competitive superiority of *M. resinosae* (McClure 1990). The six stands which had been infested only with *P. boerneri* in 1979 were invaded by *M. matsumurae* between 1981 and 1983. In each of these stands the abundance of *P. boerneri* on needles and on bark declined sharply following invasion by *M. resinosae* (Fig. 4). In three of these stands (Haddam, Middletown, and Old Lyme), *P. boerneri* was excluded by its competitor within 3 years (Fig. 4).

The earlier studies revealed that *P. boerneri* quickly excluded the ubiquitous native adelgid, *P. coloradensis*, from cohabited pine stands (McClure 1989c). Results of the later study indicated that *M. resinosae* in turn quickly displaced *P. boerneri* (McClure 1990). Unfortunately, competition among these species and the resulting sequential pattern of species displacement were of no obvious advantage to the besieged host, because even though total herbivore population density declined sharply in all pine stands (Fig. 4), the level of host damage sustained prior to that time was severe and often lethal (McClure 1990).

N. tsugae versus *F. externa*

Studies in the greenhouse and in hemlock forests in Connecticut established that *F. externa* and *N. tsugae* compete for food and space and that *F. externa* is the superior competitor (McClure 1980b, 1983c). Comparison of mortality data from solitary and coexisting populations of these scales revealed that *F. externa* had a greater adverse effect on the survival of its competitor than *N. tsugae* had on itself, while *N. tsugae* had a less significant effect on *F. externa* survival than *F. externa* had on itself. This superior competitive ability of *F. externa* resulted from the nutritional advantage gained by colonization 2 to 4 weeks earlier than its competitor, when foliar nitrogen and water are more concentrated. Early feeding by *F. externa* not only reduced the amount of foliar nitrogen by the time

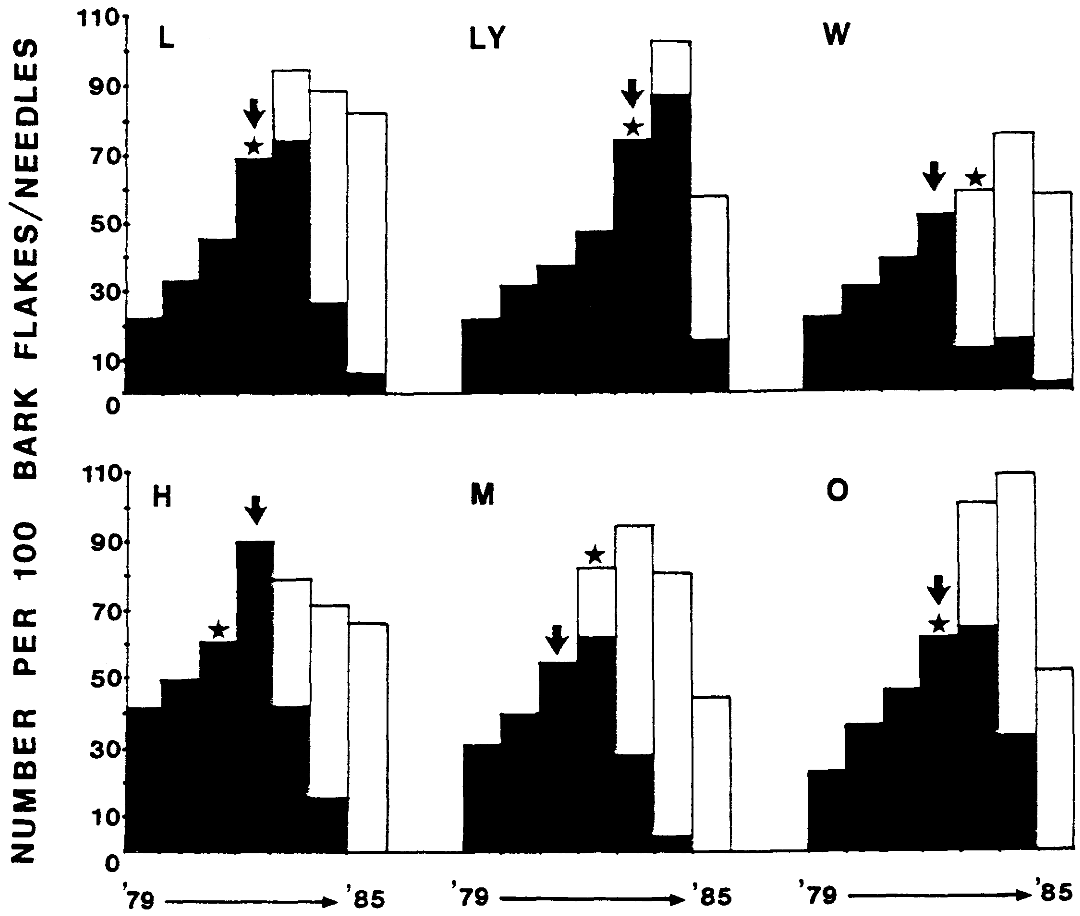

Figure 4. Mean number of adelgids and scales on 100 needles and beneath 100 bark flakes of *P. resinosa* in six cohabited stands in Connecticut from 1979 through 1985. Within each bar are the proportions of the total insects that were *Pineus boerneri* (shaded area) and *Matsucoccus resinosae* (unshaded area). Stars indicate the first year during which the crowns of all trees were at least 50 percent visibly damaged. Arrows denote the year during which *M. resinosae* first invaded the stand. Letters designate stands in the towns of Litchfield (L), Lyme (LY), Waterford (W), Haddam (H), Middletown (M), and Old Lyme (O).

that *N. tsugae* colonized the needles, but also forced *N. tsugae* to colonize less nutritious older growth where scale success was significantly reduced (McClure 1980b).

Because of its competitive superiority, *F. externa* quickly excluded *N. tsugae* from mixed infestations in a field plot and in 20 hemlock forests in Connecticut (McClure 1980b). In 12 forests in which *F. externa* outnumbered its competitor in the initial census, *N. tsugae* was eliminated after only 3 years. However, even in eight forests in which densities of *N. tsugae* were initially sevenfold higher than those of *F. externa*, *N. tsugae* was eliminated after only 4 years (McClure 1980b). Similar results were obtained in the field plot experiment, wherein the relative abundance of *N. tsugae* on cohabited trees was reduced from 66.9 percent of the total scales present to less than 1 percent in 4 years. The host-finding behavior of a parasitoid common to both scales also contributed to the rapid decline of *N. tsugae* populations (McClure 1980b).

A. tsugae versus Needle Scales

During the past 4 years, *A. tsugae* has invaded many hemlock stands previously inhabited by one or both hemlock scales in southern New England (Fig. 3). The rapid desiccation and premature drop of hemlock foliage in response to attack by this adelgid have had an obvious impact on the needle-feeding scales. The immobile stages of these scales, which are firmly attached to the needles for 11 months during the year, are immediately lost to the population when needles drop prematurely. The less obvious species interactions that occur prior to needle drop are currently being investigated. However, as in the pine guild, the level of herbivory and host deterioration needed to bring about a significant reduction in the abundance of hemlock guild species is severe and often lethal. Consequently, the intense competitive interactions among the guild species have been of no benefit to hemlock as these insects have expanded their distributions northward.

CONCLUSIONS

Factors Regulating Endemic Populations

Studies on the population dynamics of the adelgids and scales of hemlock and pine in Asia revealed that in native habitats these species were usually maintained at innocuous densities by the combined influence of host resistance and natural enemies. Experiments were conducted in Japan in pure and hybrid stands of *Pinus* species of the subsection Sylvestres (the group to which all known host species of *M. resinosae* belong) to determine their relative susceptibility to this scale. Survivorship of scale nymphs and fecundity of adults were significantly lower on the two native Japanese pines, *P. densiflora* and *P. thunbergiana*, and their interspecific hybrid than on several pure and hybrid pines of related exotic species (McClure 1985a). Maternal parents of Japanese species did not confer resistance upon the F1 progeny that resulted from hybrid crosses with susceptible exotic species. Overall trends in scale survivorship in 10 pure and hybrid stands indicated a chemical basis for host resistance. However, interspecific variation in bark texture and significant differences in survivorship of nymphs in exposed and protected sites on bark indicated a physical basis for host resistance as well (McClure 1985a).

Life table data gathered from 30 ornamental and forest pine stands in Japan revealed that predators also have an important role in the regulation of endemic scale populations (McClure 1986a). The coccinellid beetle, *Harmonia axyridis* Pallas, native to Japan, comprised 84 percent of the total number (n = 3,071) of predators captured. It killed 97 percent of the scales in one heavily infested pine stand in less than 4 weeks. When realistic densities of beetles were caged on infested pines, 81 percent of the small, inconspicuous life stages of the scale and 98 percent of the larger, more conspicuous life stages were consumed. This resulted in a 67-fold decrease in scale population growth compared with control cages containing no beetles (McClure 1986a).

Other studies in Japan revealed that host resistance and natural enemies were important regulatory factors for populations of the scale and adelgid species on hemlock as well. Samples taken from 13 natural and cultivated stands of *T. diversifolia* and *T. sieboldii* throughout Honshu revealed that densities of *F. externa* and *N. tsugae* were always innocuous and low relative to those on *T. canadensis* in North America (McClure 1986b). Density, survivorship, and fecundity of both scale species were significantly higher on hemlocks planted outside their natural range in Japan than on naturally occurring montane trees, and significantly higher on *Tsuga* species exotic to Japan than on Japanese hemlocks (McClure 1986b). I infer from these and other results (McClure 1983d) that trees growing outside their natural habitats are less resistant to insect herbivores, presumably due to stress from less adequate growing conditions and fewer natural enemies (more enemy-free space).

Data from a field plot study and life table data gathered from 13 sites in Japan revealed that endemic populations of these scales have the potential to attain densities injurious to host hemlocks, especially trees in cultivation (McClure 1986b). However, this seldom occurs because of the hymenopteran parasitoid, *Aspidiotiphagus citrinus* Craw, which regularly killed more than 90 percent of both scale species (McClure 1986b).

Implications for Developing Management Strategies

Maintenance of Host Plant Vigor and Resistance

Clearly, the Asian species of hemlock and pine are inherently much more resistant to their native adelgids and scales than are their North American counterparts. What little resistance there may be among individual North American hemlocks and pines to attack by these introduced species has been impossible to detect because of the speed with which these insects attain high and lethal population densities. This situation, combined with the relatively high degree of genetic homogeneity known for *P. resinosa*, has inhibited development of genetically resistant lines which could be used in a pest management program. Results from my studies of two sap-feeding guilds support the hypothesis that trees under stress are less resistant to attack by endemic species than are healthy trees (McClure 1983d, 1985a, 1985b, 1986b). Further studies are needed to verify that hemlocks and pines growing in cultivation or outside their natural range are stressed and are less resistant to herbivores than are naturally growing trees. Nevertheless, the rapid rates of increase of endemic species on cultivated trees emphasize the need to maintain host vigor as well as the danger of planting tree species outside their natural ranges.

A lengthy discussion of the various silvicultural practices that can be used to maintain host vigor and resistance to herbivores is beyond the scope of this report. However, one practice for improving the vigor of plants, fertilization, warrants some consideration in view of my studies. We have seen in Table 2 that adelgids and scales on hemlock were favored by increases in the soluble nitrogen component of their food; their performance on fertilized trees was significantly higher than it was on unfertilized trees. Therefore tree "feeding" as a management tool for piercing and sucking insects should be used with discretion.

Establishment and Preservation of Natural Enemies

Earlier I reported that natural enemies also play an important regulatory role in endemic populations of guild species on hemlock and pine in Asia. A popular approach for controlling injurious populations of introduced species has been the introduction and establishment of natural enemies from the homeland of the pest. Examples of successful biological control, however, are relatively scarce despite great efforts over many years. Such has been the case for biological control efforts in Connecticut against *M. resinosae* using its effective native predator, *H. axyridis*, and against *F. externa* and *N. tsugae* using their effective native parasitoid, *A. citrinus*. The reasons for the failure of these biological control agents are quite different and reflect the complexity of coevolved host-herbivore-natural enemy interrelationships.

The apparent failure of *H. axyridis* to establish itself as an effective predator of *M. resinosae* in Connecticut has been attributed to its limited ability to exploit all life stages of the scale and to overwinter (McClure 1987b). Cage experiments in Connecticut revealed that *H. axyridis* can significantly reduce the abundance of *M. resinosae* only when the conspicuous life stages (eggs, cysts, and adults) are present. This beetle is ineffective during those other times of the year when scales are first instar nymphs concealed in the cracks and crevices of the bark. In Japan, *H. axyridis* is an effective predator throughout the year because the relatively untextured bark of Japanese pine species does not afford as much protection for first instar nymphs as does the textured bark of *P. resinosa* (McClure 1985a, 1986a, 1987b). Results of two overwintering experiments in Connecticut indicated that the ability of *H. axyridis* to survive winter conditions in its new environment was also limited (McClure 1987b). Less than 10 percent of the adult beetles (n = 762) placed in cages in the field survived from November through March, a period during which weather conditions were normal for Connecticut.

Even more frustrating has been the failure of *A. citrinus* to control populations of the exotic hemlock scales in Connecticut, where this parasitoid is already widely established. Throughout Japan the seasonal occurrence of adult parasitoids and vulnerable stages of both scale species were synchronous, resulting in high parasitism rates and population regulation (McClure 1986b). In contrast, Connecticut populations of *A. citrinus* are asynchronous with their scale hosts because of phenological differences. This results in inconsistent parasitism rates and unregulated populations of these exotic scales which injure and kill their new host (McClure 1986b).

Outlook

Managing endemic populations of guild species on hemlock and pine may simply involve adherence to silvicultural practices that maintain tree vigor and preserve the natural enemy community. The management of introduced populations of these insects will be a much more difficult task. Even vigorous stands of hemlock and pine have shown no resistance to the build-up of injurious adelgid and scale populations, and important natural enemies in Asia have been ineffective in North America. Chemical control of some of these guild species has been achieved on trees where complete coverage of the foliage with pesticide was obtained. However, it has been virtually impossible to obtain complete coverage in forests, and incomplete pesticide spraying has resulted in the rapid resurgence of populations (McClure 1977b). The best and perhaps the only permanent solution for the control of the introduced species on *T. canadensis* and *P. resinosa* may be the identification or development through genetic manipulation of effective natural enemies and resistant hosts. Until more effective and persistent natural enemies are found, we must strive to maintain vigorous stands of hemlock and pine and to use pesticides only when needed, and then as prudently as possible to minimize their deleterious impact on existing natural enemies.

SUMMARY

An herbivore guild comprised of endemic species is often the product of a long coevolutionary struggle between herbivores and their host plant. Examples of neatly structured coevolved guilds permeate the literature and are highlighted elsewhere in these proceedings. Far less structured and less stable are guilds comprised of introduced species in which herbivores have had little or no coevolutionary history with their new host plants. In such guilds, resource partitioning, species packing, and other such intimate relationships that often characterize guilds of endemic species are seldom apparent. Instead, with little resistance from the new host plant, and in the absence of native natural enemies, introduced herbivores often multiply rapidly to a level at which deteriorating resources limit further population growth. Therefore hostile competitive interactions often characterize these guilds, and the success of each member species is usually measured by its relative ability to cope with the harmful effects of herbivory on the food supply. My studies revealed that the herbivore guilds comprised of Asian species of adelgids and scales on North American species of hemlock and pine are indeed highly interactive, unstable, and destructive to their host plants. Finally, I discuss the interactions between the guild species and between them and their hosts, and the ramifications for population dynamics and management of these insects.

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ADELGID HOST INTERACTIONS WITH SPECIAL REFERENCE TO THE BALSAM WOOLLY ADELGID IN NORTH AMERICA

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INTRODUCTION

The objectives of this paper are: 1) to provide a general overview of adelgid biology and the various host relationships; 2) to review the current knowledge of the interactions of the balsam woolly adelgid, *Adelges piceae* (an introduced pest), and its North American hosts; 3) to report on the most recent research involving the interactions of this adelgid with Fraser fir, *Abies fraseri*, in the southern Appalachians; and 4) to provide a synthesis of the above in the form of an hypothesis regarding host tolerance for the balsam woolly adelgid.

Adelgids are conifer-feeding insects in the super-family Aphidoidea of the order Homoptera. They are frequently referred to as aphids and have similar features such as a soft body and membranous wings. Both feed on plant sap. However adelgids are placed in a separate family, Adelgidae, because they differ from true aphids in having short antennal segments, a reduced wing venation, glandular body surface, no siphunculi, and because all the female forms are oviparous (Carter 1971).

The life cycles of species within the Adelgidae is either holocyclic, requiring a primary and secondary host, or anholocyclic, occurring only on one host. In the holocyclic life cycle the primary host is always a spruce (*Picea*) and the secondary host is a conifer of another genus such as fir (*Abies*), larch (*Larix*), pine (*Pinus*), Douglas-fir (*Pseudotsuga*), or hemlock (*Tsuga*).

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

The holocyclic life cycle (e.g. *Adelges laricis*), as described by Carter (1971), is shown in Fig. 1. On the primary host, eggs are laid by a fertilized female (apterous sexuales). The egg hatches into a fundatrix nymph that settles on the current year's shoot. After overwintering, feeding activity is closely synchronized with the flow of sap in the spring. The mature fundatrix females lay a large cluster of parthenogenetic eggs which hatch into gallicolae nymphs. As the nymphs feed on the sap of the young tissue the characteristic adelgid gall forms. During the summer the deformed needle bases which form most of the gall become separated, and the winged gallicola is released. Throughout the summer the gallicolae migrate to the secondary host (*Larix* in the case of *A. laricis*) where they settle on the needles and lay eggs.

The parthenogenetic eggs of the gallicolae give rise to sistens and the first generation on the secondary host begins (Fig. 1). After overwintering as first or second instar sistens, the sistens mature in the spring and lay large clusters of eggs which hatch into progrediens nymphs. Two morphs of the progrediens nymph develop simultaneously into apterous oviparae and alate sexuparae. The latter migrate back to the new needles of spruce and lay eggs which hatch as males and females of the sexuales generation, and the entire life cycle is completed. The apterous progrediens may produce additional generations of progrediens or sistens during the summer. They overwinter as sistens and give rise to sexuales and progrediens the following spring.

Anholocyclic adelgids do not have all the morphs in Fig. 1 and reproduction is by parthenogenesis exclusively. The life cycle may be confined to any one of the conifer genera. Carter (1971) described four types of anholocyclic adelgids. Two types are on spruce: one has gall-forming morphs that have the appearance of the fundatrices and gallicolae (e.g. *Adelges abietis*), the other type has only apterous forms and no galls are formed (e.g. *Pineus pineoides*). The other two types occur on the secondary host and produce sistens and progrediens; one type may produce sexuparae that are incapable of producing males (e.g. *P. pini*), the other type does not produce sexuparae although alates are produced which give rise to sistens (e.g. *A. piceae*).

The focus of this paper, *Adelges piceae*, the balsam woolly adelgid, infests *Abies* species and is believed to be native to the silver fir, *A. alba*, forests of central Europe. The adelgid was introduced into North America around 1900. European firs are not seriously affected by this insect, but North American firs frequently experience either crown dieback or tree death or both. Adelgid-caused damage has been extensive and, at times, intense.

Europeans place the true fir-infesting adelgids in the genus *Dreyfusia* (Borner 1908). The British and North Americans follow a classification that places all the sub-family Adelginae into two genera, *Pineus* and *Adelges*, based on the number of abdominal spiracles (Annand 1928, Carter 1971). This latter classification is used here. Three subspecies of *A. piceae* have been identified on the basis of morphometric analysis (Foottit and Mackauer 1980, 1983): *A. piceae piceae*, Pacific Northwest, British Columbia, and southeastern United States; *A. piceae canadensis*, eastern Canada and New England; and *A. piceae occidentalis*, British Columbia.

The balsam woolly adelgid was introduced into Maine and Nova Scotia in 1908 on nursery stock and became established on balsam fir, *A. balsamea* (Balch 1952). The adelgid was discovered in the southern Appalachians in 1955[1] infesting Fraser fir, *A. fraseri*, on Mt. Mitchell, North Carolina. Since then it has been found on Fraser fir in Virginia and Tennessee, and on bracted balsam fir, *A. balsamea* var. *phanerolepis*, in Virginia and West Virginia (Amman 1962). Balsam fir has the most extensive

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[1] J.S. Boyce. Memorandum of October 7, 1955, to North Carolina National Forests, Toecane Ranger District, Burnsville, North Carolina. Southeastern Forest Experiment Station, Asheville, North Carolina. As reported in Amman 1966.

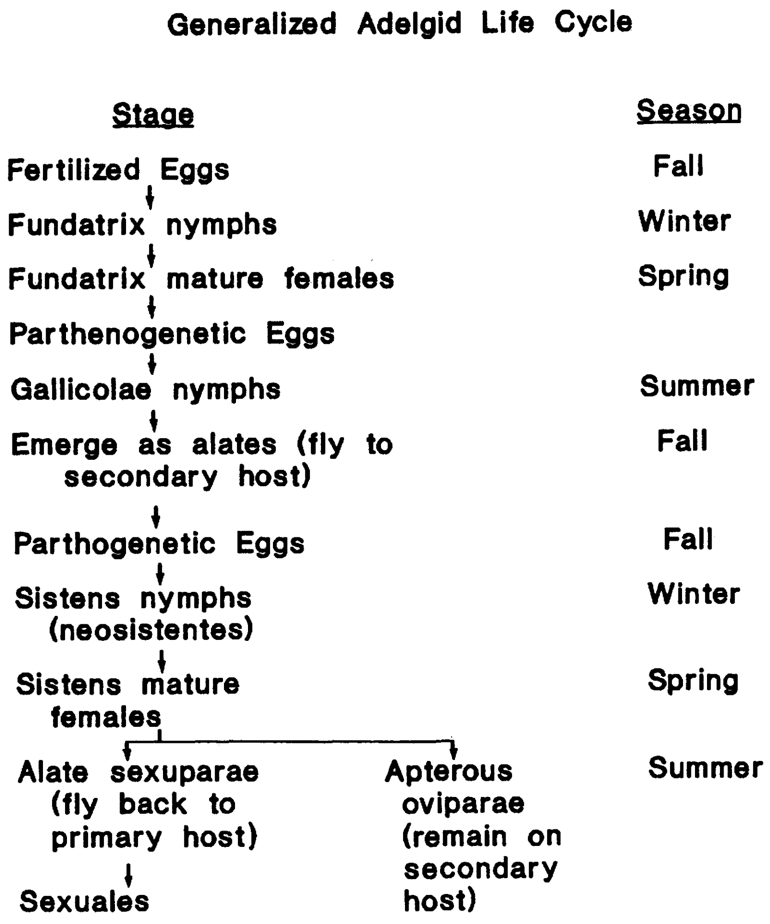

Figure 1. Holocyclic and anholocyclic life cycles of adelgids.

range of all the North American true firs, occurring from Newfoundland to Alberta, Labrador to Pennsylvania; however the adelgid is only found on balsam fir in New England (as far south as New York), Newfoundland, Nova Scotia, New Brunswick, and Quebec (Greenbank 1970, Mitchell et al. 1970). A separate introduction occurred in the Pacific Northwest, where the principal hosts are grand fir (*A. grandis*), subalpine fir (*A. lasiocarpa*), and Pacific silver fir (*A. amabilis*) (Mitchell 1966).

The life cycle of the balsam woolly adelgid consists of the egg, three larval instars, and the adult. The first instar, or crawler stage, is about 0.4 mm in length, and is the only form capable of movement (Fig. 2). Within 24 to 48 hours after hatching, the crawler locates a suitable feeding site, inserts its stylets into the bark of the host, and transforms, without molting, into a flattened, wax-fringed resting stage (neosistentes). The insect is sessile, remaining permanently attached to the feeding site which is usually a bark lenticel or other roughened area of the main stem, branch, twig node, or bud base (Bryant 1974). Dispersal occurs when the crawlers or eggs are passively transported by wind, birds, or other animals. The second and third instars are about 0.50 and 0.65 mm in length, respectively. They closely resemble the adult and are covered with secretions of waxy threads that appear as a dense white wool mass. The second instar through the adult are considered the sistentes. The adult females are about 0.80 mm in length, dark purple to black, nearly spherical, and wingless. As many as 248 amber-colored eggs are laid within the woolly mass. The dense woolly secretions provide protection for all of the life stages except the crawler (Balch 1952). The progrediens stage has been observed in Europe and the Maritime Provinces of Canada (Mitchell et al. 1970), although it is rare. There are winged and wingless forms of the progredientes. The wingless form is similar to the sistentes, while the winged form has conspicuous membranous wings and five-segmented antennae and generally lack wax pores. The progrediens stage gives rise to the neosistens stage.

The winter is passed as a dormant first instar nymph, and this generation is referred to as hiemosistens. Development is completed in the spring (Balch 1952, Greenbank 1970). The first instar nymphs of the second generation (aestivosisten) also undergo a dormant period (summer aestivation) ranging from 2 to 8 weeks (Amman 1969). At lower altitudes or warmer climates, additional generations may be produced (Arthur and Hain 1984, Mitchell et al. 1961). A third generation usually results from faster development, and a partial fourth may occur during years of extremely early development.

The amount of damage sustained by an infested tree is related to the size of the attacking adelgid population, to the part(s) being attacked, and to the physiological state of the tree. Adelgids generally concentrate in the outer portions of tree crowns or on the main stem and large branches. The precise location of the infestation depends on the tree species and geographic location. Stem infestations usually cause more damage and tree mortality than do crown infestations. Heavy stem attacks give the lower bole a white-washed appearance because of the conspicuous presence of white woolly masses. In some cases, stem infestations may virtually disappear after a few years without killing the tree--this is especially true in Europe. However, many North American firs are killed within 2 to 6 years of a sustained infestation.

The anatomical, structural, and physiological changes in host tissue caused by an *A. piceae* infestation include the production of abnormal wood (rotholz) in the xylem tissues, an increase in outer bark thickness, bark resinosis and sometimes copious resin flow from within the feeding zone, and the production of juvabione and juvabione-like compounds. The stimulation of the cambium to produce rotholz is particularly intriguing, since the physical presence of the stylets only extend to the living bark cells. In young and thin bark tissue, the stylets occasionally reach the phloem but do not enter it (Balch 1952).

Rotholz is usually reddish in color and resembles compression wood (Balch 1952, Busby 1964, Varty 1956). The intensity of the red coloration varies from barely noticeable to dark red. The xylem tissue from infested fir contains higher amounts of ray tissue (Mitchell 1967, Smith 1967), thickened cell walls, shorter tracheids (Doerksen and Mitchell 1965, Foulger 1968), a reduced number of conducting pits in the tracheids (Puritch and Petty 1971), and encrusted pit membranes that resemble those of normal heartwood (Puritch and Johnson 1971).

Water flow through sapwood samples from infested trees was greatly reduced (Mitchell 1967), almost to the level of non-conduction (Puritch 1971). There are no distinguishable differences between normal heartwood and the heartwood formed as a response to adelgid attack (Puritch 1971, 1977, Puritch and Petty 1971). Since the cambium and ray cells are not physically damaged, it appears that the adelgid merely enhances the normal pattern of heartwood formation. An infestation is also associated with the production of chemical compounds in the sapwood (Puritch 1977). In contrast to uninfested trees, water transport in infested trees is limited to narrower bands of early wood and does not ascend as high (Mitchell 1967). The tree is in a state of physiological drought. As fluid movement is impaired, photosynthesis and respiration are reduced, contributing to the death of the host. European firs do not form rotholz in response to attack (Mitchell 1966), which may explain the innocuous status of the pest.

When the periderm tissue of conifers is injured a layer of impervious tissue (Biggs 1985, Mullick 1975) followed by necrophylactic (secondary) periderm is formed internal to the wound (Mullick and Jensen 1973a, 1973b). This impervious tissue isolates the necrotic cells of the wound response from the unwounded portion of the stem. In a susceptible response to an adelgid infestation, the formation

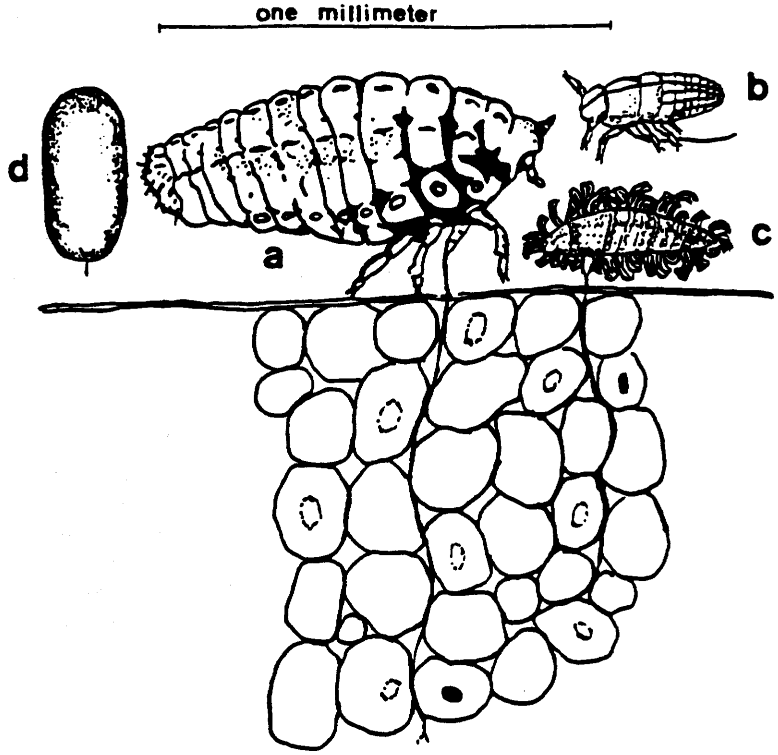

Figure 2. Life stages of the balsam woolly adelgid: a) adult with stylets piercing bark tissue, b) crawler, c) neosisten with wax fringe and stylets piercing bark tissue, and d) egg.

of the impervious layer may be inhibited (Mullick 1975, 1977), perhaps as a result of stylet secretions. The wound response continues into deeper tissue layers and ultimately into the xylem, where rotholz is formed. By contrast, tolerant firs may complete the formation of the impervious tissue without delay and thus avoid any permanent damage to the underlying cells. Eventually nutrients in the outer bark become exhausted and the adelgid disappears leaving the tree relatively unharmed.

The wound response of some fir, especially grand fir, *Abies grandis*, produces such copious amounts of resin that it flows down the bole. Grand firs are considered one of the more resistant North American fir species to adelgid attack with only 20 to 30 percent of the infested trees dying (Mitchell 1966). Adelgid-infested grand firs do not always produce rotholz (Puritch and Petty 1971), although the anatomical and chemical features of the xylem are altered and permeability reduced (Puritch 1973, 1977, Puritch and Petty 1971, Puritch and Johnson 1971).

Also juvabione-like substances may be produced by the host in response to an adelgid infestation. The substances were not found in uninfested fir, nor were they found in infested fir except in the vicinity of the adelgid (Puritch and Nijholt 1974). Perhaps the juvabione-like compounds interfere with the metabolism of the insect and render the tree resistant to a prolonged infestation.

We have reviewed the general life history of adelgids that attack spruce and fir, focusing on an adelgid introduced into North America, the balsam woolly adelgid. Research into the interactions of the adelgid with its new hosts has shown that the infested trees respond, in varying degrees, by the production of rotholz in the xylem, wound periderm in the bark, resins, and juvabione-like substances.

The objective of our research at North Carolina State University has been to clarify the importance of each of the reaction components (rotholz, wound periderm, resin, and juvabione-like substances) to the tolerance or susceptibility of Fraser fir to the balsam woolly adelgid. This paper will review that work and propose a hypothesis for the cause of tree susceptibility or tolerance.

METHODS

Most of these studies were conducted on Fraser fir, *Abies fraseri*, in the southern Appalachians of North Carolina. However, some comparative studies were also conducted on European silver fir, *A. alba*, in the Black Forest of Germany.

Rotholz Formation and Water Potential

Several methods were used to determine the presence of rotholz. The first was wood coloration. Wood cores were taken from opposite sides of trees. When a growth ring from both cores showed a high proportion of latewood, giving it a reddish coloration, the ring was considered to contain rotholz. Some cores were also treated with perchloric acid (a heartwood indicator) to enhance the difference in coloration. Other cores were examined by electron microscopy. Rotholz is anatomically similar to compression wood (Balch 1952), having thick-walled tracheids which are circular (rather than rectangular) in cross-section (Doerksen and Mitchell 1965, Timell 1986), and encrusted pit membranes which appear similar to those of heartwood (Puritch and Johnson 1971).

Water potential of individual trees was measured using a Scholander pressure chamber (Scholander et al. 1965) and all readings were taken at dawn. When necessary, extension clippers were used to remove a branch from the upper crown and a 2-year-old twig was cut from the branch for use in the chamber.

Sapwood flow rates were measured through Fraser fir stems previously infested by the balsam woolly adelgid and containing rotholz. Four pairs of Fraser fir were cut and removed from an infested Christmas tree plantation. Each pair included one tree which had been heavily attacked by the adelgid and a second tree which did not show symptoms of a heavy infestation. Ten-cm long bole sections were placed with the bottom portion in a reservoir of distilled water, and a partial vacuum pressure of 10 psi was applied to the upper portion. The amount of water drawn through the sample during two consecutive 2-minute intervals was recorded. Water dyed with food color was then drawn through the sample at 27 psi. Flow rates were calculated on a per unit area of sapwood basis. Sapwood was defined to include all wood except heartwood.

Wound Periderm and Bark Thickness

The formation of wound periderm was evaluated by artificially wounding individual trees using a scalpel to make several shallow cuts (5 mm x 3 mm x 1 mm deep) in the bark surface. Trees were examined for suberized impervious tissue by removing a circular bark plug (with the wound in the center) about 3 weeks after wounding. The formation of impervious tissue was determined by the F-F test (Mullick 1975). The bark plugs are held phloem side down in a 2 percent solution of $FeCl_3$ for 3 days, and then in a 4 percent solution of $KFe(CN)_6$ for an additional 3 days. After drying, a radial cut through the bark plug exposes a light brown zone of necrotic tissue surrounding the wound. Immediately below this tissue is a thin layer of dark brown tissue, the suberized impervious tissue. The remainder of the plug will be colored dark blue. If the impervious layer is not formed, the entire sample will be dark blue.

Outer bark thickness was determined also using the F-F test. Unwounded plugs were taken from two sides of a tree. After staining, the samples were cut, and the maximum depth of any impermeable layer present (i.e. outer bark) was measured.

Monoterpene Analysis

We quantified the volatile fraction of resin, the monoterpenes, that was present within the necrotic tissue surrounding an artificial wound produced as described above. The monoterpenes found in healthy Fraser fir have been identified (Zavarin and Snajberk 1965, 1972, Thor and Bennett 1974), but there was no information concerning the monoterpene fraction of wounded tissue.

Wounded trees were sampled using a cork borer (dia. 11 mm) to remove a circular bark plug from the wound surface. All samples were placed in individual vials containing 4 ml of n-pentane, placed in a container of dry ice and taken to the laboratory and held at 0°C until analyzed. Control samples of unwounded tissue were handled in the same manner to determine the constitutive monoterpene composition.

The monoterpene content of each sample was analyzed by gas chromatography using one microliter of paracymene as an internal standard. All monoterpenes were identified by comparing their retention times with that of known standards. The amount of each monoterpene was quantified using a recording integrator. After this analysis, the dry weight of each bark sample was determined.

Juvabione Analysis

Juvabione analyses have been reported earlier (Puritch and Nijholt 1974, Manville 1975, 1976, Manville and Bock 1977, Manville and Kriz 1977). However, our procedures were different. We analyzed air-dried 5/8 inch woodcores rather than cross-sections of felled trees. The most recent annual ring and any annual rings showing evidence of rotholz were analyzed. The wood sections were ground up and subjected to a Soxhlet extraction (24 hr) with methanol. The extract was eluted through a C18 Waters sep-pak with 10 ml of methanol, and then analyzed by capillary gas chromatography. The retention times were compared to those of pure samples of extracts of Douglas-fir supplied by Dr. John Manville (verified by GC-MS).

Genetic Variations of Fraser Fir

Because of the wide variation in mortality caused by the balsam wooly adelgid within the natural range of Fraser fir, a related study assessed the genetic architecture of the southern Appalachian endemic Fraser fir by analyzing seven polymorphic allozyme loci found in five major mountain populations. Mature mother trees and their respective progeny were sampled in groups of 5 to 10 at the peaks of the mountains, and at other representative locations within populations. Samples consisted of cones with ripe seed.

Cleaned seed were germinated on moist filter paper and then subjected to electrophoretic analysis. Megagametophytes and embryos were excised from the seed coat, crushed separately, and inserted into the vertical slice of a gel. Of the approximately 25 enzymes tested in preliminary trials, 12 were chosen for scoring because of their good resolution in embryos and gametophytic, or their polymorphic character.

RESULTS AND DISCUSSION

Rotholz Formation and Water Potential

Although rotholz production is a common occurrence in infested fir species of North America, not all infested trees show the visual signs of rotholz. However, the lack of any visible indications of rotholz does not necessarily indicate that the xylem has been unaltered by the infestation. Heavily infested grand firs, grown as exotics in Scotland, were found to contain no visible evidence of rotholz, yet the sapwood of these trees was only one-twentieth as permeable as sapwood sampled from nearby uninfested trees. The adelgid-altered wood stained the same color as heartwood (Puritch 1971). The reduced permeability was due to a combination of tracheid pit membrane encrustation and accelerated embolism (Puritch and Johnson 1971, Puritch and Petty 1971).

Rotholz formation in infested Fraser fir was evaluated by studying wood cores taken from six sites near Mt. Rogers, Virginia, and five sites in the Black Mountains of North Carolina. Average adelgid densities were higher for trees sampled at Mt. Rogers. At moderate-to-high infestation densities, the proportion of trees producing rotholz was similar between locations. However, a significantly higher proportion of trees from the Black Mountains produced abnormal wood when lightly infested.

Pressure chamber measurements, made on cut shoots of Fraser fir, add additional evidence that adelgid infestations might interfere with water transport through the sapwood. Measurements taken in June showed that infested trees at Mt. Mitchell and Roan Mountain, North Carolina, had lower xylem pressure potentials (an indication of poorer water status) than uninfested controls, while the infested and uninfested trees at Mt. Rogers, Virginia, did not differ from one another. In mid-summer, there were no significant differences at any site. However, infested trees at all locations showed lower water potentials than uninfested trees when measured in September (Arthur and Hain 1986). Increment cores taken from infested trees at all three sites contained visible rotholz, and nearly all cores from uninfested trees at Mt. Mitchell also contained rotholz. This suggests that the uninfested trees at Mt. Mitchell may have recovered from an earlier infestation. As September was a low-rainfall month in the southern Appalachians during this study, these results may indicate that the physiological effects of adelgid-caused damage are more severe during periods of low rainfall.

In a comparative study in the Black Forest of Germany, xylem and phloem potential measurements were made on ca. 10-year-old silver fir infested with a closely related adelgid, *Adelges* (= *Dreyfusia*) *nordmanniana*, which infests branches and twigs. Trees were classified as uninfested, lightly infested, and heavily infested. Table 1 shows that both the phloem and xylem potential readings of the infested trees were considerably higher than that of the uninfested. In fact, the phloem of many of the infested trees had liquid oozing out of just one or two spots rather than the entire phloem area. When tested for rotholz with perchloric acid, many of the smaller twigs tested positive. *A. nordmanniana* was introduced into the Black Forest and is considered a pest. It is also capable of causing rotholz formation on the thin-barked twigs, while the native *A. piceae* does not cause rotholz formation on the thicker-barked boles of silver fir.

When sapwood flow rates were measured through Fraser fir stems previously infested by the adelgid, areas of rotholz generally did not transport dye. Rotholz inclusion is associated with reduced sapwood permeability and an increase in the proportional area of heartwood (Hollingsworth and Hain,

Table 1. Water potential readings of *Abies alba* infested with *Dreyfusia nordmanniana*

	Water potential (-bars)	
Degree of infestation	Xylem	Phloem
Heavily infested (n = 16)	10.09 ± 3.27	1.46 ± 1.06
Lightly infested (n = 10)	7.95 ± 1.96	1.75 ± 2.55
Uninfested (n = 15)	8.03 ± 2.67	0.73 ± 0.44

unpubl. data). These results lend support to the hypothesis that rotholz leads to water stress in the crowns of infested trees.

Wound Periderm and Bark Thickness

Adelgid attack causes chemical and structural changes within the tissue of susceptible hosts (Balch 1952). Initially the number and size of bark parenchyma cells increase within the area surrounding the insect's stylets. Within a year, these enlarged cells become surrounded by purplish cork cells which are produced by secondary phellogen. The parenchyma cells disintegrate, and the area becomes infiltrated with resin and completely enclosed within cork tissue. In heavily infested stems, this secondary cork cambium forms two or more millimeters beneath the surface of the bark, forming a localized, thickened layer of dead outer bark cells which physically prevents feeding by future generations.

The response described above is typical of conifers injured by biotic or abiotic factors. It serves to isolate the damaged area from the living tissues of the bark, while adding additional layers of protection in the damaged area. Many woody plants (Mullick 1977) exhibit this type of non-specific response when living bark cells are damaged.

In fir trees, the wound response initially involves the formation of a layer of suberized impervious tissue (Mullick 1975) to wall-off the damaged tissue, followed by the formation of a reddish-purple sequent (necrophylactic) periderm internal to the impervious layer. To determine if inherent variation in the formation of the layer of suberized impervious tissue could account for the observed mortality patterns of Fraser fir in the southern Appalachians, we tested 89 firs from seven locations for the complete formation of the suberized impervious tissue at artificial wound sites. The F-F test (Mullick 1975) showed that all the trees except one formed the impervious layer in a time period that was considered normal (3 weeks) during the growing season, with no delays due to tree age, location, or presence of balsam woolly adelgids.

There are a few instances where specific chemicals have been associated with a balsam woolly adelgid attack. The saliva of the adelgid contains auxin-like compounds (Balch et al. 1964) and pectinase (Adams and McAllan 1958). A juvabione-like substance, todomatuic acid, was found in the bark of infested grand fir (Puritch and Nijholt 1974). To determine the effect of these chemicals on the formation of the suberized impervious tissue at wound sites, we artificially wounded 86 fir trees (including 10 European silver fir planted at Mt. Mitchell) at three locations in the southern Appalachians. The wounds were treated with either napthalene acetic acid (NAA), pectinase, or todomatuic acid (Arthur and Hain 1985). None of the chemicals delayed formation of the impervious tissue.

Observations on other fir species indicate that outer bark, formed in response to attack by the balsam woolly adelgid, is frequently associated with recovery of infested trees (Brower 1947, Pschorn-Walcher and Zwölfer 1958, Schooley and Bryant 1978). Apparently the outer bark forms a physical barrier to adelgid feeding, or forces the insect to feed on other portions of the tree. Of 94 trees measured for bark thickness at Mt. Rogers, and 99 at Mitchell, a higher proportion of infested trees had outer bark thickness greater than 1.5 mm (the average length of a balsam woolly adelgid stylet) in comparison to uninfested trees. This was especially true of trees with a high infestation density and for trees with old wool only. Trees with old wool were recently infested (the woolly masses had not washed off yet), but not currently infested.

There was some indication that the "outer bark" detected in the Mt. Mitchell trees (defined by its impermeability to staining solutions) was not completely impermeable to the passage of moisture from the inner bark. When a new periderm layer is formed internal to the old one, all of the bark tissue between the two layers should gradually desiccate, becoming hard and compressed. Because of its distinct texture, this tissue is easily identified, and was classed as "dry outer bark" at the time we measured the thickness of the impermeable tissue. From Mt. Rogers, there were 23 trees which contained a measurable amount of outer bark, and 16 of these also contained "dry outer bark" as a proportion of the total outer bark thickness. By contrast, only 8 of 37 Mt. Mitchell trees with outer bark also contained "dry outer bark."

Average thickness of the dry outer bark was considerably greater for the silver fir trees from Germany, regardless of infestation class, than for Fraser fir trees of the southern Appalachians (Hollingsworth and Hain, unpubl. data). Silver fir trees generally contained more moist outer bark as well. It seems probable that silver fir trees naturally produce more outer bark than Fraser fir. An alternative explanation is that many of the silver fir studied may have formed the outer bark in response to previous infestations.

Monoterpene Deposition

The bark of 22 mature Fraser fir from Mt. Mitchell and Mt. Rogers was artificially wounded. Two to six weeks after wounding, wound tissue and unwounded tissue were sampled and analyzed for monoterpenes.

The results of the bark wound reaction study showed that there were no differences in total monoterpene content between wound tissue and normal bark tissue at either Mt. Mitchell or Mt. Rogers. However, there were differences between the two sites. Trees from Mt. Rogers had lower amounts of delta-3-carene relative to Mt. Mitchell. The variation between trees at Mt. Mitchell (which probably reflects historical harvesting and planting practices) could indicate differences in susceptibility to adelgid attack. Because Mt. Rogers trees have experienced little adelgid-caused mortality, it has been hypothesized (Arthur and Hain 1987) that those Mt. Mitchell trees that more closely resemble Mt. Rogers trees (and may in fact be a Mt. Rogers seed source) are more tolerant of an adelgid infestation.

In a similar study in Germany's Black Forest, monoterpene composition of wounded and unwounded tissue was compared between infested trees from a low elevation site and healthy and declining trees at a high elevation site. The cause of the decline at the high elevation site was unclear (perhaps it was influenced by atmospheric deposition) but none of the trees showed any sign of a balsam woolly adelgid infestation.

As seen in Fig. 3, the amount of monoterpenes found in the phloem tissue was considerably higher in the trees from the infested site. This was especially true for the wounded tissue. The monoterpene composition (Fig. 4) for the wounded tissue of the infested trees was similar to that of the wounded tissue of the declining trees at the high elevation. The amount (Fig. 5) of limonene in the unwounded tissue of the infested trees was also very high compared to the other trees.

It appears that the silver fir of the Black Forest, as opposed to Fraser fir, do respond to wounding of the phloem tissue by an accumulation of monoterpenes around the wound site.

It is not clear whether monoterpenes contribute to the tolerance mechanisms of fir trees infested by the balsam woolly adelgid. However, for other conifer species, monoterpene contents are thought to be important for host resistance to a number of insect pests and diseases (Rockwood 1973, Shrimpton 1973).

Juvabione

In addition to monoterpenes, some members of the genus *Abies* produce sesquiterpenoids which act as insect juvenile hormones (Slama and Williams 1965). Two such compounds, todomatuic and dehydrotodomatuic acids, have been identified from Pacific silver fir and grand fir infested with the adelgid (Puritch and Nijholt 1974). These compounds were found only in the vicinity of attack and

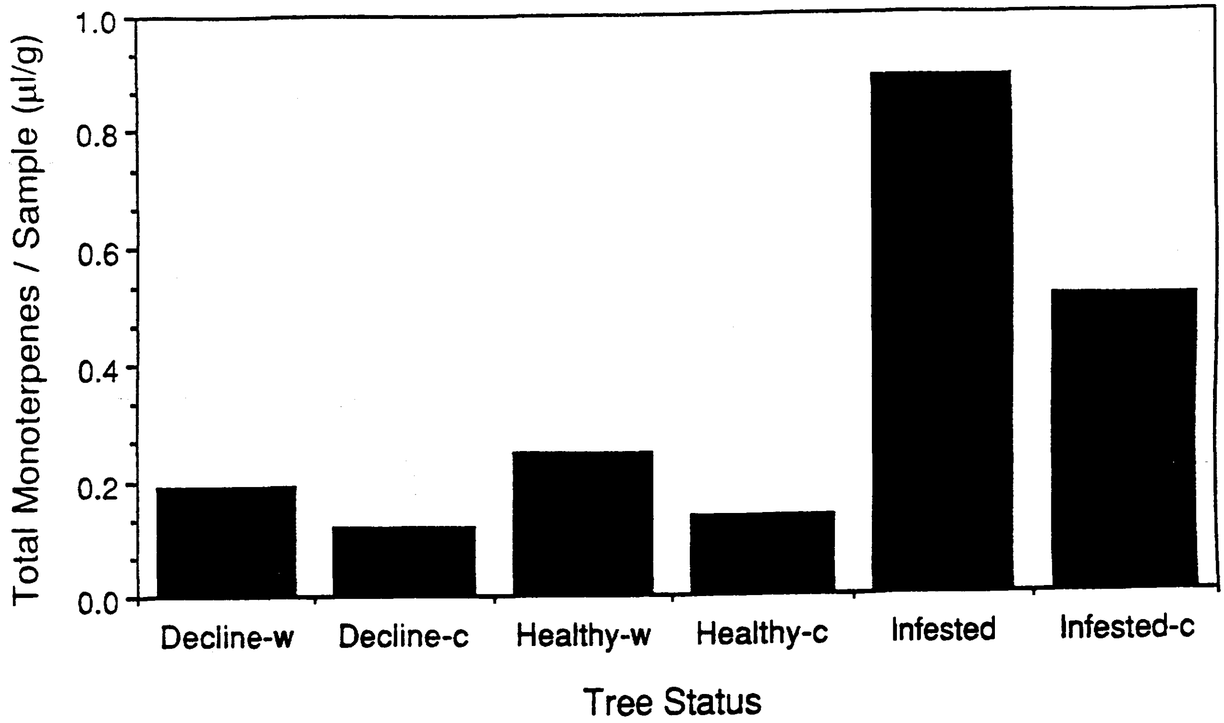

Figure 3. Total monoterpenes of European silver fir in the Black Forest of Germany. Decline-W = wound tissue from an uninfested declining tree, Decline-C = unwounded control tissue, Healthy-W = wound tissue from an uninfested healthy tree, Healthy-C = unwounded control tissue, Infested = wound tissue from an infested tree, and Infested-C = unwounded control tissue.

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were not present in uninfested trees. Todomatuic acid and juvabione have been isolated from seedlings of infested Fraser fir (Sanchez, unpubl. data).

The trees at the two sites in the Black Forest were also examined for the presence of juvabione and todomatuic acid (Table 2). Both compounds were detected but in very small amounts, especially the todomatuic acid. The concentration of these compounds was about 100-fold less than that detected in the infested Fraser fir seedlings (Sanchez, unpubl. data), and about 10-fold less than that detected in some of the infested mature grand and Pacific silver fir (Puritch and Nijholt 1974). However, the compounds were detected in the mature European silver fir, even in uninfested trees.

It has been hypothesized that juvabione-related compounds may interfere with adelgid development (Puritch and Nijholt 1974). The effective level of concentration, however, is unknown.

Genetic Variation of Fraser Fir

This study (Ross 1988) assessed the genetic architecture of Fraser fir throughout its restricted geographic range by analyzing seven polymorphic allozyme loci. The five major mountain populations differed slightly but significantly from each other with respect to allele frequency for both mature tree and progeny populations. The Mt. Rogers trees had the most extreme allele frequencies and appear to be an outlier among the five mountain populations. These differences may be due to local, restricted

Table 2. Presence of juvabione and todomatuic acid in *Abies alba*

Type	Age ± SE	Bark thickness MM ± SE	ul/g ± SE Juvabione	ul/g ± SE Todomatuic acid
Declining	96 ± 8	8.25 ± 1.66	1.60 ± 0.38	0.13 ± 0.20
Healthy	91 ± 5	9.39 ± 1.68	1.34 ± 0.13	0.03 ± 0.02
Infested	55 ± 7	6.28 ± 0.96	1.88 ± 0.52	0.01 ± 0.01

mating and genetic drift. Therefore, the distinctiveness of the Mt. Rogers fir trees is demonstrated genetically as well as entomologically with regards to adelgid tolerance. However, it has not been demonstrated that the genetic distinctiveness is in any way related to adelgid tolerance.

SUMMARY AND HYPOTHESIS

The balsam woolly adelgid's life cycle is anholocyclic with parthenogenetic reproduction on fir trees only. The adelgid is native to the fir trees of central Europe but has been introduced into North America. European firs are not seriously affected, but North American firs frequently experience either crown dieback or tree death, or both. Fraser fir, in the southern Appalachians, is one of the most susceptible North American species to an adelgid infestation. Research into the interactions of the adelgid with its new North American hosts has shown that infested trees respond by the production of rotholz in the xylem tissue, wound periderm in the bark tissue, resins, and juvabione substances. The objective of this paper has been to clarify the importance of each of the reaction components to the tolerance or susceptibility of Fraser fir to the adelgid. Comparisons with European silver fir were also made, and the genetic architecture of the major mountain populations of Fraser fir was examined.

Balsam woolly adelgid infestations interfere with water transport through the sapwood and undoubtedly interfere with phloem transport as well. Whether rotholz is visible or not, water potential measurements were lower in infested trees. In trees with rotholz, dye transport within the rotholz zone did not occur and there was an increase in the proportional area of heartwood. A significantly higher proportion of trees from the Black Mountains produced rotholz when lightly infested than did trees from Mt. Rogers, suggesting a greater sensitivity to an adelgid infestation in some mountain populations of Fraser fir.

Outer bark formed in response to attack by the balsam woolly adelgid appears to be associated with recovery of infested trees. Infested trees, at both Mt. Mitchell and Mt. Rogers, had a higher proportion of trees with an outer bark thickness greater than 1.5 mm. However, a higher proportion of Mt. Rogers trees contained "dry outer bark" as a proportion of the total outer bark thickness. The average thickness of the dry and moist outer bark of the silver fir trees in Germany was considerably greater than that of Fraser fir, regardless of infestation class. This suggests that the formation of outer bark, especially dry outer bark, is an important tolerance mechanism for mature trees infested by the adelgid.

While differences in monoterpene composition of bark tissue did exist between Mt. Mitchell and Mt. Rogers trees, there was no significant accumulation of monoterpenes in wounded bark tissue. This is in contrast to the silver fir of the Black Forest where wound tissue surrounding an artificial wound had a significantly higher accumulation of monoterpenes than unwounded tissue, especially in currently infested trees.

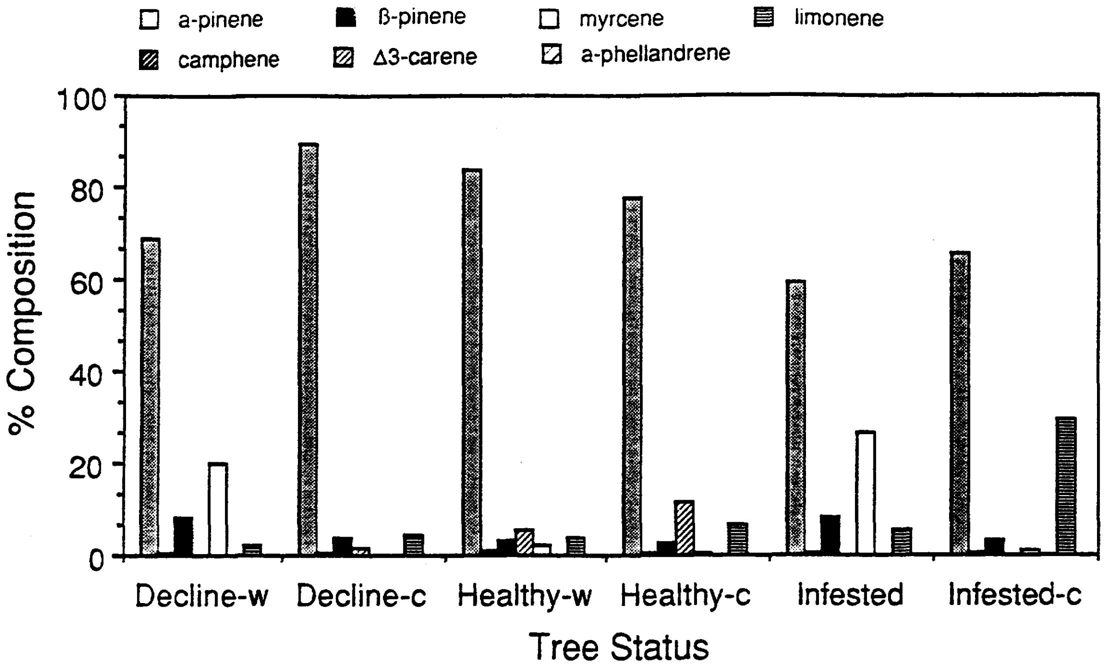

Figure 4. Composition of monoterpenes of European silver fir in the Black Forest of Germany. See Fig. 3 for description.

Juvabione-related compounds have been found in several fir species and may cause abnormal adelgid development. In some North American fir species the compounds were only found in infested trees. Infested Fraser fir seedlings had extremely high quantities of these compounds. Both infested and uninfested mature silver fir of Germany had detectable amounts of the chemicals, but in very low quantities. If these compounds do interfere with adelgid development, the effective concentration level is not known.

The balsam woolly adelgid studies in the southern Appalachians have demonstrated that the fir population at Mt. Rogers is unique with regards to adelgid/fir interactions. A genetic study of allele frequencies has also demonstrated the distinctiveness of the Mt. Rogers fir population. The Mt. Rogers trees had the most extreme allele frequencies and appear to be an outlier among the fir populations of the southern Appalachians.

Although our knowledge of the balsam woolly adelgid/Fraser fir interaction is incomplete, we know enough about the system to offer the following hypotheses about susceptibility, resistance, and tolerance of fir to an adelgid infestation.

In a susceptible fir there is an inadequate response tissue to the infestation within the bark. There is no immediate accumulation of monoterpenes or juvabione-related compounds, and an inadequate accumulation of outer bark. Both the phloem and the current xylem rings become non-translocating because of chemical and structural changes within the tissue. Continuous infestation over a period of years results in accumulation of non-translocating tissue that eventually kills the tree, especially during periods of drought.

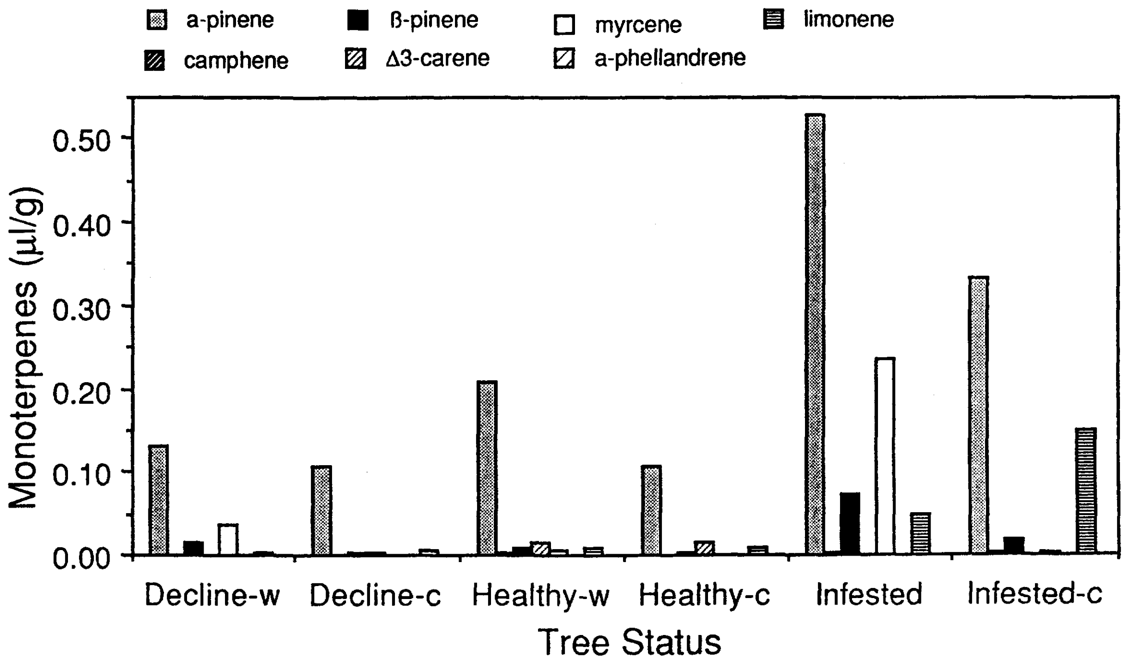

Figure 5. Amounts of monoterpenes of European silver fir in the Black Forest of Germany. See Fig. 3 for description.

In a resistant or tolerant fir there is a rapid accumulation of monoterpene and juvabione-related compounds surrounding the invasion site. In mature trees the chemical accumulation serves to inhibit survival and development of the adelgid. In younger trees, especially seedlings, the accumulation of juvabione-related compounds is so high that abnormal adelgid development prevents the insect from successfully reproducing. Older trees, which accumulate less juvabione-related compounds, begin to produce secondary periderm and a thick layer of outer bark. As the outer bark thickens and dries, it becomes unsuitable as an adelgid substrate. The insect either abandons the host, or abandons that part of the host, to infest another tree or another part of the same tree. If the process occurs rapidly, minimum damage is inflicted and the tree survives.

Future work will examine the above hypotheses in greater detail.

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SIGNIFICANCE OF PHYTOHORMONES IN SIBERIAN LARCH-BUD GALL MIDGE INTERACTION

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INTRODUCTION

Interrelations of the bud gall midge and the Siberian larch are of scientific and practical interest because of the bud gall midge's role as a plant endoparasite. We know that attack by the gall midge sets off a reaction in the entire plant. Invasion by the insect results in a certain interaction between physiological mechanisms of the insect and the plant which leads to a complex range of interdependent shifts in the metabolism of the tree, the final result depending on the character of those shifts. The reactions of both the plant and the insect are determined both by genetic factors and by environmental conditions.

The bud gall midge has long been considered a pest of the larch in Siberia even though it does not cause significant mortality among the trees. Some papers have been written on the effect of the gall midge on morphological and physiological parameters of the larch (Isaev et al. 1988). Damage to the larch by the bud gall midge involves reduction of the assimilative apparata. The gall midge infests the buds of the brachyblasts. Where the eggs have been laid under the cover scales of the buds, a gall appears, functioning during one season in which the whole cycle of insect development takes place.

MATERIALS AND METHODS

The balance of phytohormones in the plant, which is upset by the insect, has not been studied enough, though hormonal changes in damaged plant tissue have been recorded. In our study, phytohormone dynamics were examined in the needles, buds, and galls from the time of needle initiation up to the time of their yellowing and fall in the autumn, taking into account insect development stages, and tree differentiation according to the rate of pest invasion. To study the phytohormones, we used a set of methods including extraction, purification, chromatography, and biological activity tests. Identification by bioassays was made according to the growth of pieces of wheat coleoptiles and larch and lettuce hypocotyls, the capacity to produce color reactions, luminescence in the UV-light, and rechromatographing in different systems of solvents.

RESULTS

If larch is chronically infested by the gall midge, an increase occurs in the quantitative and qualitative composition of indole compounds and in their biological activity. The levels of endogenous auxins depend on the ratio of their synthesis and inactivation rates. The activity of indoleacetic oxidase in different parts of the larch does not change considerably as a result of midge invasion. Activity of

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the gibberellin-like and cytokinin-like substances increases, however. The rise in the activity of these phytohormones correlates with the start of pathological growth of bud tissue in the infested trees. Their maximal activity coincides with the period of intensive growth and formation of the gall. A concomitant accumulation of abscisic acid inhibitors occurs during the ending of growth. Chronically infested trees complete their vegetation cycle with a minimum of growth-promoting substances, leading to retardation of needle flushing in the spring.

Gall tissue developing in response to insect infestation is characterized by a great variety and activity of growth-promoting substances. The greatest amount of natural activators is found in galls during the first 10 days of July, when the growing process is intensive. At the end of vegetative growth, the growth-promoting activity of the gall extract is reduced by nearly half. Gall tissue is hormone-dependent, i.e. it cannot synthesize phytohormones while in tissue culture, as is the case for tumor tissue. Formation of gall tissue is a response by the tree to the midge infestation and is a necessary condition for normal development of insect larvae. Mechanical destruction of the gall causes mortality of the insect larva.

Increases in the activity of phytohormones occur at definite times, corresponding to the first and second larval instars. Invading the tissue of the host plant, the larva changes the plant's metabolic pattern. By using the attractive capacity of auxins, the midge larva attracts and accumulates mobile metabolites in the gall tissue. Thus one can see that gall-forming insects can cause shifts in the hormonal balance of the host plant, changing the content of its natural regulators.

DISCUSSION AND CONCLUSIONS

Most believe that whatever agent has caused the pathological tissue to form (mutations, infections by fungi, bacteria, insects), does so by eliciting changes in the activity or synthesis and degradation of plant hormones. Increases in auxins can be related to the accumulation of auxin protectors in the tissues and organs of the larch tree. The role of protector is performed by the phenols of the ortho-diphenol type, which serve as inhibitors of IAA disintegration. At the same time, some authors suggest that in natural conditions, loss of resistance to pathological growth is connected with a drop in the level of endogenic gibberellic acid or decreased sensitivity to it. Cytokinins are found in various parasitic organisms and seem to play a role in the development of anomalous tissue. Growth promotion based on elevated cell division and/or growth and a rise in mitotic activity is regulated by phytohormones. The specific effect of the bud gall midge on the buds connected with the gall occurs through induction. Induction starts the process (under the influence of the phytohormone) and does not occur in cells in the absence of the requisite hormones. In the case of gall tissue formation, two mechanisms, induction and promotion, operate together. Induction of pathologic growth is caused by secretory exometabolites of the bud midge larva. In line with the classic theory of mechanisms of realization of genetic information in the bacterial cell, Bonner (1967) suggested that hormones function by activating the genes which have previously been suppressed. Experimental data however, do not support this hypothesis. Though accumulation of natural growth stimulators and inhibitors in the larch tree damaged by the midge does not constitute direct evidence for the participation of phytohormones in the induction of anomalous growth, it does indicate that a change in the hormonal status of the host plant has occurred under the impact of the insect.

One may conclude, then, that the network of protective reactions to the pathologic growth stimulated by the bud midge is based on a shift in the balance of natural stimulators and growth inhibitors, reflecting complex interrelations between the plant and the insect.

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MANIPULATION OF HOST PLANT BIOMASS ALLOCATION AND RESOURCE REGULATION BY THE LARCH BUD GALL MIDGE

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INTRODUCTION

Intensive herbivory may influence the resources available to the next generation of herbivore in three ways: quantity may decrease, be unchanged, or increase. There are now two good examples of the last possibility. One of them concerns *Monochamus* beetles on firs in Siberia (Isaev et al. 1984), and the other a galling sawfly on willow in Arizona (Craig et al. 1986). The highly intimate and sedentary way of life of galling insects should predispose them to evolve the means to manipulate their hosts. Therefore, it is not surprising that a third example which we report herein deals also with a gallmaker.

The larch bud gall midge, *Dasyneura rozkovi* Mamaev et Nykolsky, forms galls in the vegetative buds of Siberian larch shoots, causing gall-bearing buds to die. In South Siberia during persistent and heavy infestations, trees may lose up to 95 percent of their buds. Such trees produce no flower buds, so commercial seed production on infested seed orchards is impossible (Isaev et al. 1988).

RESOURCE REGULATION

Our data deal with sixty, 45-year-old sample larch trees in a single seed plantation near Krasnoyarsk which varied considerably in the level of gall infestation. Though the increasing level of bud infestation decreases the number of flowers, it does not influence the current year's crown biomass production. Forming galls appear to function as metabolic sinks working as "redirectors" of tree resources. The tree translocates nutrients to branch periphery where last year's infested shoots are situated. The biomass of newly formed galls is negatively correlated with the biomass increment of older branches. In spite of a great shortage of living buds on 3- to 4-year-old shoots, the infestation level does not influence the total biomass of needles on the branch. This is because the needles of galled buds are much longer than those of ordinary buds on the same tree: the weight of a single needle may increase by 40 percent and the number of needles in the cluster by 11 percent.

The quantity of galls per shoot correlates positively with the incidence of shoot tip mortality and increasing lateral branching. Newly formed shoots have 10 to 15 percent higher bud density per shoot and increase simultaneously with the level of tree infestation. On galled larches, the growth rate of gall midge population density is limited only by the number of newly appearing buds. So in our case we have an example of resource regulation by the herbivore, i.e. the maintenance of higher food base

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by the gall midge that impacts immediately the subsequent generation of the same midge population on the same individual plant.

There is no evidence of induced defenses against gallmaker by the larch even though midge infestation has a large impact on tree growth and reproduction. The reaction of larch to defoliation and shoot tip mortality is unspecific: increased branching and bud density following severe defoliation by needle-chewing insects and frost damage (Pleshanov 1982). By redirection of intershoot supplies of nutrients, the gallmaker stops the apical dominance in the shoot system, and in this way simply stimulates dormant meristems, i.e. provokes the process of general response to damage in larch trees (Haukioja et al. 1990).

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GALL MIDGES (DIPTERA: CECIDOMYIIDAE) IN FOREST ECOSYSTEMS

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INTRODUCTION

The family Cecidomyiidae is one of the largest of the Diptera. Gall midges are small, inconspicuous flies, but they may be very important both in forest ecosystems and in agroecosystems. Many phytophagous gall midge species attack forest trees, and some of them can be serious pests, such as the *Dasineura rozhkovii* Mamaev and Nikolsky, which develops in bud galls of *Larix sibirica* Ledeb (Isaev et al. 1988). More than 1,200 species in 125 genera are known to occur in the Nearctic Region (Stone et al. 1965), and about 2,200 species in 300 genera occur in the Palearctic Region (Skuhravá 1986). It has been estimated that the world fauna of gall midges includes four or five thousand species.

Adult gall midges have small bodies, usually only 0.5 to 3 mm long, rarely up to 8 mm long, and long antennae. Adults do not take food and therefore cannot cause damage to humans in any way. The larvae of gall midges feed and develop in various environments. On the basis of larval feeding habits, gall midges may be divided into three ecological groups: the mycophagous (= fungivorous), the phytophagous, and the zoophagous (Skuhravá et al. 1984). The majority of described species belong in the group of phytophagous gall midges, the larvae of which develop in, or on, various organs of many host plant species, where they feed by sucking sap from the tissues. Many of them induce development of some type of abnormal plant growth, called galls. The larvae of gall-producing species develop on most plant parts: roots, stems, vegetative tops, leaves, flowers, and fruits.

Gall midges usually have only one generation per year, although some species have two or more generations per year. Adults have very short lives, sometimes only several hours long, sometimes 1 to 4 days. Males usually perish shortly after mating, females very soon after oviposition. The typical life cycle begins early in the spring with emergence of the adults either from the gall or from the soil where they hibernate as larvae. Females lay their eggs on the surface of the organs of the host plants. Galls develop and the larvae develop inside them, sucking sap. Development of the larvae from hatching to maturity (three or four stages) requires usually 2 or 3 weeks. Many species drop to the soil, where they hibernate. Larvae of other species live in their galls through pupation.

Gall Midges as Forest Pests

Barnes (1951) has reviewed of about 240 gall midge species associated with coniferous and broad-leaved trees in the world. The larvae of 80 species develop on various species of 14 genera of coniferous trees, making galls on buds, terminal shoots, needles, fruits, seeds, and cones, or living under bark, in resin masses, in scolytid burrows, and in aphid galls. In Europe only seven species may be

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considered serious pests: *Thecodiplosis brachyntera* Schwagr. on needles of *Pinus silvestris* L. and *P. mugo* Turra, *Resseliella piceae* Seitner on seed of *Abies alba* Mill., *Plemeliella abietina* Seitner on seed of *Picea excelsa* Link., *Dasineura kellneri* Henschel (= *Dasineura laricis* [F. Low 1878]) on bud of *Larix decidua* Mill., *Paradiplosis abietis* Hubault on needles of *Abies alba* Mill., *Taxomyia taxi* Inchbald on terminal buds of *Taxus baccata* L., and *Janetiella siskiyou* Felt (= *Craneiobia lawsonianae* de Meijere) on the seed of *Chamaecyparis lawsoniana* Parl. imported from North America. The larvae of about 160 gall midge species develop on various species of 35 genera of broad-leaved trees in the world, producing various types of galls on terminal buds, stems, twigs, leaves, petioles, flowers, flower-stalks, fruits, and pods, or living under the bark, in decaying wood and bark, or as predators in the galls of mites or aphids.

Most gall midges cannot be considered pests, but some of them may increase and then attain the status of pest. For example, in Central Europe, in Czechoslovakia, more than 500 gall midge species have been identified (Skuhravá 1987), 92 of which are associated with forest trees and may be considered as actual or potential pests. Thirteen species develop on coniferous trees and 79 develop on broad-leaved trees (Skuhravá 1983). At present, the following eight species of gall midges damage forest tree species and are actual pests: *Contarinia fagi* Rubsaamen on young trees of *Fagus silvatica* L., in forest nurseries or planted trees in submontane and montane areas; *Contarinia querccina* Rubsaamen on young oaks, *Quercus robur* L. and *Q. petraea* Liebl., in hilly country; *Dasineura irregularis* Bremi (= *Dasineura acercrispans* [Kieffer]) on developing young leaves on terminal parts of the twigs of maple, *Acer pseudoplatanus* L., in lowlands and hilly countries; *Harrisomyia vitrina* Kieffer and *Drisina glutinosa* Giard. on leaves of young, medium-aged and old maple trees, *Acer pseudoplatanus* L., in submontane regions; *Dasineura fraxinea* Kieffer on leaves of young, medium-aged and old ashes, *Fraxinus excelsior* L., in hilly regions; *Dasineura thomasiana* Kieffer on leaf buds of young trees of *Tilia platyphyllos* Scop. and *Tilia cordata* Mill. in hilly areas; *Dasineura kellneri* Henschel (= *D. laricis* F. Low) on buds of larch, *Larix decidua* Mill., in central and southwestern parts of Bohemia.

The following 15 gall midge species represent potential pests of forest trees in Czechoslovakia: *Thecodiplosis brachyntera* Schwagr. and *Contarinia Caeri* Prell. on *Pinus silvestris* L. and *P. mugo* Turra; *Paradiplosis abietis* Hubault on *Abies alba* Mill., *Taxomyia taxi* Inchbald on *Taxus baccata* L., *Plemeliekla abietina* Seitner on *Picea excelsa* Link., *Resseliella piceae* Seitner on *Abies alba* Mill., *Contarinia marchali* Kieffer on *Fraxinus excelsior* L., *Mikiola fagi* Hartig on *Fagus silvatica* L., *Dasineura fraxini* Bremi on *Fraxinus excelsior* L., *Zygiobia carpini* F. Low on *Carpinus betulus* L., *Didymomyia tiliacea* Bremi on *Tilia platyphyllos* Scop. and *Tilia cordata* Mill., *Dasineura tortilis* Bremi on *Alnus glutinosa* Gaertn., *Dasineura populeti* Rubsaamen on *Populus tremula* L., *Wachtliella rosarum* Hardy on various species of Rosa, and *Dasineura* (*Rhabdophaga*, *Helicomyia*) *saliciperda* Dufour on various species of willows, *Salix* sp. The distribution areas of some of these gall midge species in the Palearctic Region were elaborated by Skuhravá (1987).

Gall Midges as Members of Forest Ecosystems

In relation to ecosystem studies, most gall midges may be considered part of the grazing food chain: the majority of gall midge larvae suck the sap of the plant tissues making or not making the galls. Another, but smaller part of the gall midge population belongs to the detritus food chain in which those species occur which suck sap from decaying or dead plant matter, i.e. the phytosaprophagous and mycophagous gall midges. Data about species composition, seasonal dynamics and function of gall midges in two types of forest ecosystems were obtained from studies organized within the International Biological Program on the Territory of Czechoslovakia. In 1973, stationary emergence traps were used to collect spiders, harvestmen, and insects, including Diptera, from the soil in a spruce monoculture at Kunicky, in the area of the Drahanska vrchovina Highlands, about 16°E and 49°N, at an elevation of 620 m a.s.l. The plant community was a type of unnatural woodland with unsuitable composition of *Picea excelsa* Link. The soils belong to the acid brown forest soil type (Vanhara 1983). In 1973, from the beginning of May up to the beginning of November, 1,108 specimens of adult gall midges emerged from soil under the tree traps. The majority of gall midges emerged in the spring. In terms of composition, most belonged to the zoophagous genera, *Lestodiplosis* (57 percent) and *Trisopsis* (11 percent). About 19 percent belonged to the phytosaprophagous species *Porricondyla neglecta* Mamaev. Strictly phytophagous gall midge species formed only 1 percent of the emerging specimens (Table 1).

In 1971, 1972, and 1981, other ecosystem studies were carried out in a lowland forest of the Ulmeto-Fraxinetum-Carpineum type near Lednice na Morave using the sweep samples (Vanhara 1981, 1986). In all, 7,815 specimens of Diptera were obtained in 1971, among them 3,417 specimens representing 711 species (9 percent) of gall midges. In lowland forest ecosystems, the family Cecidomyiidae is one of the richest families of Diptera.

From late April to early October in 1981, 319 adult gall midges were collected. In lowland forests, the flight period of gall midges has two peaks, the vernal maximum in May and the autumnal one in early September. The species composition is more varied than that in the monoculture of *Picea excelsa*, with a predominance of the phytophagous species, *Contarinia tiliarum* and *Dasineura thomasiana* (Table 2).

Table 1. The composition of gall midge species emerging in 1973 from soil of a spruce monoculture (*Picea excelsa* Link.) at Kunicky in the Drahanska vysocina Highlands, Czechoslovakia, by means of stationary collecting emergence traps.

Species or genus	Number of individuals			Percent of total	Feeding habits[1]
	Males	Females	Adults		
Lestodiplosis	254	373	627	57	Z
Porricondyla neglecta	80	126	206	18.5	PS
Trisopsis	54	71	125	11	Z
Thecodiplosis brachyntera	2	4	6	0.5	P
Kaltenbachiola strobi	2	3	5	0.5	P
Cecidomyiidae, undetermined	46	93	139	12.5	-
Total:				100	

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[1] Abbreviations: Z - zoophagous, PS - phytosaprophagous, P - phytophagous.

Table 2. The gall midge species composition in the flood plain forest, Ulmeto-Fraxinetum-Carpineum type, near Lednice na Morave, Czechoslovakia, obtained by the sweeping method in 1981

Species or genus	Number of individuals			Percent of total	Feeding habits[1]
	Males	Females	Adults		
Contarinia tiliarum	30	46	76	24	P
Porricondyla neglecta	19	40	59	18.5	PS
Lestodiplosis	16	44	60	19	Z
Clinodiplosis cilicrus	13	30	43	13.5	PS
Mycodiplosis	10	6	16	5	PS
Dasineura thomasiana	3	8	11	3.4	P
Macrolabis	4	7	11	3.4	PI
Craneiobia corni	1	5	6	1.8	P
Dasineura	6	-	6	1.8	PI
Trisopsis	2	2	4	1.2	Z
Jaapiella	3	-	3	0.9	PI
Lasioptera tiliarum	-	2	2	0.6	PI
Didymomyia tiliacea	1	1	2	0.6	P
Tricholoba	-	2	2	0.6	PI
Aphidoletes aphidimyza	1	-	1	0.3	Z
Parallelodiplosis galliperda	1	-	1	0.3	PI
Therodiplosis persicae	1	-	1	0.3	Z
Cecidomyiidae, undetermined	8	7	15	4.8	-
Total:				100	

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[1] Abbreviations: P = phytophagous (gall-producing), PI = phytophagous--inquilines, PS = phytosaprophagous, and Z = zoophagous

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SEED GALLS OF SEMUDOBIA BETULAE (DIPTERA: CECIDOMYIIDAE) ON SPECIES OF BIRCH (BETULA SPP.)

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INTRODUCTION

Semudobia betulae Winnertz, described in 1853, is the most common species of gall insect occurring on the genus *Betula* in the Palearctic and Nearctic regions of the world. *S. betulae* has been observed on four species of *Betula* according to Barnes (1951) and on 14 additional species according to Roskam (1977).

At the Arboretum of Mlynany affiliated with the Institute of Dendrobiology of the Slovak Academy of Sciences, eight species of *Betula* from the Palearctic and Nearctic regions have been planted. Three of them are mentioned in the papers of Barnes and Roskam: *B. pendula*, *B. ermanii*, and *B. papyrifera*.

In 1987 and 1988, the galls of *S. betulae* on the eight species of *Betula* were collected and their forms studied. Ten catkins were collected from each species and the number of attacked fruits recorded.

RESULTS

Normal seed of the birch consists of two parts: the middle part, i.e. the seed itself, and the large, round, rudimentary wings which assist in its dispersal.

Gall form differed among various birch species. We found a great number of fruit having larvae or parasites inside the deformed seed gall and normal large seed wings. In some *Betula* species, on the other hand, the seed gall consists only of the middle part, without the wings. In other species, there are still other types of seed galls, which the wings are very small or only one part of the wing is developed.

Normally developed galls were found only on *B. ermanii*, *B. nigra*, and *B. pumilla*. Great variability was found in *B. pendula* from Europe. The galls without wings were found on *B. chinensis*, *B. microphylla*, *B. nigra*, and *B. papyrifera*. Only *B. maximowicziana* was not infested. Since the fruit of this *Betula* species does not develop until 3 weeks after the flight period of *S. betulae* commences, its infestation is impossible.

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The results are summarized in the following table:

Betula species	Distribution	Number of galls per 10 catkins	
		1987	1988
B. microphylla Bge.	Middle Asia	8	12
B. ermanii Cham.	Northeastern Asia, Japan, Korea	16	7
B. chinensis Maxim.	Northern China, Japan, Korea	115	10
B. pendula Roth. (= *B. verrucosa*)	Europe, Asia	30	62
B. maximowicziana Regel.	Japan	-	-
B. nigra L.	Eastern U.S.A.	2	15
B. pendula Roth.	U.S.A.	115	19
B. pumilla L.	Northeastern U.S.A., Labrador	135	105
B. papyrifera Marsh.	North America	95	33

The form of galls depends on the time when the first instar larvae start to develop in the fruit.

Our data indicate that *S. betulae* are present on seven species occurring in the Palearctic and Nearctic regions. It appears that *S. betulae* can live on many species of the genus *Betula* in the northern hemisphere. It is interesting to note that the galls of *S. betulae* were also found on *B. nana* L. in the Sumava Mountains of southern Bohemia, at an elevation of 1,000 m a.s.l.

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STRUCTURE, SPECIFICITY, AND EVOLUTION OF INSECT GUILDS RELATED TO CONES OF CONIFERS IN WESTERN EUROPE

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INTRODUCTION

Patchy and ephemeral resources, such as the cones of conifers, can be very useful in the study of plant-insect relationships. Studies of such relationships in forest entomology are typically complicated by the spatial and temporal characteristics of the host plants, which occur over vast areas and have lifespans of decades or even centuries. The reproductive structures of conifers, on the other hand, are much more easily studied because they mature within 1 to a few years and occur as discrete, easily sampled units. They also play a unique role in forest ecosystems.

Seed cones, which correspond to female flowers in most gymnosperms (Pinaceae, Taxodiaceae, Araucariaceae, most Cupressaceae), develop both as singular units and as integral parts of cone-bearing trees. Though development varies with tree species, general trends appear similar, corresponding to the progressive development of the female flower into a lignified cone that can release mature seeds. These overall similarities in cone development among most conifers facilitate a comparison of the fauna inhabiting cones (Roques 1988a).

Cone maturation is always extremely rapid compared to tree lifespan. The morphological, physiological, and biochemical changes which occur during the lifetime of the reproductive structures are thus condensed into a much more limited time and space (cone size varies from 0.6 cm in *Juniperus sabina* to 15 cm in *Abies alba*, and time from flowering to seed release ranges from 6-1/2 months in *Larix decidua* to 2-1/2 years in *Pinus silvestris*, for instance). Very distinct environmental conditions are thus offered to insects during successive and temporally restricted periods. Moreover, in most conifers spatial distribution of cones is heterogeneous among trees as well as within trees (Mattson 1979) and cone crop appears to vary over time, generally being neither annual nor cyclic (masting phenomena, according to Fenner 1985).

Individual cones may therefore be viewed as temporary subunits of the forest biocenosis which form discrete habitats with a limited carrying capacity for possible inhabitants. Niche characteristics, especially size limitations, would predict a highly specific entomofauna adapted to host discontinuity in space and time.

Though a large body of literature has dealt with the functioning of insect guilds of similar structures of angiosperms (among many others, Janzen 1969, 1970, Zwölfer 1979, 1982, 1987, 1988), very few studies have provided a synthesis of the relationships between cones and associated insect guilds, with the exception of some notable work done in eastern Europe (Stadnitskii 1971, Stadnitskii et al. 1978, Skrzypczynska 1977, 1981, 1982, among others). In this contribution, which is part of a

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wider study of cone-insect relationships (Roques 1988a), I synthesized the European literature with the following goals: 1) analysis of the structure of ecological groups in cones of native and introduced conifer species in western Europe, 2) specificity of the host of individual cone-insect relationships, and 3) exploration of the consequences for the structure and evolution of insect guilds.

ECOLOGICAL GROUPS RELATED TO CONES: DIVERSITY AND LIMITATION

Insects inhabiting cones in western Europe can be divided into three ecological groups in relation to trophic habits: a) phytophagous insects with their parasite and predator complexes, b) mycophagous and detritivore species developing in the detritus food chain deriving from the previous group, with their own natural enemies, and c) insects using the galleries made by phytophages as hibernating shelter sites. This structure of entomological communities is, naturally, based upon the phytophagous group, whose previous damage creates conditions that support development of the other groups.

Insects Using Cones as Hibernating Sites

These species are uncommon. Only a few species with no accurately defined tropic relation, are regularly encountered overwintering within cones: adults of *Rhizobius chrysomeloides* Hbst. (Coleoptera: Coccinellidae) and some stages of *Leptothorax affinis* L. (Hymenoptera: Formicidae) in *P. silvestris* (Roques 1977); some stages of *Crematogaster* spp. (Hymenoptera: Formicidae) in Mediterranean pines; adults and nymphs of *Gastrodes abietum* Bergroth and *G. grossipes* De Geer (Hemiptera: Lygaeidae) in spruce (Roques 1983). These insects will be excluded from the following discussion.

Mycophagous and Detritivore Species

Larvae of several species commonly develop on fungi and detritus in cone galleries made by phytophages. Dipterous larvae are exclusively observed in western Europe: Chloropidae, one species, and Cecidomyiidae, one species. These larvae do not directly attack cone structures but may, as does *Camptomyia pinicolana* Mam. (Cecidomyiidae), seed browning that leads to seed abortion (Roques 1983). The detritivore subguild is more important in other European regions. In addition, 15 other species, mainly Diptera but also Coleoptera (Cryptophagidae, Anobiidae, Lathridiidae) have been noted in Poland and in the European part of the Soviet Union (Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1978).

Phytophagous Species

By contrast, diversity in families and orders is a dominant feature of the phytophagous group. Larvae of weevils, microlepidoptera, gall-midges, and seed-chalcids, among others belonging to 13 families and four orders of insects are known to feed on cones of the various conifers growing in western Europe (Fig. 1a, from data in Roques 1983). In addition, mites of the family Eryiophiidae have been reported, e.g. *Trisetacus* spp. (Roques 1983, Roques et al. 1984).

This diversity, however, is only superficial. The number of species and, more importantly, the number of genera observed in the cones are limited. Fifty-nine species from only 30 genera are currently recorded in western Europe (Fig. 1b, from Roques 1983, Roques et al. 1984, Roques and Raimbault 1986). The subsequent total of recorded phytophages and detritivores is 61 species and 32 genera. The same values total only 72 and 33, respectively, when all of Europe, including the European part of the Soviet Union, is considered (calculations from data in Annila 1976, Wiersma 1978, Skrzypczynska 1977, 1981, 1982, Stadnitskii et al. 1974, 1978). This shows both relative stability

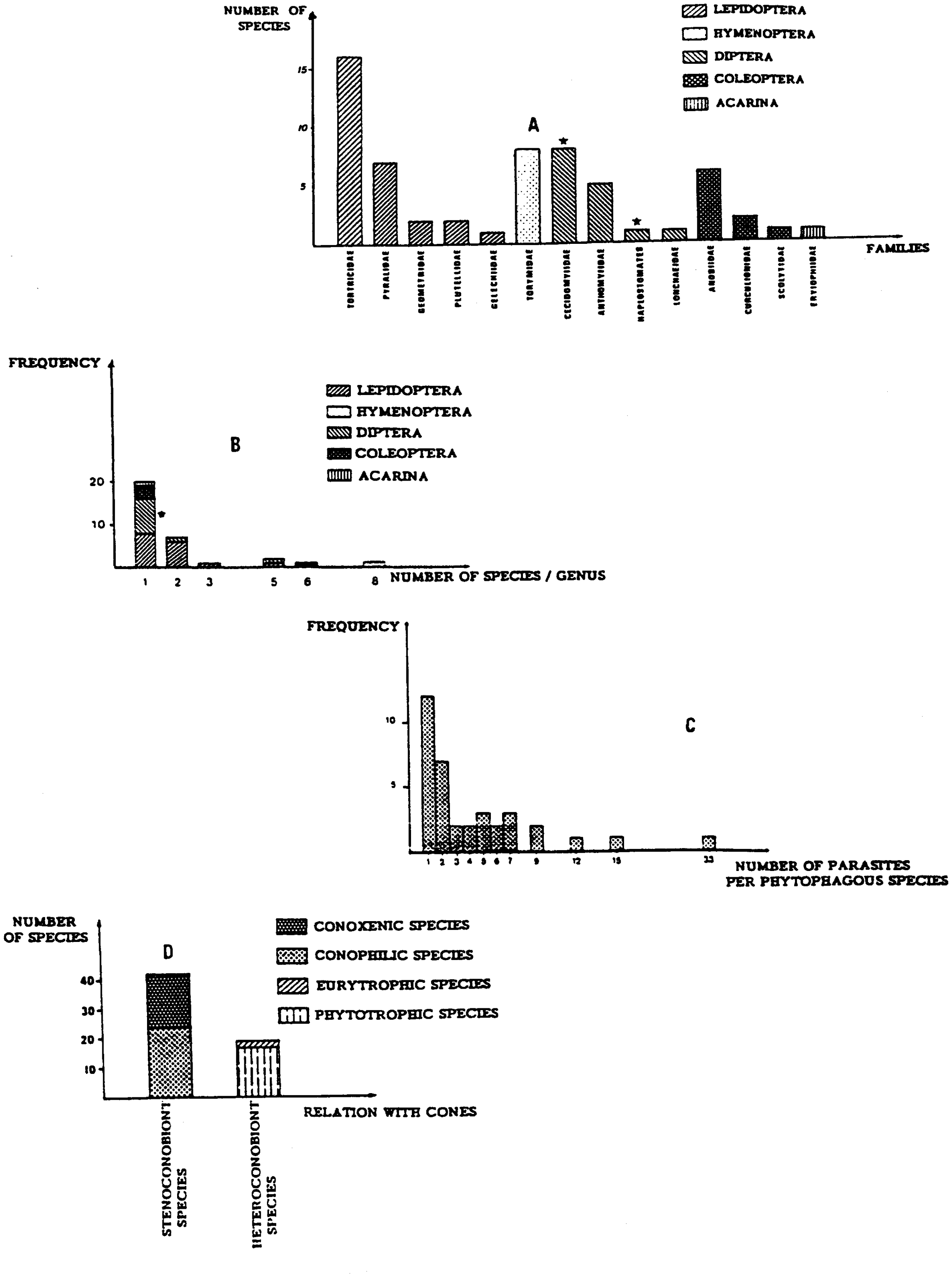

Figure 1. Faunal characteristics of insect guilds related to cones in western Europe: a) families and orders involved in phytophagous and detritivore species (* 1 detritivore species), b) extent of speciation within phytophagous genera (* 2 genera with 1 detritivore species), c) frequency of entomophagous species per phytophagous species, and d) specificity to cones and developmental features shown by the phytophagous and detritivore species.

in cone-insect relationships at the continental level and the present limitation of speciation processes within cones to a reduced number of genera, whose species are specializing in the exploitation of these distinct substrates (especially Anthomyiids of the genus *Strobilomyia*, Chalcids of the genus *Megastigmus*, Pyralids of the genus *Dioryctria*, and Anobiids of the genus *Ernobius*).

The guilds of phytophagous insects associated with cones include three trophic strategies by which the resource is partitioned. A first group, representing 40 percent of the insects (27/59), feeds on cone tissues as well as on seeds: conoseminiphagous insects, e.g. members of the Anthomyiid genus *Strobilomyia*, members of the tortricid genera *Barbara*, *Petrova*, *Cydia*, and *Pammene*, and the weevil *Pissodes validirostris*, among others. The second group, less important (19/59), develops only on cone tissues: conophagous insects, e.g. some members of the Pyralid genus *Dioryctria* and Argyresthiidae of the genus *Blastotere*). The third group (15/59) is specialized in seed exploitation: seminiphagous insects, e.g. members of the chalcid genera *Megastigmus* and *Torymus* and members of the Cecidomyiid genera *Plemeliella* and *Resseliella*, among others. It must be noted that all the insect species from a single genus exploit the same cone level, independently of tree species. These characteristics of the phytophagous group--diversity of families and limited speciation process related to a similar specialization in resource exploitation by species of the same genus--may be viewed as the result of an evolutionary process leading to complete utilization of the niche.

Parasite and Predator Complexes

Only 38 of the 61 phytophagous and detritivore species are presently known to have parasites and predators within cones in western Europe (data compiled by Roques in Yates 1988). One hundred twenty-two species, mainly Hymenoptera, have been identified in this group (Table 1).

The number of parasite species per host species is limited, generally fewer than 10 (Fig. 1c). It has been assumed that the cryptic nature of most cone insects underlies this phenomenon (Yates 1986). Thus the number of natural enemies observed in phytophagous insects that can feed on structures other than cones is strongly affected by the type of tissue occupied, e.g. three parasites in cones versus 20 in shoots for the pine shoot moth, *Rhyacionia buoliana* Schiff., in the same French localities (Roques 1977).

DEGREE OF SPECIFICITY OF THE VARIOUS INSECT GROUPS

High Host Specificity for Most Phytophagous Insects

Seventy-one percent of these species, defined as stenoconobiont species (after Stadnitskii 1971), need to complete their larval development, at least in part, within cones (Fig. 1d, from Roques 1988a). More than half--the conophilic show an extreme adaptation in spending their entire larval and pupal development within cones species as opposed to the conoxenic species, which exit the cone to pupate--(Fig. 1d). All seminiphagous species exhibit this former type of development. Close adaptation to seed substrate thus appears as the result of an extreme niche specialization.

Conversely, less than one third of common phytophages, the heteroconobiont species, are able to develop in other tree structures, such as buds and shoots. Most of them (14/19) damage the cones only occasionally, when insect population density is out of proportion to the resources offered by the normal host, e.g. as in outbreaks of the larch bud moth, *Zeiraphera diniana* Guenée (Roques 1988b), and as with pine shoot moths, *Rhyacionia pinicolana* Dbld. and *Rh. buoliana* Schiff., in young stands (Roques 1977). A minority of heteroconobiont species do prefer the cones and feed occasionally on other vegetal structures. *Dioryctria mutatella* Fuchs may develop in pine shoots in case of cone crop

Table 1. Parasites and predators associated with phytophagous cone insects in western Europe

Order	Family	Number of species
Hymenoptera	Ichneumonidae	43
	Braconidae	28
	Pteromalidae	22
	Torymidae	5
	Eulophidae	4
	Eupelmidae	3
	Tetrastichidae	2
	Platygasteridae	1
	Eurytomidae	1
	Encyrtidae	1
	Trichogrammatidae	1
	Cynipidae	1
Diptera	Tachinidae	5
	Lonchaeidae (predator)	2
Neuroptera	Chrysopidae (predator)	1
	Rhaphidiidae (predator)	2

failure (Charles and Roques 1977). This certainly confers an adaptive advantage upon these latter species, allowing their populations to minimize the consequences of irregular cone crops.

Despite appearances, however, no European cone and seed insect species is entirely host-specific. The apparent specificity observed in western Europe results from the present range of conifers in this geographical region, where in several cases only one species per genus survived after Quaternary glaciations, e.g. *Larix*, *Picea*, and *Abies*.

The example of the *Megastigmus* species is significant. The speciation process is highly developed in this genus as compared with other cone insects, resulting in seven native species, to which, subsequently, four species introduced from North America have been added (Roques 1983). Larvae of these chalcids developing entirely in seeds are completely at the mercy of host selection pressure, with no possibility of escape (Labeyrie 1977). Therefore, conifer taxa may be assumed to serve as platforms for adaptive radiation of *Megastigmus*, insect species ultimately mirroring conifer speciation. Such a process is observed, but with a substantial evolutionary lag. Native conifer species in western Europe are each attacked by a single *Megastigmus* species, with the exception of *Pinus* spp., in relation to which disappearance with glaciations probably explains the absence of chalcids (Roques 1988a). However, where sympatric stands of congeneric host species exist, e.g. *Juniperus* spp. in central and mediterranean France, they are colonized by the same chalcid species (Roques et al. 1984). In addition, records in arboreta where exotic and native tree species are mixed show that each *Megastigmus* species is still capable of attacking allopatric Eurasian congeners of the natural host (Table 2), whereas these allopatric species are colonized by other chalcid species in their native areas. Similar results have been obtained with most other cone insects, e.g. *Strobilomyia* spp. and *Cydia* spp. (Roques 1983). Host specificity thus remains at a superspecific level, though local adaptive differences in insect populations probably exist.

Table 2. Host range of *Megastigmus* species observed within seeds of native and exotic species growing at the Arboretum des Barres (France)

CONIFER SPECIES MEGASTIGMUS SPECIES	Abies alba	Abies bornmulleriana**	Abies cephalonica**	Abies cilicica**	Abies grandis**	Abies nordmanniana**	Abies pinsapo**	Cedrus atlantica**	Cedrus brevifolia**	Cedrus libani**	Larix decidua	Larix sibirica**	Picea abies	Picea orientalis**	Picea obovata**	Pseudotsuga macrocarpa**	Pseudotsuga menziesii**
M.suspectus	■	■	■	■		■	■										
M.suspectus var. pinsapinis	■					■	■	■	■	■							
M.pictus											■	■					
M.strobilobius													■	■	■		
M.pinus*					■												
M.spermotrophus*																■	■

* Insect species introduced along with host species
** Introduced host species

High Phenological Synchrony with Cones

There is close phenological coincidence of attack period in phytophagous insects with the appearance of unique, ephemeral stages in cone development. This is observed in all conifer species (Roques 1983, Roques et al. 1984). Most phytophagous insects are univoltine species, apart from some *Dioryctria* spp. (Roques 1983), and close synchrony in attack period is probably an adaptation to structural changes occurring within the cone which differentiate it from other tree structures, especially buds and shoots.

Fig. 2, based on the homology in cone development observed in western conifers, presents a synthesis of colonization of successive cone development phases by the 59 European phytophages. The stenoconobiont core of cone entomofauna is essentially recruited during cone growth and onset of seed development, when physical and chemical changes are both more substantial and more rapid. By contrast, previous and subsequent development phases, during which cones may be less distinct from surrounding tree structures, are dominated by heteroconobiont species.

Fig. 2 also shows the decrease in conoxenic species, due to successive departures from the cone, after the completion of cone growth. This may be considered an "evasion" strategy (sensu Zwölfer 1982), minimizing intra- and interspecific competition for limited cone resources.

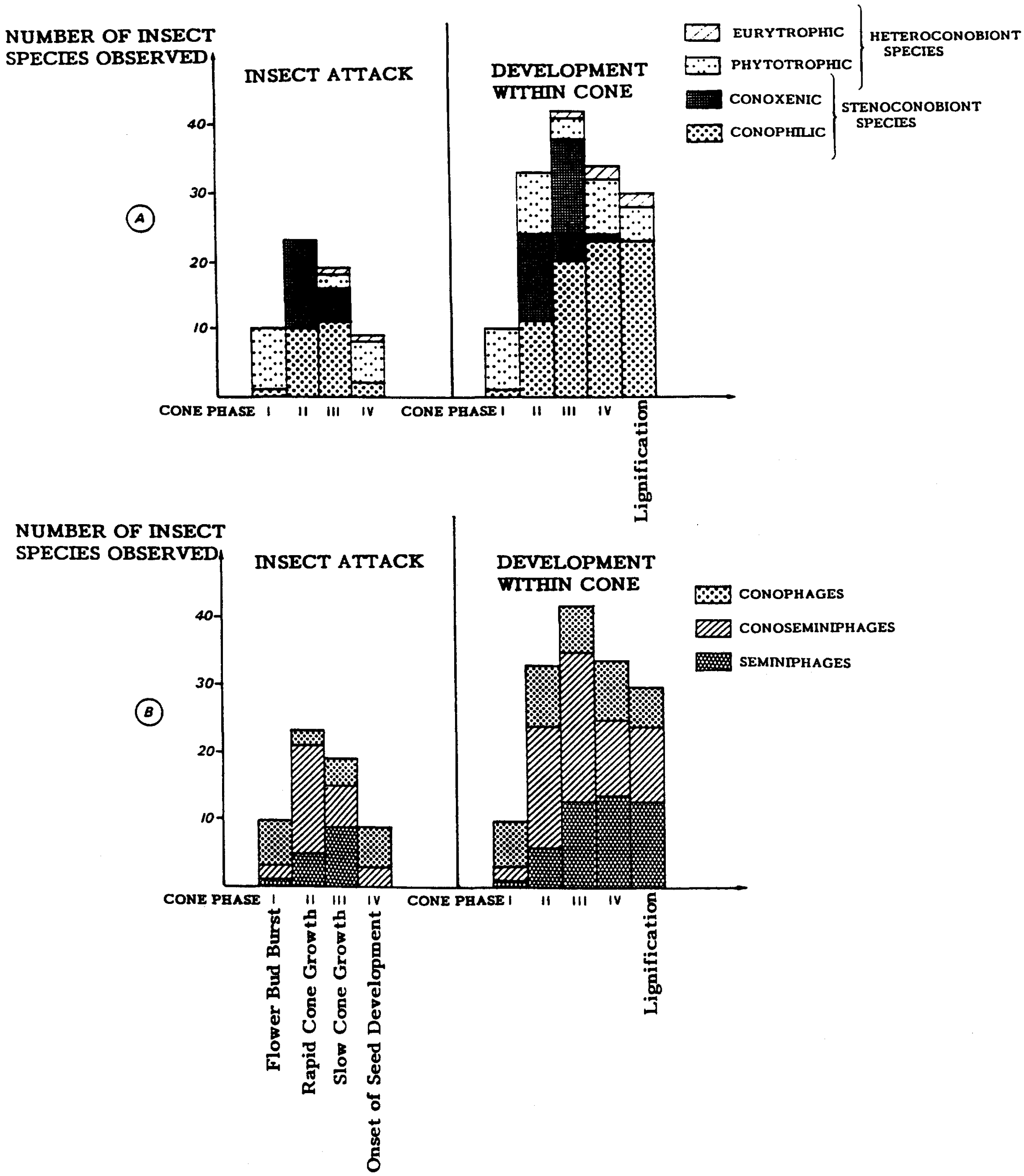

Figure 2. Patterns of cone colonization by the phytophagous and detritivore guilds during cone development as a function of a) host specificity and b) trophic level. Calculations based on the 61 species commonly observed in cones in western Europe.

Comparative Polyphagy of Etomophages and Phytophages

In *P. silvestris*, for instance, 14 of the 15 entomophages, whose cone insect host is identified, also prey on insects from other structures of scots pines (trunk, shoots, buds) or insects developing in the cones of other tree species (Roques 1988a). Similar relationships have been established in larch (Roques 1988b) and spruce (Stadnitskii 1971). More generally, at least 80 of the 122 entomophages (i.e. 66 percent) recorded in cones in western Europe show alternate hosts that do not develop in cones. Only a few chalcids of the genera *Mesopolobus*, *Anogmus*, *Amblymerus* (Pteromalidae), *Eupelmus* (Eupelmidae), and *Torymus* (Torymidae) seem specialized for the attack of seminiphagous insects. Polyphagy of entomophages effectively decreases from conophagous to seed insects, in relation to the increasing specialization of hosts (Roques 1988a).

The parasite speciation process in adaptation to phytophagous hosts thus appears to be more delayed than phytophage adaptation to conifers. Several factors may be involved. Differences in parasite complexes in regard to the plant substrate have previously been noted in heteroconobiont species. A substantial similarity is also observed in some phytophagous species of the same genus colonizing various tree structures, e.g. *Pissodes* spp. (Mills and Fisher 1986). It can be assumed that the parasite complex evolved from preadapted entomophages of these other insects. The slow progress of this process can be inferred from the variations in parasitism rate observed when a phytophagous cone insect colonizes a new introduced host. *P. validirostris* Gyll. immediately adapted to cones of *Pinus contorta* when this tree species was introduced into Europe. However, *Pissodes* parasites apparently faced barriers in locating their normal host in an introduced conifer. Parasitism levels remain low in *P. contorta* (2 percent versus 40 percent in *P. silvestris*) in Finland (Annila 1976) as well as in France (Delplanque et al. 1988). Parasite colonization thus apparently requires adaptation to both phytophagous host and cone host.

CONSEQUENCES FOR GUILD STRUCTURE AND EVOLUTION

Analogies in Cone Phytophage Succession in Native Tree Species

Similar specializations in cone resources are shown by congeneric insect species with respect to the synchrony of insect attack period with cone development; this results in a relative similarity of faunal structure within each native conifer species. Three main groups, within which fauna are homologous, are clearly distinguishable (Fig. 3).

Pinaceae with annual seed-cone development (i.e. *Picea abies*, *L. decidua*, *A. alba*) show quite homothetic fauna where distinct insect species from the same families (and often from the same genus) colonize the same cone development stages in four successive attack periods.

Although tree species fauna also appear homologous, insect families and genera colonizing Juniperaceae are quite different from the previous ones. In addition, sympatric *Juniperus* spp. (*J. communis* and *J. nana* in northern areas versus *J. oxycedrus* and *J. phoenicea* in mediterranean areas) have common fauna. The peculiar case of *J. thurifera* will be considered further on.

Pinaceae with superannual seed-cone development (i.e. *Pinus* spp.) have comparatively fewer cone phytophages and their fauna are more dissimilar. Three subgroups can be delimited: pine species of the *silvestris* group (*P. silvestris*, *P. nigra*, *P. uncinata*, *P. mugo*), mediterranean pines (*P. pinea*, *P. pinaster*, *P. halepensis*), and *P. cembra* (subgenus *strobus*). The single common component among these species is the occurrence of *Dioryctria* spp. (Pyralidae) and, in the two former groups, the weevil, *Pissodes validirostris*. The latter tree species is colonized only by three nonspecialized insects.

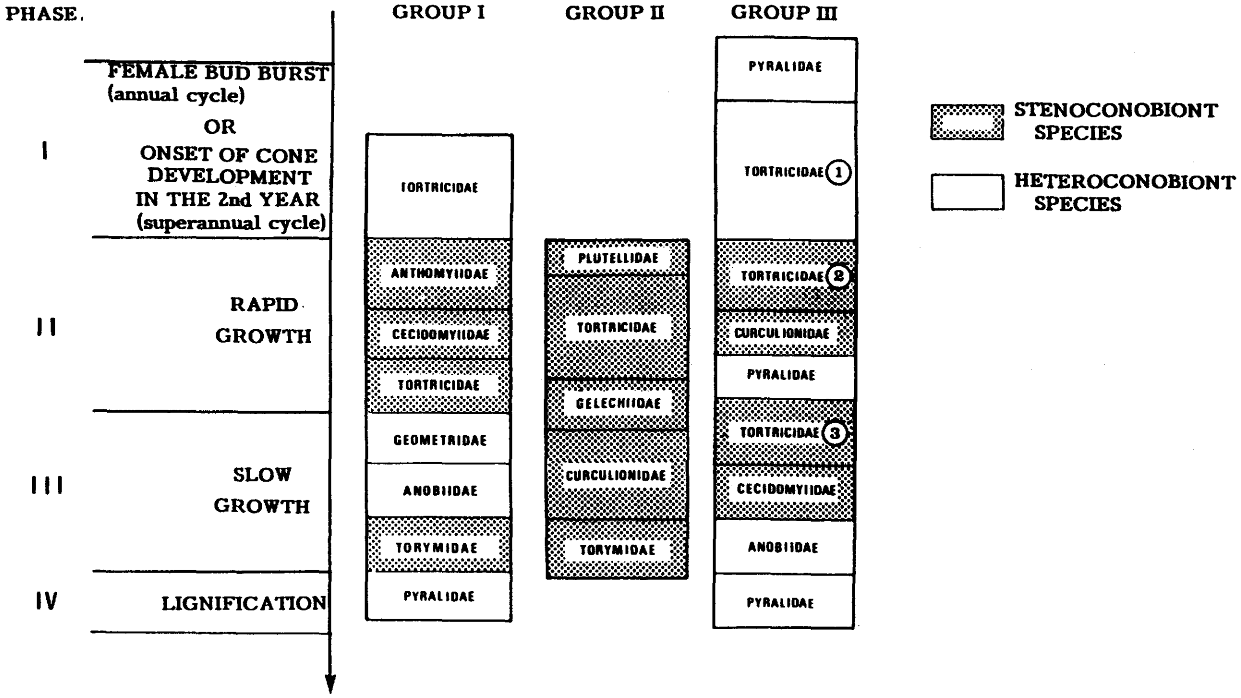

Figure 3. Classification of conifer species native in western Europe as a function of homologies seen in successive attacks of insect and mite families during cone development. Group I: Pinaceae with annual seed-cone development; Group II: Juniperaceae; Group III: Pinaceae with superannual seed-cone development.

The magnitude of the differences between groups with respect to the structural regularity within each group suggests a common origin for the fauna occupying cones of conifer species from groups with similar reproductive cycles. The insect fauna occurring at present may be the result of a further parallel diversification within each group.

Variation in Phytophage Guild with Tree Species and Stands

The total number of phytophagous species recorded in western Europe (species richness) varies with tree species, irrespective of cone size (Fig. 4a). However, an analysis of the respective contributions of stenoconobiont and heteroconobiont insects to species richness leads me to group tree species in a way similar to that above (Fig. 4b).

This confirms the existence of similarities or links in the colonization process within each of these groups. Pinaceae other than *Pinus* spp. show the largest diversity in cone insects, including a majority of stenoconobiont species. Juniperaceae have fewer species, but all are specialized in cones. Mediterranean pines and pines of the *silvestris* section are clearly separated, specific characteristics of the former being close to Juniperaceae. Fauna of the latter subgroup, though more diverse, is less closely adapted (50 percent of heteroconobiont species). Last of all, *Pinus cembra* appears similar to most introduced species: it is characterized by very low colonization, mainly by heteroconobiont species.

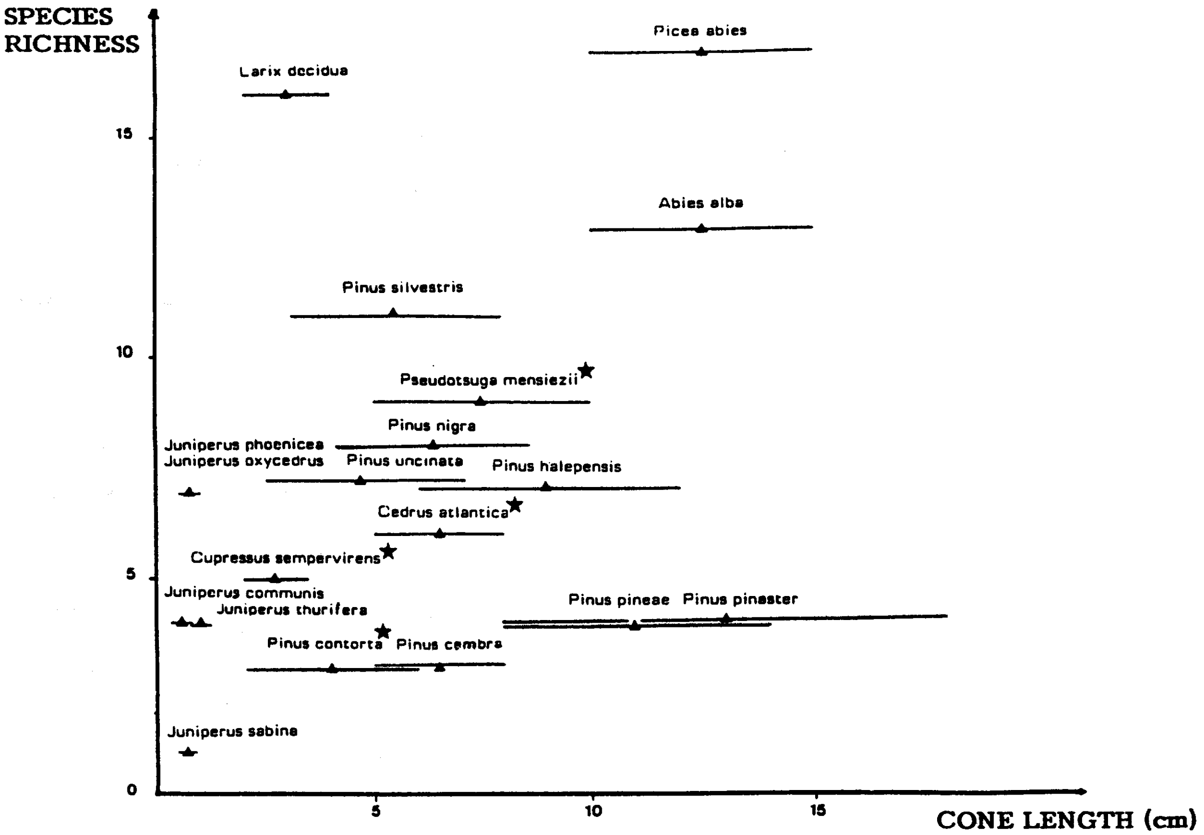

Figure 4. Species richness in phytophagous guilds related to cones in western Europe: a) relation with cone length and b) respective contribution of stenoconobiont vs. heteroconobiont species. *Introduced conifer species.

However, species richness provides a biased view of relationships between tree species and insect guilds by hiding possible variation with geographical range. When species packing (i.e. the number of species recorded in a given stand under standard sample collections) is the measure used, such variation appears in most conifers (Fig. 5).

Interspecific variation within a given area does not seem significantly related to the date of first reappearance of tree species after Quaternary glaciations, at least in French regions where sufficient paleobotanical data are available (Roques 1988a).

Conversely, intraspecific variation within tree ranges appears related to species reappearance in a species like *Picea abies*, which has a continuous distribution (Fig. 6). Species packing varies along a gradient following the postglaciation development of spruce from eastern Europe. The relative importance of closely adapted insects decreases from the location of the secondary evolution center of *P. abies*; Zwölfer (1987) noticed a similar pattern in thistle-head phytophagous guilds. The asymptotic curve indicates that insect evolutionary delay is limited in regard to host range expansion. When this progress is continuous, the faunal composition, including very specialized seed insects, can occur in less than 2,000 years. This development lasts longer in isolated stands of human creation, such as in the Pyrénées (Fig. 6). First colonization is, nevertheless, carried out by a certain number of insect species that are cone-specialized without being tree-specific. Faunal recruitment consequently results from

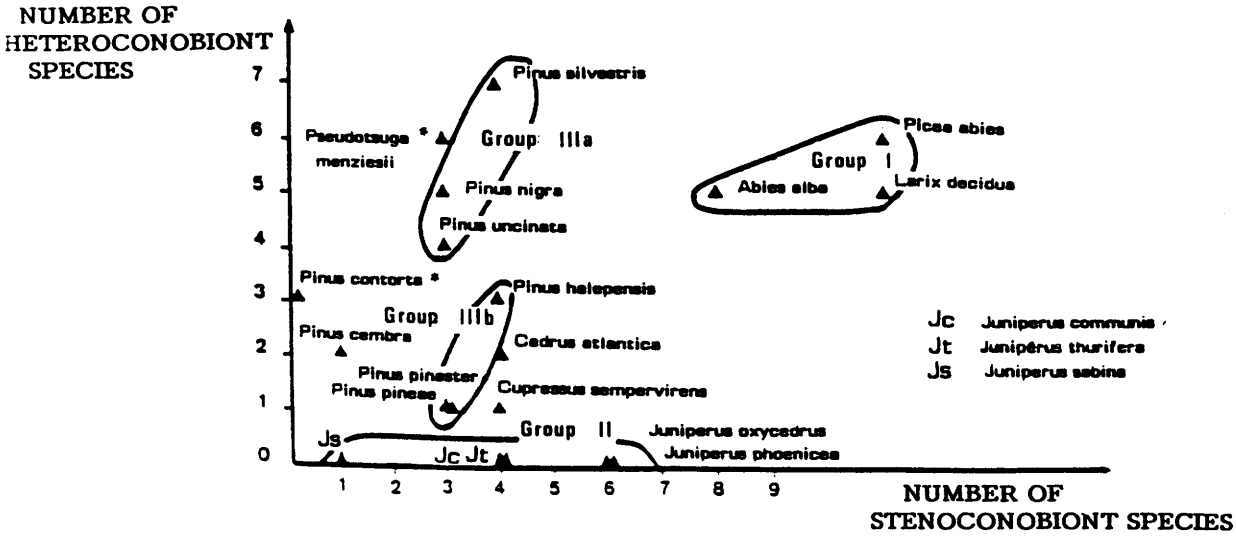

Figure 5. Variations in species packing of phytophagous guilds observed within cones through the natural range of four conifer species. Species packing is indicated by numbers within circles, host range by either hatching or points.

development of preadapted insects in cones of native conifer species. Early occurrence of insect species more adapted to tree species may be explained by insect flight capacity relative to stand isolation, ornamental trees being "relays" for the spread of insects, as shown for Douglas-fir (Roques 1986) and mediterranean cypress (Roques and Raimbault 1986).

Observations in species showing a relictual natural range following Quaternary glaciations confirm these results. In *J. thurifera* and *P. cembra*, cone fauna probably disappeared partially or completely during that period. Fig. 7 presents their respective recolonization patterns (from data in Roques 1983, Roques et al. 1984). In *J. thurifera*, differences among species result from local recruitment of insects occupying similar cone structures in either northern or mediterranean junipers, depending on stand location. In *P. cembra*, the recolonization progresses from insects observed on other sympatric conifers of genera *Pinus* and *Picea*, one of them, *Cecidomyia pini*, feeding on other structures than cone (i.e. foliage) in the usual host. Nevertheless, this last process has barely begun, no conoseminiphagous or seminiphagous (i.e. specialized) insects having been observed.

In introduced tree species, relative taxonomic isolation--number of congeneric species in the area of introduction (Zwölfer 1982)--also plays a decisive role in the rapidity of insect colonization. Exotic species without native European congeners (e.g. *Pseudotsuga*, *Tsuga*, *Sequoia*, *Cryptomeria*, *Chamaecyparis*, and others), or even without taxonomically close species in the same genus in some cases (pines of the *strobus* section), generally show a majority of conophagous insects (Roques 1983, 1988a). The conoseminiphagous minority is observed to include heteroconobiont or ubiquitous stenoconobiont species related to the insect genera commonly found in cones in the tree's native area. No seminiphagous insects are noted, except when *Megastigmus* chalcids have been introduced along with the host. Conversely, the phytophagous guild is much more complete in *Pinus contorta* or Asian spruce species: specialized insects passing to these new hosts from taxonomically close European pines of the *silvestris* section and from Norway spruce, respectively (Roques 1983 1988a).

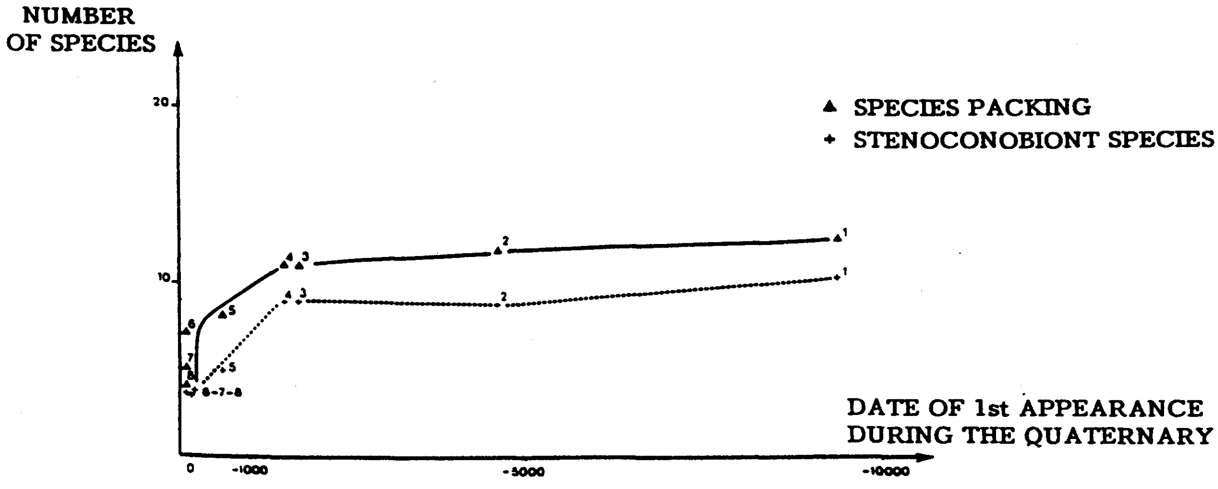

Figure 6. Relationships of species packing and host specificity in the phytophage guild of cones of *Picea abies* with the date of reappearance of this tree species during the Quaternary era in several regions of Europe: 1) Polish Carpathians (from Skrzypczynska 1982), 2) Upper Adige (from Del Favero and Masutti 1974), 3) Maurienne Valley, 4) Briançonnais, 5) Vosges; 6) southwestern France, 7) western Pyrénées, and 8) Fontainebleau Forest (from Roques 1983).

CONCLUDING REMARKS

The structure and composition of the phytophagous cone and seed insect guilds, the most characteristic among cone insects in western Europe, thus appear to result from an adaptive process which began largely before the Quaternary era. I have previously discussed the assumption of a common original fauna colonizing the new cone niche based on its presumed appearance during the lower Carboniferous period in conifer ancestors, the Cordaitales, from nonspecialized insects feeding on other tree structures (Roques 1988a). Though this idea remains highly questionable, the present results clearly suggest a common colonization during the Tertiary era, at least in Pinaceae and Juniperaceae. From these fauna three distinct patterns of phytophagous guilds would have evolved through adaptation to the different length of vegetative reproductive cycle, followed by parallel diversification in regard to increasing cone specialization. It must be noted, however, that the current situation may be substantially distorted because it results from an evolutionary process that involved many conifer species and genera that are now extinct in Europe--10,000 gymnosperm species existing in the Cretaceous period as opposed to the 600 existing today, according to Wieland (in Gaussen 1955).

From this point of view, the present heteroconobiont species may be considered precursors of future new stenoconobiont species, but the large dominance of this latter group in phytophagous guilds also indicates that the niche may be full in native tree species. The current range of host acceptance in stenoconobiont species shows, however, the probable direction of the actual evolution of phytophages related to cones: new species diversification through adaptation to a single host in response to relative geographic isolation in many conifers in western Europe.

Evident similarities in structure and functioning are noticeable when one compares cone insect guilds to those of other habitats characterized by limitation in space and time, especially the thistle-heads, as described by Zwölfer (1979, 1982, 1987, 1988). In the two cases, insect specialization

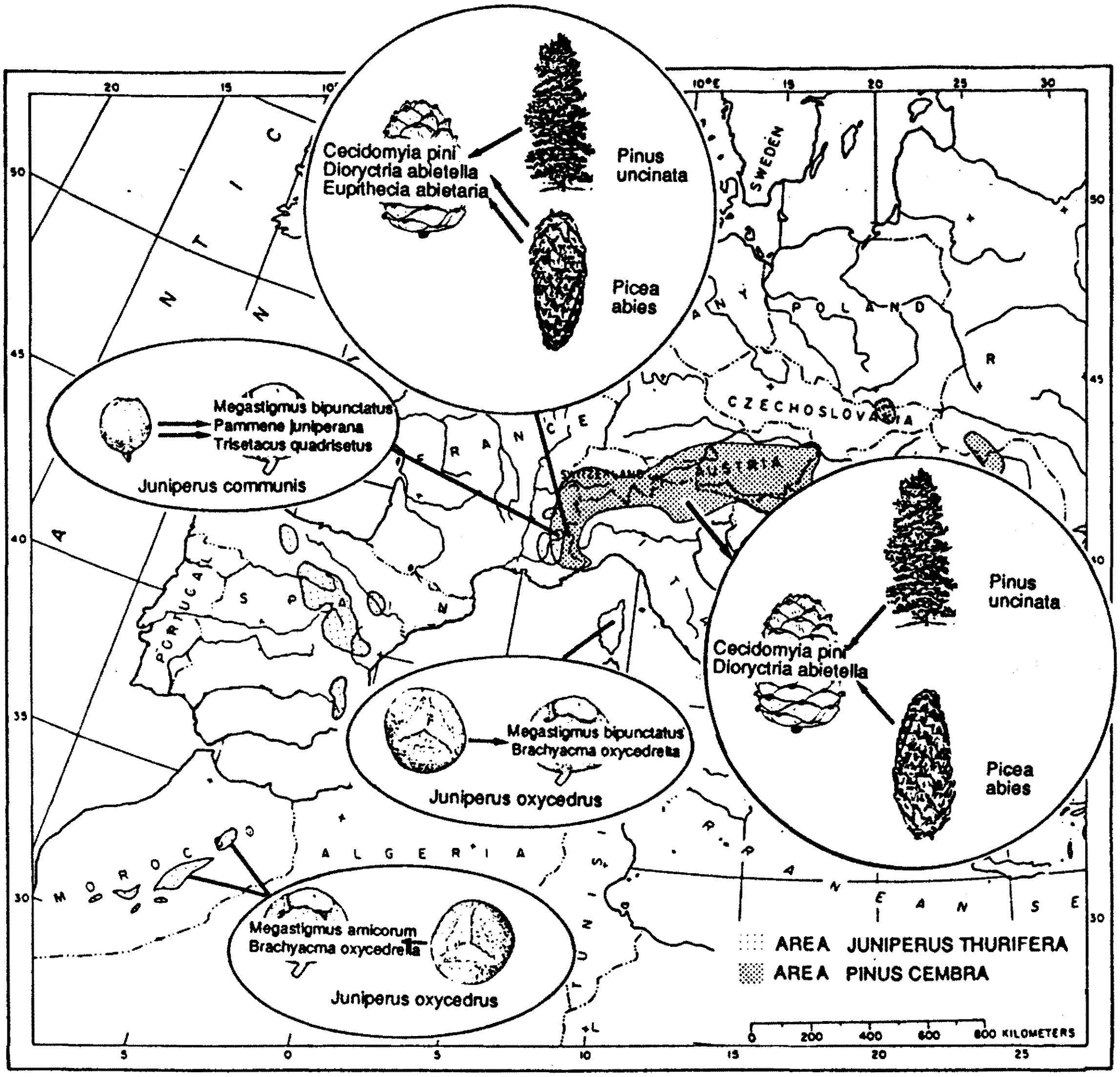

Figure 7. Recruitment of new cone phytophages in certain parts of the range of *Pinus cembra* and *Juniperus thurifera* from preadapted fauna of related sympatric conifer species.

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is directly associated with the occurrence of evasion strategies minimizing competition for limited food resources. Thus cone-insect systems are similarly observed to include partitioning of cone space, both by insect specialization in specific cone structures and by limitation in the number of competitors for the same structure, and sharing of time by adaptive differentiation of both arrival and exit of insect species (Rappaport and Volney 1986). However, this system faces an additional limit in food resources imposed by annual crop fluctuations, which do not occur to this extent in other systems. The latter evasion strategies are ineffectual when cones do not exist over large areas.

Other adaptive mechanisms, especially prolonged diapause, have been shown to allow the survival of insect species depending on cone occurrence (Bakke 1963). It is particularly interesting to note that prolonged diapause is not only limited to stenoconobiont species (at least 55 percent show it, to our present knowledge), but this phenomenon is also more effective in insect species attacking conifers with an annual seed-cone development (Roques 1989). This confirms the existence of previous differences in faunal evolution pattern. Prolonged diapause is also a general characteristic of seminiphagous insects, emphasizing the occurrence of seed-insects as "indicators" of the current status of phytophage guild specialization in each tree species.

Particular relationships between the cones and the remaining forest biocenosis are initiated by the consequences of the following factors: insect evolutionary delay in regard to conifer speciation and occurrence of heteroconobiont species and dominant polyphagy in entomophages. Cones, then, constitute a nutritional reservoir for insects damaging other tree structures as well as corresponding to a potential reservoir of alternate hosts for parasites and predators commonly found in the biocenosis. Cones also develop in competition with other vegetal structures for the consumption of photosynthesis products (Kozlowski 1971). These interrelations imply that no intrinsic regulation can exist at quantitative levels in cone-insect systems considered separately from the biocenosis, though the qualitative composition of cone entomofauna depends mainly on cone development. The definition of merocenosis, as used by Balogh (1958), has previously been proposed to qualify such a functioning in the case of *Pinus silvestris* (Roques 1977). Concordant data recorded in other species (Roques 1988a) suggest that the notion of merocenosis can be generalized to insect guilds related to cones in each native conifer.

SUMMARY

Cones can be regarded as dynamic plant microunits, with both limited lifespan and size and highly variable spatial and temporal distribution. Fifty-nine phytophages, two detritivores, and 122 entomophages have been regularly observed to develop within cones in western Europe. Entomofauna structure in native conifer species is characterized essentially by phytophagous guilds highly specialized in cone utilization, the other insect groups being mainly polyphagous. However, specialization shown by most phytophages appears delayed in regard to the evolution of conifers, each insect species being still capable of attacking cones of congeneric tree species. Possible origin, evolution, and direction of future diversification of fauna in further adaptation to hosts are discussed. Finally, entomofauna related to each conifer species is defined as a merocenosis, whose regulation is under the control of forest biocenosis.

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SEED PRODUCTION AND CONE-FEEDING INSECTS OF PINUS PUMILA ON THE KAMTCHATKA PENINSULA: ASPECTS OF COEXISTENCE

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INTRODUCTION

Insects attacking seeds and cones of trees are significant for their economic consequences as well as for the ecological role in vegetation dynamics. Currently much is known about seed and cone insects feeding on upright trees (see Roques, this volume), but almost nothing is known about cone inhabitants of prostrate pines *Pinus pumila* (Pall.) Rgl., *P. albicaulis* Engelm., *P. mugo* Tur. These three vicariant species from young mountain systems of the northern hemisphere have evolved in unfavorable environments which have favored peculiar patterns of seed production and insect-host relations. Cone insect populations are strictly determined by well known periodicity of seed production which often causes the evolution of diapause in cone-feeding insects. This phenomenon occurs in upright trees and is perfectly illustrated by *Lasiomma melania* on *Larix kamtchatica* on the Kamtchatka Peninsula. Unlike *Larix*, *Pinus pumila*, whose seeds develop over 2 years, has peak crops every 2 to 3 years but in fact produces some cones every year. This happens because seeds are produced on mosaically dispersed local patches of trees varying in micro-climate and other environmental factors. There are small, contiguous patches of good seed production in almost each region. Another important feature of the stochasticity of seed production is that seed dispersal is affected by the nutcracker, *Nucifraga caryocatactes* L., which leads to wide exchange of genetic material, and, consequently, to high ecological valency of the tree species. In sharp contrast to the typical strong antibiosis towards xylophagous insects: the trees apparently tolerate parasitic-commensal relationships with the seed and cone feeding species.

On the other hand, the plant is highly vulnerable to the attack of highly specialized insects. *Pinus pumila* cones, growing on the Kamtchatka Peninsula, are damaged by only two insect species-- *Cecidomyia pumila* Mamaev et Efremova sp.n. (Diptera: Cecidomyiidae) and *Eupithecia abietaria* Goeze (Lepidoptera: Geometridae).

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

Seed Yields of *Pinus pumila*

Pinus pumila on the Kamtchatka Peninsula produces seeds along the whole altitudinal profile of its range, from the sea coast almost up to the timber-line (about 1350 to 1400 m. above sea level). It can occur practically in all sites (Fig. 1), if not overshaded for more than 50 percent.

Cone size (length and diameter) declines with increasing altitude more definitely than their mass (correspondingly r.l = -0.73; r.d. = -0.79; r.m. = -0.41). Cumulative seed quantity increases very definitely with altitude (r = 0.76), mainly owing to increasing numbers of imperfect seeds. Seed output per cone (seed mass percent of cone mass) is practically invariable at each altitude (r.o = -0.11). Cone mass and seed quantity achieve their maximum between 300 and 700 m above sea level. Here one can observe the highest stability of crops and large numbers of mosaically dispersed patches of different seed producing levels. Mean characteristics of *Pinus pumila* seed production in central and eastern Kamtchatka (Table 1, data from 30 sites, confidence level 95 percent, coefficient of variation doesn't exceed 28 percent) are as follows: cone length = 42 mm (range: 25 to 62), cone diameter = 27 mm (range: 18 to 37), mean air-dry full cone mass = 7.3 g (range: 4.4 to 10.0), mass of a thousand of seeds--84.4 g (range: 52 to 116), percent of nuclei mass--48 to 54 percent. A typical cone includes about 45 seeds, about 39 (range: 26 to 52) seed scales, 11 (5 to 18) of which are undeveloped and don't contain seeds.

Conophagous Insects on *Pinus pumila* at Kamtchatka

Pinus pumila cones in general, for unknown reasons, are not damaged by a polyphagous cone feeders (at least not at Kamtchatka). This may be caused by specific physical and chemical characteristics of tree resin which is, in particular, a well-known defense for polyphagous xylobionts.

Biology of *Cecidomyia pumila* Mamaev et Efremova sp.n.

This insect was first recorded on *Pinus pumila* by L.S. Efremova in 1969, but serious difficulties in collecting adults and other reasons prevented it from being described as a new species until 1990. The description has been made by B.M. Mamaev (in press). The species has never been recorded on

Table 1. Average properties of *Pinus pumila* cones at different altitudes in the central and eastern Kamtchatka

Cone	Height above sea level--m											
trait	4	200	400	400	600	650	700	750	900	940	950	1,000
CM	5.7	5.6	6.7	9.0	9.4	10.0	9.3	9.0	6.6	4.4	5.8	5.7
SMP	44	45	43	49	45	43	51	55	50	42	46	32
SSS	35	26	42	31	38	43	43	52	42	38	39	40
SWS	12	6	12	5	10	13	18	14	12	10	12	11
SQT	26	27	40	42	50	46	45	68	54	47	47	50
SMT	73	100	84	116	94	100	109	78	67	52	75	65

Note: CM - cone mass, g; SMP - yield (seed mass percent from cone mass), %; SSS - seed scale quantity; SWS - quantity of the scales without seeds; SQT - seed quantity in a cone; SMT - mass of seed thousand, g; (data are taken from various parts of the central and eastern Kamtchatka)

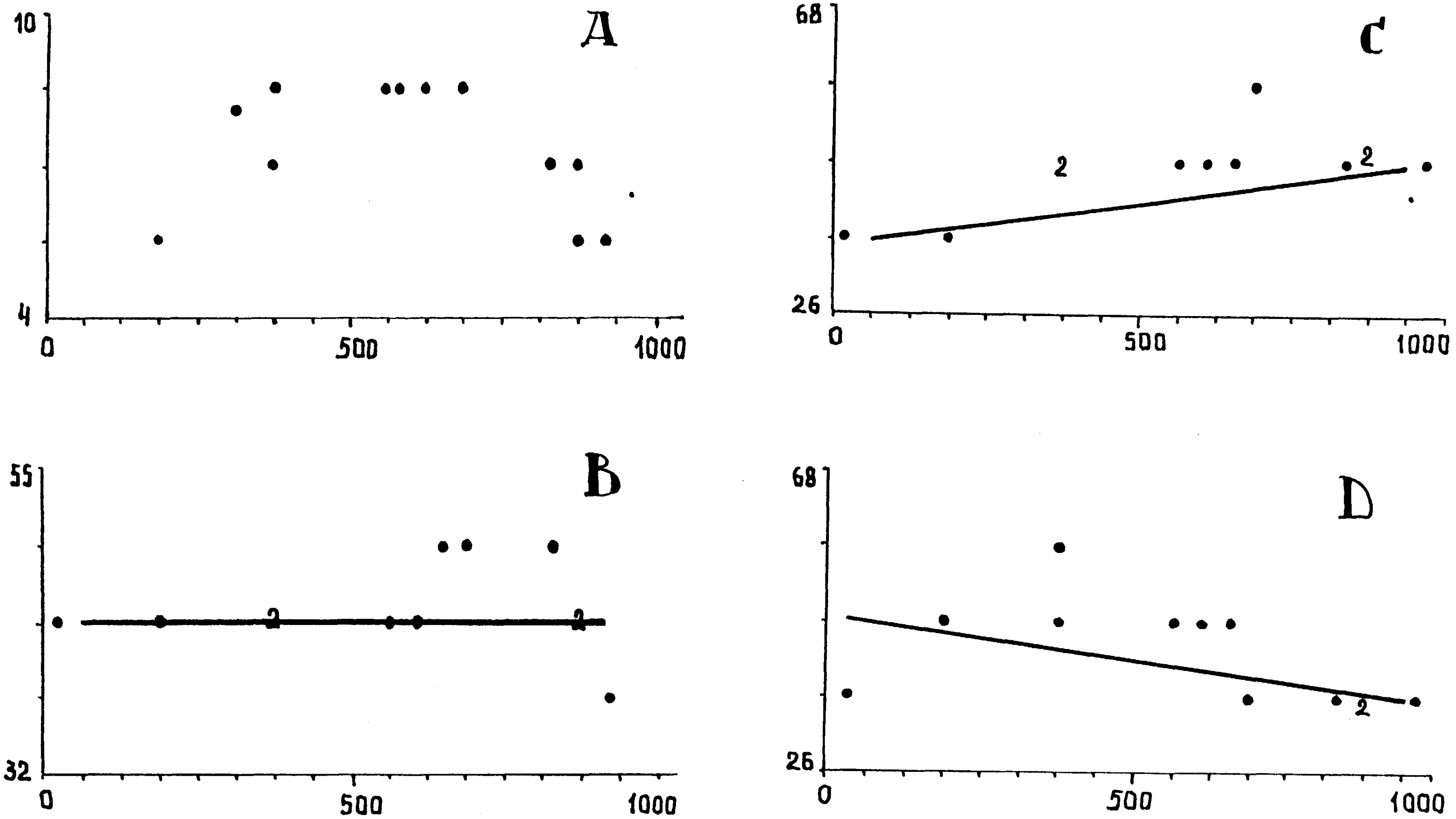

Figure 1. Seed production dynamics in changing ecotope disposing altitudes (combined data from various parts of Kamtchatka Peninsula). Horizontal axis - height above sea level, m. Vertical axis - (A) cone mass, g.; (B) seed yield, %; (C) seed quantity in a cone; (D) thousand nuclei mass, g.

other Kamtchatka conifers. Flying imagos appear in the early July and can be rarely seen in the early September even though you can find young and mature larvae in the same cone. Insects feed on the first-year cones where adults usually lay about 1 to 5 eggs. In the case of abundant crop, about 70 percent of cones are occupied by one larva, 20 percent by two, and 10 percent by three larvae. It has been noticed that in 50 percent of cases, insects occupy the middle part of the cone, in 30 percent of cases--the upper, and in 20 percent--the lowest part. After the hatching a larva bores into the seed scale causing the appearance of resin drops on scale surface or between the scales which serve as galls. The resin spots are quite visible, and the next year the cone damage is clearly indicated by the surface deformation and retarded development of some seed scales. Larvae leave the cones in the middle of August and pupate in the soil litter. The insect has a one generation per year. The adult has an orange body, with dark thorax and dark, almost black eyes. Male body length is about 2 to 3 mm, that of female--3 to 5 mm, the length of wings and legs is about 3 and 5 mm, respectively. Male antennae are about half as long as the body. In the laboratory, adults live for about 2 days, both with and without food. Insects don't like bright light, they usually die under the lamp heat and prefer semi-shadowed sites. Larvae of this genus have cherry-orange or red-orange color, and are 3 to 4.5 mm long and 1 to 1.5 mm thick. The pupal stage takes about 4 to 5 days in laboratory conditions at room temperature.

Biology of *Eupithecia abietaria* Goeze.

This species was first recorded on the Kamtchatka Peninsula by L.A. Ivliev and D.G. Kononov (1962). It has not been recorded on other conifers (*Larix kamtchatica*, *Picea ajanensis*). This fact and some other reasons cause us to suspect that the Kamtchatka population of *Eupithecia* is a new species because *Eupithecia abietaria* is well known throughout the palearctic as an oligophagous insect of conifers (Stadnitsky et al. 1978). Adults fly from the middle of June, larvae appear in the middle of July. Insects feed on the second-year cones. In the year of large crop, a cone is occupied by one larva, but in the year of low crop--by two or three larvae. Damaged cones are easily distinguished by visible holes and abundant excrements. Larvae feed on seed scales, cone stem, etc., but never on mature seeds. They pupate in soil litter in September, and the pupa overwinters. The insect has one generation per year.

Seed Damage by Insects

Cecidomyia pumila occupies about 70 percent (50 to 100) of *Pinus pumila* first-year cones in various sites and altitudes (Table 2).

Table 2. *Cecidomyia pumila* occupation of *Pinus pumila* cones at central and eastern parts of Kamtchatka peninsula

	Height above sea level--m						
Cone trait	5[1]	100[2]	400[2]	600[3]	950[3]	1000[2]	Mean
Percent damaged	60-100	50-70	50	65	100	60	70

Note: Sites: [1] - sea shore: [2] - subcontinental climatic conditions; [3] - continental climatic conditions (all within the Kamtchatka).

All estimates are certainly rough because of great variety of habitat conditions, weather, and crop yield. Nevertheless, two features were revealed. Firstly, cone damage by *Cecodomyia pumila* varies insignificantly between sites. Second, in the many moderately shaded sites both on the seashore and continental climatic conditions, in spite of altitude, the cone damage is substantial in nearly all cases. *Cecidomyia pumila* larvae destroy seed scales thus preventing normal seed development without their direct injury to seeds. Defective seed quantity often amounts 20 to 30 percent in a cone. But it has been demonstrated that the mean seed quantity in normal and deformed cones appeared to be the same. Neither are mean cone diameter and length seriously influenced by the insect injury. *Eupithecia abietaria*, in contrast as has been stressed above, occupies cones during the second summer, in the final 2 to 3 months of cone development. Very often it chooses cones previously damaged by *Cecidomyia pumila*. The occupation rate is significantly lower than of the previous species and varies from 5 to 10 percent in the year of large crops to 40 percent in the years of low crop. *Eupithecia abietaria* prefers plains and foothill sites, being rather rare in middle and high mountain sites, i.e. in the main *Pinus pumila* habitats. Its injury does not significantly influence the seed output and cone size.

CONCLUSION

Perhaps the main conclusion is that neither insect species damages seeds directly and hence cannot seriously influence the seed yields despite their high level of cone occupation. Assuming coevolution between producer and consumers, we believe that those cone feeders demonstrate both parasitic and commensal relations with the host plant as a whole: parasitic relations prevailing in the case of *Cecidomyia pumila* and commensal one prevailing in the case of *Eupithecia abietaria*. In general, the tree species show sharp antibiosis towards all insects, and only resin-gall species *Cecidomyia pumila* has managed to overcome this threshold very successfully. The main thing is that neither this nor the second cone feeding species causes significant injury to the seeds and therefore does not influence tree fitness. Taking into account the origin of *Pinus pumila* in unfavorable and even extreme abiotic conditions, it is not surprising to see the host specific gall-forming insect being the only one which is apparently fully adapted. Here we see support of the "harsh environment" hypothesis (Fernandes and Price 1988), which states that harsh environments favor the evolution of gall-forming plant-insect relationships probably due to hydrothermal stresses facing herbivores. The "harsh environment" hypothesis seems to favor other kinds of concealed feeders, e.g. xylophages *Urocerus gigas* L. (Hymenoptera, Siricidae) and *Pissodes gyllenhali* Gyll. (Coleoptera, Curculionidae) which feed in dying trunks in the mountain habitats. We admit that *Pinus pumila* is a young species and hence coadaptation with its herbivores and plant neighbors is far from complete.

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IPS TYPOGRAPHUS AND OPHIOSTOMA POLONICUM VERSUS NORWAY SPRUCE: JOINT ATTACK AND HOST DEFENSE

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INTRODUCTION

During the years 1971 to 1982, major epidemics of the spruce bark beetle, *Ips typographus* L., occurred in southeastern Norway and adjoining parts of Sweden. The outbreaks were triggered by large-scale wind-fellings and long-lasting drought (Worrell 1983). This "epidemic of the century," hitting our important timber tree, Norway spruce, *Picea abies* (L.), stimulated research in Norway and other countries of the region on the relationship between the beetle, its fungal symbionts, and the host tree.

It is assumed that the outcome of a bark beetle attack generally depends on 1) the local density of beetles that can respond to aggregation pheromones and 2) the resistance of host trees to attack (Berryman 1978, 1982). Field experiments lend support to this hypothesis (Waring and Pitman 1980, 1983, Raffa and Berryman 1983, Mulock and Christiansen 1986).

In this paper, I describe the relationship between the spruce bark beetle and its fungal symbionts and discuss how the symbiosis enables the beetle to successfully attack living trees. I also outline the method by which the trees defend themselves against the joint beetle/fungus attacks and discuss the important factors in that defense.

THE BEETLE-FUNGUS ASSOCIATION

In the 1970s we discussed with colleagues in the Section of Forest Pathology of the Norwegian Forest Research Institute the role that fungi might play in the colonization of trees attacked by *I. typographus*. Looking into the literature, we found that there existed a good deal of interesting information.

Discoloration of wood in connection with insect damage had already been noted by Hartig (1878), and early in this century bark beetles were directly associated with blue-staining fungi (Münch 1907, 1908). In 1928 the American forest entomologist F.C. Craighead demonstrated that blue-stain fungi play a primary role in the rapid death of pines infested with *Dendroctonus* beetles. He argued that mere girdling by the insects would not kill a tree within a few weeks, since artificially girdled trees often live on for months and years. Instead, he suggested, the fungi interrupt the tree's transpiration stream, thus causing its desiccation and death.

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Following Craighead's suggestion, a number of researchers conducted experiments with American pines. Several staining fungi of the family Ophiostomataceae were inoculated into the trees, and in some cases caused their wilting and death (Horntvedt et al. 1983). Over the years several Ophiostomataceae have been isolated from blue-stained sapwood of Norway spruce (Horntvedt et al. 1983, Solheim 1986). An early attempt to establish some of these fungi in spruce trees through artificial inoculation proved futile (Münch 1907, 1908).

In 1980 our pathologist, Richard Horntvedt, decided to try an inoculation experiment using two *Ophiostoma* (= *Ceratocystis*) species that had frequently been mentioned as associates of the spruce bark beetle, *Ophiostoma piceae* H. and P. Syd. and *O. penicillatum* Siem. Three cambium-deep girdles were cut around the stem of each tree. Cotton ropes soaked in agar and thoroughly infected with the fungi were placed in the girdle and covered by tape. The experiment failed as Münch's had done; no fungal infection of the xylem could be observed.

At this time a mycologist, Halvor Solheim, had just joined our group to study the succession of microorganisms in beetle-killed spruce trees. He soon made a very significant discovery: the species *Ophiostoma polonicum* Siem., to which no one had hitherto paid much attention, was always found at the advancing front of blue stain in the sapwood of beetle-attacked trees. In 1981 we inoculated both *O. polonicum* and *O. penicillatum* under the bark of young and old spruce trees, using the cork-borer technique (Wright 1935) and infected wood-chips inserted under the bark (Reid et al. 1967). The inocula were placed 2 cm apart along rings encircling the stem. We discovered that *O. polonicum*, but not *O. penicillatum*, was able to kill trees of normal health. It penetrated sapwood of normal water contents, and in doing so caused a blockage of the transpiration stream through the stem (Horntvedt et al. 1983).

Repeated experiments have verified that *O. polonicum* will kill healthy spruce trees provided an adequate load of inoculum is given (Christiansen and Horntvedt 1983, Christiansen 1985a, 1985b, Christiansen and Ericsson 1986, Horntvedt 1988, Solheim 1988). On the other hand, further studies confirmed that our isolates of *O. penicillatum* and *O. bicolor* are unable to kill trees of normal health (Solheim 1988). The differences in pathogenicity between the fungal species can probably be explained by their differential abilities to colonize wet sapwood. *O. polonicum* seems to tolerate low oxygen conditions better than the other species mentioned here and consequently also tolerates a wetter growth substrate (H. Solheim, pers. comm.).

The relationship between *I. typographus* and its fungal symbiont is an example of true mutualism, since both parts benefit from it. The pathogenic fungus helps the beetles kill trees, thus making them available for beetle reproduction. The benefit for the fungus is transportation to new hosts and effective inoculation under the bark. Since the mutualists have joined forces in such a deadly way, there must be a means by which the trees defend themselves against attack, thereby securing their own future existence as well as that of the parasites.

DEFENSE MECHANISMS OF THE TREES

Coniferous trees have coevolved with insects and parasitic microorganisms, including fungi, for over 200 million years. To survive they have developed effective systems of defense. Whereas a tree can lose large parts of its crown and root biomass and still survive, loss of the cambium around the stem constitutes a mortal threat. In several important conifers, the defense of stem tissues is based upon secretion of resinous materials.

"Resin" in its broadest sense has long been regarded as important for the defense against bark beetles in Norway spruce (Gmelin 1787) and other conifers. The pioneering work of Reid et al. (1967) on lodgepole pine, *Pinus contorta*, in Canada added a new dimension to the concept. It became clear that the resin observed in the case of beetle/fungus attack has two different origins: on the one hand, there is the preformed (or "constitutive") resin in ducts in the bark and sapwood, and on the other hand, there is the resin produced by an induced reaction to wounding and infection. The two types of resin are termed "primary" and "secondary," referring to the order of their appearance in the tree.

Preformed Resin: The "Standing Forces"

Preformed resin originates from an interconnected system of ducts in the phloem and xylem. This system comprises the "standing forces" of the tree, which become operative once a resin duct is severed, e.g. by a mining beetle. After the resin has been flowing for a short period of time, its surface will crystallize to form a hard, protective surface over the wound. A system of resin ducts exists in some coniferous genera (e.g. *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*), but is absent in others (e.g. *Cedrus*, *Sequoia*, and *Thuja*). *Abies* species have resin blisters in the bark, but these can in some cases be avoided by bark beetles (Ferrell 1983).

The preformed resin has been subjected to extensive studies in pines, partly in connection with its commercial use. Investigations related to bark beetle attack on ponderosa pine have emphasized the importance of oleoresin exudation pressure (OEP) because OEP would influence the quantity of resin that an attacking beetle would have to cope with (Vité 1961, Vité and Wood 1961). Because OEP is often correlated with the turgor pressure of the epithelial cells surrounding the resin ducts, droughty conditions could lower OEP and possibly facilitate beetle attack.

Studies of pines in the southern U.S.A. have, however, indicated that the exudation flow (OEF) largely depends on the storage capacity of the resin duct system and the viscosity of the resin, whereas OEP seems to be less important (Hodges and Lorio 1971). It seems logical to assume that OEF and total quantity exuded are the critical factors for an attacking beetle. The formation of resin ducts seems likely to be influenced by the growth-differentiation balance of the tree (Lorio 1986).

Induced Resinosis: The "Mobilization Defense"

Preformed resin may repel, flush out, and even drown attacking beetles. If these "standing forces" of the tree are inadequate for arresting the beetles, however, the phloem, cambium, and outer sapwood become infected with propagules of microorganisms. Most important of these are the spores of blue-stain fungi, which are specially adapted for transportation by insects by being covered with an adhesive, mucilaginous sheath. After these spores germinate, the fungus may soon spread into the surrounding tissues. It has been pointed out that since the preformed resin does not permeate the host tissues in advance of fungal growth, it is unlikely that it can prevent the spread (Berryman 1972).

When infected by microorganisms, whether fungi, bacteria, or vira, most plants have a hypersensitive reaction (Klement and Goodman 1967). A necrotic area forms around the point of infection so that the invading organism is deprived of food. Such necrotic reaction zones forming in the cambial region of conifers may also become impregnated with resinous and phenolic compounds, which creates an environment very unfavorable to beetles and fungi (Reid et al. 1967, Berryman 1969, Shrimpton 1973, Wong and Berryman 1977). The wound resin is produced by living parenchyma cells of the phloem and sapwood, including new-formed callus parenchyma. It is synthesized from carbohydrates stored in parenchyma cells of the phloem and xylem (Reid et al. 1967, Shrimpton 1978, Cheniclet et al. 1988, Lieutier and Berryman 1988), the reaction being elicited by substances produced by the fungus (Lieutier and Berryman 1988).

The induced response constitutes the "mobilization forces" of the defense, which come into action more slowly, but can stay active for an extended period of time. In lodgepole pine, where this reaction has been studied most intensively, it is considered the main defense against bark beetle attack, the preformed resin merely delaying the beetles and allowing more time for the secondary response (Raffa and Berryman 1982). The induced response is concentrated in a small area surrounding the infection, thereby keeping the loss of cambium to a minimum (Raffa and Berryman 1982). The process is highly energy-demanding (Wright et al. 1979) and probably related to the overall vigor of the host tree (Raffa and Berryman 1982).

STUDIES OF THE DEFENSE IN NORWAY SPRUCE

In 1983 we carried out a field experiment to establish the number of *I. typographus* attacks necessary to kill a Norway spruce tree (Christiansen 1985b). Pheromone dispensers were attached to a number of trees, and shortly after the main flight of the beetles, the number of attacks was recorded.

In several trees, the attack appeared to be successful, only dry frass being expelled from the entrance holes. However, about 1 month after attack, we observed that liquid resin was now seeping from formerly dry holes. Removing the outer cork bark, we found resin-impregnated reaction zones surrounding egg galleries of different lengths (Fig. 1). Obviously, the preformed resin had been inadequate to prevent the beetles from excavating their nuptial chambers and initial egg galleries. Later, however, secondary resinosis had put an end to the breeding. This was one of the reasons why we wanted to take a closer look at the relative importance of the two defense systems in Norway spruce.

The Preformed Defense

Schwerdtfeger (1955) studied the efficiency of the resin duct system under different conditions by making cambium-deep cuts of a standard size in the bark and measuring resin exudation within a maximal period of 3 days. One of his conclusions was that the quantity of resin exuded by a standard wound in the phloem-cambium region will rapidly taper off when the number of wounds increases. He also established a clear seasonality in resinosis, the quantity of exudate showing a strong positive correlation to ambient temperature. The amount of preformed resin exuding from a mechanical wound varies greatly from tree to tree, and even between places on a given tree (Christiansen and Horntvedt 1983). Within a stand, there is a trend toward a higher yield of duct resin per wound among the larger trees (Fig. 2), also suggested by Schwerdtfeger (1955). Likewise, older trees seem to exude at least as much resin as younger (Schwerdtfeger 1955, Christiansen and Horntvedt 1983).

There are several sources of seasonal and annual variation in amounts of duct resin. Newly formed resin ducts of the sapwood may not become connected with phloem ducts until most of the year-ring has been laid down, as observed in pines (P.L. Lorio, Jr., pers. comm. 1986). Also, different year-rings of Norway spruce may hold highly variable numbers of resin ducts, which can be formed in response to external stresses, i.e. frost, drought, or attack by insects and fungi. During extremely dry years of the mid-1970s, unusually high numbers of ducts were formed in connection with drought rings in the spruce trees we examined. Due to this variability, pioneer beetles may encounter "standing forces" of variable strength depending on where and when they attack.

An experiment we conducted in Norway in 1985 sheds some light on the relative importance of the two defense systems. It was just after the recent large epidemic and very few trees were spontaneously killed by *I. typographus* that year. In the experiment, pheromone dispensers were attached to 77 spruce trees of variable vigor. All 77 came under attack, but only 20 of them died. Shortly after the main flight of the spruce bark beetle, we counted the number of attacks on each tree. In doing so, we distinguished between entrance holes where liquid resin or moist frass occurred and holes where only dry frass was expelled. Very few attacks occurred after this major inspection.

Figure 1. The spruce bark beetle has been able to enter the phloem and initiate its galleries without being stopped by the preformed resin of the tree. Later, however, the induced defense has produced abundant resin that permeates the phloem locally around the galleries. The eggs have been killed, and the fungus is contained inside the resin-soaked areas.

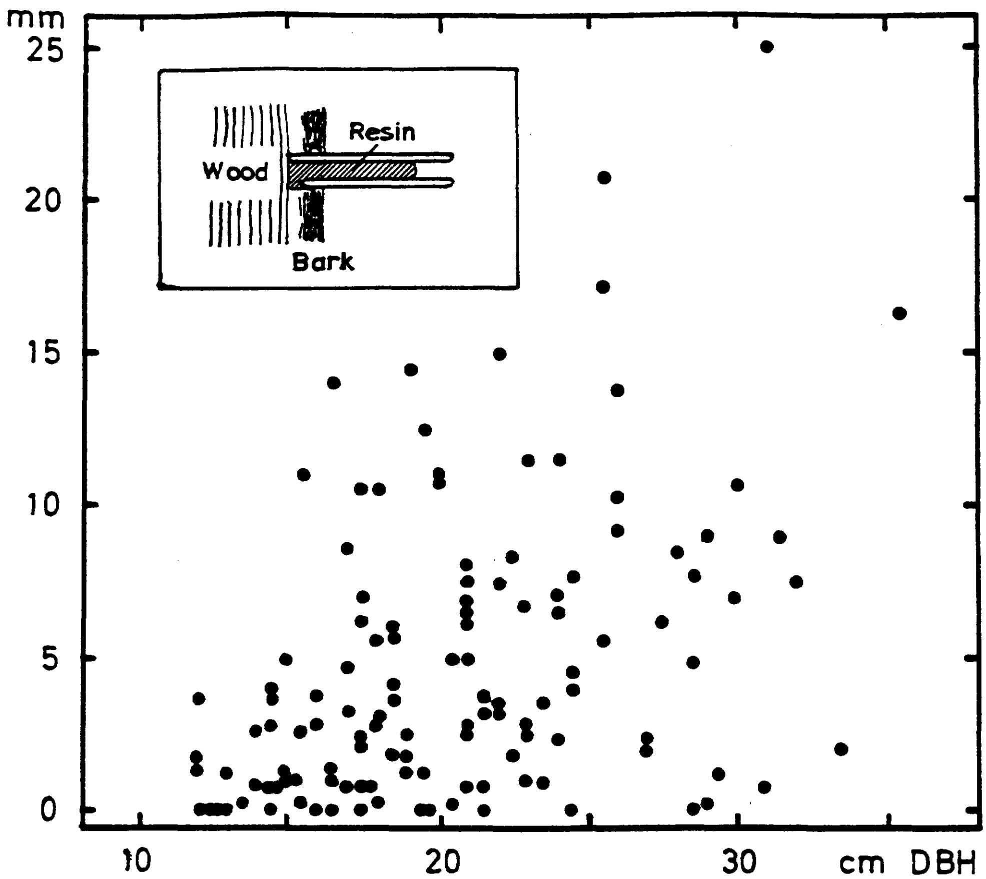

Figure 2. The inserted drawing shows measurement of the yield of constitutive resin: plastic tubes are cut at an angle and fitted into holes cut to the cambium with a cork borer. After 24 hr the length of the resin column is measured. The main figure gives mean values of 10 measurements per tree for 128 spruce trees growing in a small stand.

There was great variation in total number of attacks per tree (Fig. 3). Surviving trees showed a maximum of about 500 entrance holes, whereas killed trees had no less than 200 to nearly 1,200. In the killed trees only a small percentage of the boring holes had resin exudation; the proportion was almost zero in some trees. Surviving trees had fewer attacks in general and a higher, but extremely variable proportion of holes with primary resin. On one of these trees, over 300 boring holes were recorded, all of which were oozing resin, whereas in others only a small share of the entrance holes exuded resin.

Although the results mentioned here are only fragmentary, I think it is safe to conclude that the "standing forces" of the resin duct system are inadequate as a sole defense against a mass attack of *I. typographus*. It should be pointed out that in other trees, such as certain pines, this first line of defense may be much more important (Christiansen et al. 1987).

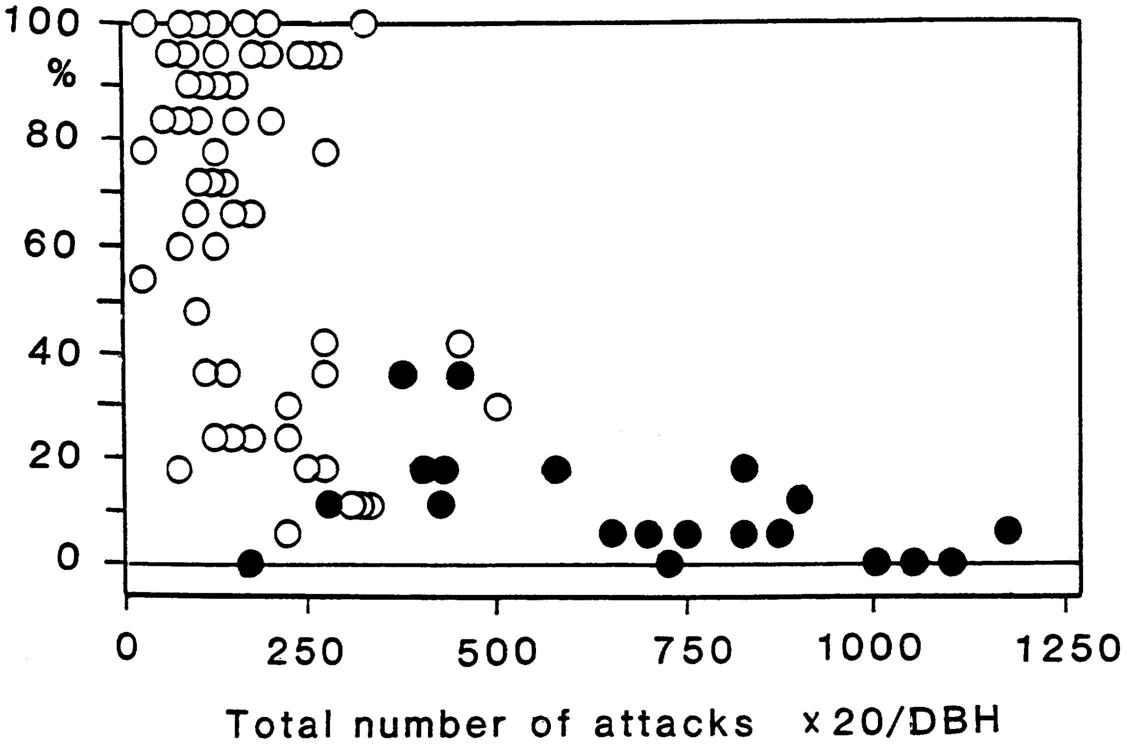

Figure 3. Performance of the constitutive defense in Norway spruce: percent of beetle entrance holes with liquid resin or resinous frass in relation to total number of attacks per tree. Black circles = trees killed by the attack; white circles = trees surviving.

The Induced Defense

The induced defense reaction in Norway spruce has been studied using artificial inoculations with *O. polonicum*. It turns out that other *Ophiostoma* species will produce reactions of a similar type (Horntvedt et al. 1983, Solheim 1988), but we have concentrated on *O. polonicum*, which is able to penetrate the sapwood and kill experimental trees.

Artificial inoculation offers an interesting opportunity for experimental study of the relative resistance of individual trees. By using this technique, we can administer exact numbers of infections to a given tree. Theoretically, this can also be achieved by subjecting the tree to a controlled number of beetle attacks. In practice, however, it is very difficult and laborious because the experimental beetles inevitably attract "wild" conspecifics to the tree. Thus the part of the bole which is suitable for *I. typographus* would have to be screened in order to prevent unwanted attacks.

It is possible that the reaction of a tree to one single inoculation could be used as a predictor of its resistance to mass inoculation, as demonstrated for lodgepole pine (Raffa and Berryman 1983). This might possibly be used to assess resistance to beetle attack as well. In our experiments, however, we have studied only the tree's reaction to mass inoculation. Our technique has been to mark out a belt on the stem, 60 or 80 cm high, around breast height. Within this belt, the trees are inoculated at different densities, ranging from one to eight inoculations per square decimeter. A template is used to ensure even spacing of the points of inoculation. Alternatively, the inocula are placed along rings encircling the stem, virtually covering the same area as the inoculation belts. The cork borer technique has been used as a standard. Placing the inoculations so densely within a limited area, instead of spreading them out over a larger section of the bole, is considered a "worst case" for the defense. However, a pilot study in which an equal number of inoculations was given over 60, 120, or 240 cm of the stem did not reveal any dramatic differences in fungal success (unpubl. data).

The experiments have demonstrated a clear threshold of successful infection (Christiansen 1985a, 1985b). When the number of infections in a tree increases, there is a point where the resin concentration of the phloem reaction zone drops (Fig. 4). At this critical point, the fungus is able to break out of the enclosure and spread out into the phloem. This is parallelled by increasing success of the fungus in penetrating the sapwood.

There also appears to be a difference in defensive capacity between spruces of different vigor. Suppressed, slow-growing trees appear to tolerate fewer infections than dominant and vital ones (Christiansen 1985a). This accords with a study of host resistance to *I. typographus* attacks by Mulock and Christiansen (1986).

Role of Carbohydrates in the Induced Defense

From the threshold response described above, it may be inferred that defensive capability is influenced by the availability of some limited resource. Since it is known that carbohydrates (C) are both raw material and energy source for the wound response, availability of C in the infected area would seem one likely candidate for a critical factor. I have tested this assumption experimentally (Christiansen and Ericsson 1986). Our first hypothesis was that if substantial amounts of sugar are mobilized for the induced defense, then C (starch) reserves of the surroundings should be depleted. Second, we assumed that trees with low reserves should be more vulnerable to fungal attack than trees with high starch concentrations.

We inoculated spruce trees in belts as described above, and measured the starch concentrations at different distances above the belt. Our first hypothesis was supported in that starch concentrations were significantly reduced as far as 1.5 m above the inoculated belt. But the experiment failed to support our second hypothesis. Trees ranging from 12 to 20.7 percent in starch concentration showed no differences in defensive capacity. Similar results were found in a later investigation (Horntvedt 1988).

In a second experiment (Christiansen and Ericsson 1986), we girdled some of the trees above the inoculation belt to manipulate their starch reserves. A cambium-deep girdle at 2 m above ground shut off the assimilate flux from the crown. One group of trees was girdled in April, before the spring build-up of C reserves. In these trees the starch concentration reached only half the normal (Fig. 5). Another group was girdled at the time of inoculation (i.e. mid-May) and consequently had normal starch reserves. In this experiment we had carefully chosen our inoculation dose so that inoculated, ungirdled trees withstood the infection quite well; only a small fraction of their sapwood became blue stained (Fig. 5). Low-starch (i.e. early-girdled) trees were much more stained, but so were trees girdled at the time of inoculation. We therefore concluded that it may not be the size of the C reserves (starch) per se, but rather the efficacy of C (sugar) translocation that is critical for the mobilization defense. Our conclusions are corroborated by a study of lodgepole pine in the U.S.A. (Miller and Berryman 1986) performed simultaneously, but independently.

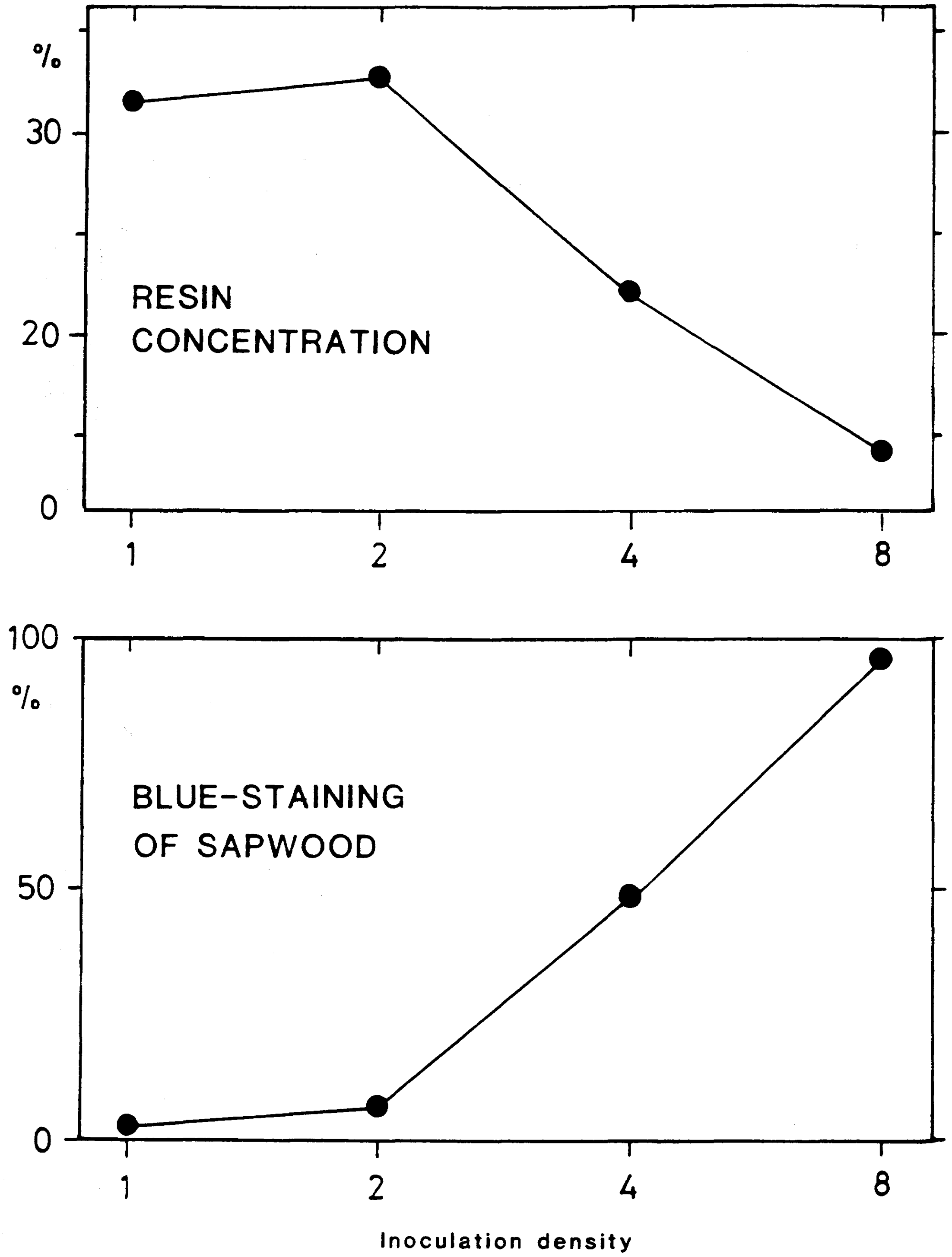

Figure 4. Performance of the induced defense in Norway spruce: resin concentration in phloem reaction zones and fungal success in relation to inoculation density. Data from Christiansen 1985a.

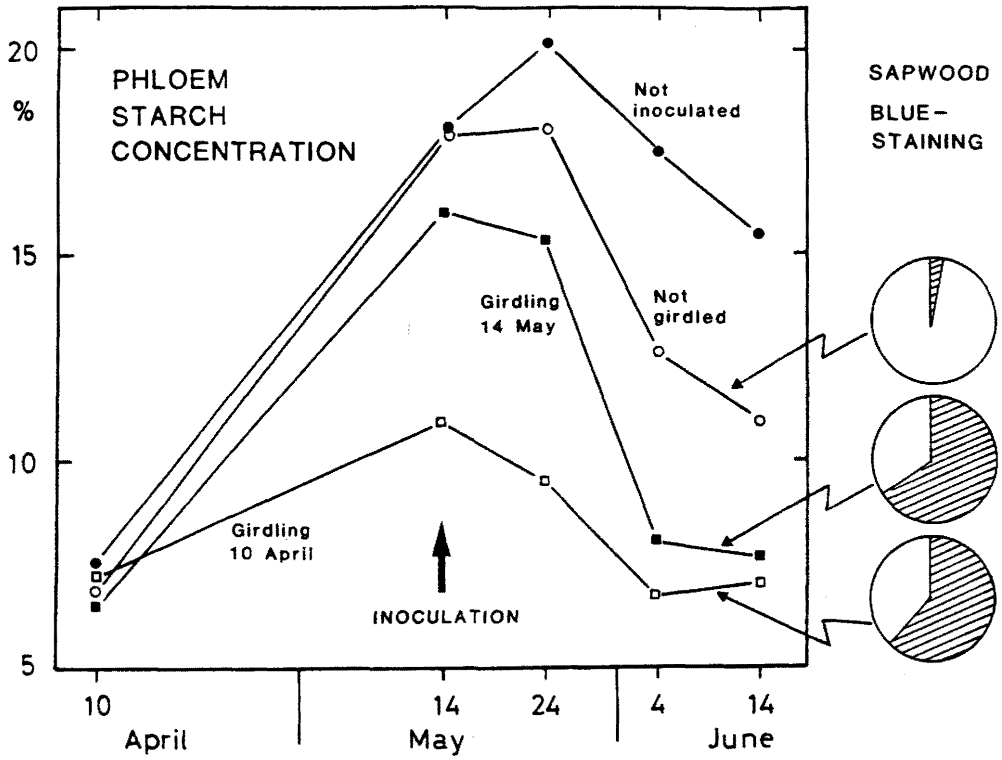

Figure 5. Starch dynamics of Norway spruce in relation to fungal inoculation and girdling of the stem and fungal success in invading the sapwood. Data from Christiansen and Ericsson 1986. See text for further explanations.

During the growth season, many sinks compete for the available C in a tree. Priorities for C allocation seem to exist. In a defoliation experiment with Scots pine, Ericsson et al. (1980) found the following order of allocation (moving from high to low priority): 1) bud formation, 2) needle biomass, 3) shoot length, and 4) year-ring width. Allocation for defense may not be the highest priority (Waring and Pitman 1985), but a high drain on C by numerous induced defense reactions considerably affects year-ring growth in Norway spruce (Christiansen 1985a).

Since carbohydrate availability varies during the growing season (e.g. Ericsson et al. 1980), this is likely to affect the defensive capacity of the trees. An experiment with monthly inoculations of Norway spruce showed considerable variation in defensive efficacy over the season (Horntvedt 1988). The success of *O. polonicum* in infecting the sapwood was very low in May, moderate in June, and high in July, then declined through August and September. The lack of fungal success in spring could not be explained by lower temperatures only; the trees were evidently more resistant in the early season.

Because *I. typographus* has its main flight in spring (mid-May in South Norway), the beetles appear to encounter host trees in a highly resistant state. Nevertheless, they are able to overcome the resistance of the host given an adequate number of attackers. On the other hand, during an epidemic, when the parent beetles produce one or more sister broods, increasing susceptibility late in the season may reduce the number of beetles necessary to kill a tree. This may have a bearing on population dynamics, as pointed out by Horntvedt (1988).

It has been suggested that tree resistance in general may be closely related to the amount of photosynthate that is immediately available for defense (Christiansen et al. 1987). A wide variety of factors is known to predispose trees to bark beetle attack, among them drought, flooding, wind-swaying, defoliation, lightning strike, fire, rot fungi, competition, and old age. These seemingly unrelated factors may have a common denominator: they all reduce the C availability. It would thus be interesting to test the relationship between limitations on the transfer of C to the sites of attack and host tree resistance.

At present, we are testing this hypothesis in experiments with Norway spruce. We are trying to reduce C stores--and hence, presumably, availability--by two techniques: 1) by exposing the trees to prolonged drought and 2) by reducing the crown biomass considerably through branch pruning. Later the trees will be inoculated with *O. polonicum* to test their resistance.

EPILOGUE

Together, the two defense systems will define the "threshold of successful attack" for a given tree. Both defenses become exhausted when the number of attacks reaches the critical level. Given the high population densities of an epidemic, any tree can be killed in a mass attack. When the trees are rapidly overwhelmed by a large number of beetles, no constitutive defense will suffice and no evidence of the induced defense can be observed, as there is no time for the reaction to take place.

Even though the described defense mechanisms are no safeguard during an epidemic, they do protect the spruce trees in a normal situation. They prevent the tree from being conquered by a handful of attackers, and they contribute to reduction of the beetle population. Since at least the induced defense reaction seems related to the vigor of the host tree, the forest manager can probably reduce the possibility of beetle outbreaks by maintaining a vigorous forest.

SUMMARY

This paper describes the relationship between the bark beetle *Ips typographus* and its fungal symbionts, in particular *Ophiostoma polonicum*, attacking Norway spruce, *Picea abies*. Against a joint beetle-fungus attack, coniferous trees defend themselves by means of 1) their preformed (constitutive) duct resin and 2) an induced reaction producing highly resinous zones around the points of infection in bark and outer sapwood. The performance of the two defense systems is discussed, with particular reference to Norway spruce. The importance of carbohydrate availability for the induced defense reaction is discussed.

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RELATIONS BETWEEN WOOD-INHABITING INSECTS AND FUNGI

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INTRODUCTION

It is widely known that xylophagous insects do not usually attack healthy, resistant trees. In order to overcome these defenses, inner-bark feeding insects have developed symbiotic interrelationships with various organisms, fungi in particular. In this paper, using our own data together with that available in the literature, we analyze the forms of relationships between insects and fungi and the role of these interactions at various stages of wood decomposition. In doing so, we distinguish between the following fungal-insect relationships:

1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi
2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi (auxiliary ambrosia fungi according to Batra 1985)
3) xylophagous insects, symbiotically associated with fungi causing vascular mycoses
4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi.

The representatives of the first three groups develop in living wood or fresh timber. Representatives of the last group develop in dead wood, though in the earliest stages they can colonize living, but irreversibly weakened wood.

REVIEW

Ambrosia Mycetophagous Insects

This group includes insects which have necessary ectosymbiotic connections with a specific group of fungi imperfecti, the ambrosia fungi, and several characteristic features. The ambrosia fungi are highly sensitive to drought and develop only in moist wood. They are host specific, associated with certain species of insects, and are located only in colonized galleries or on the body of xylobionts. The fungi form the pellicle on the gallery walls--ambrosia--consisting of separate cells and fragments of filaments (Batra 1985 and others). Ambrosial cells can form vegetative mycelium under certain conditions.

Typical representatives of the ambrosia fungi are *Ascoidea*, *Ambrosiella*, *Raffaelea*, and *Phialophoropsis* (Batra 1967, 1985). The taxonomy of this group of fungi is poorly studied, representatives of other ecological groups, considered by us below, often being confused with them.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

Typical representatives of the ambrosia insects group are Platypodidae, Lymexylonidae, and some Scolytidae--*Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. (Francke-Grosmann 1967, Nakashima 1971, 1972, 1975, Mamaev 1977, Batra 1985, Nakashima et al. 1988). Some peculiar beetle representatives, Curculionidae and flies--Axymyiidae and Syrphidae--should also be classed among this group. The complex of ambrosia mycetophages is formed on both living wood and fresh timber. It has been said of the pin hole borer, *Austroplatypus incompertus* (Schedl.), that one and the same system of galleries can be used over 36 years (Harris et al. 1976). Ambrosia fungi have been obtained from the galleries of borers, pin hole borers, and bark beetles (Lymexylonidae, Platypodidae, Scolytidae) (Francke-Grosmann 1967, Baker and Norris 1968, and Nakashima 1971).

It has been ascertained that ambrosia fungi constitute the main food source for ambrosia insects (Kaneko and Takagi 1966, Norris and Baker 1967), and this determines insect behavior. The bark beetle *Xylosandrus compactus* Eichh. (Scolytidae) lays eggs only during the four to 14 days after colonization of the trunks of the coffee tree, i.e. after spreading of the ambrosia fungus mycelium throughout the surface of the gallery (Hara and Beardsley 1979). Successful larval development and imago reproduction are determined mainly by insect feeding on the ambrosia fungi (French and Roeper 1972, 1975, Barras 1973). Mamaev (1966) considered ambrosia insects xylomycetophagous. However, recent data show convincingly that they should be considered ambrosia mycetophages. This identification is indirectly confirmed by the peculiar intestinal structure of Axymyiidae larvae, without additional chambers or folds, which is pronounced in xylophages (Mamaev and Krivosheina 1966).

Apparently ambrosia insects are associated with fungi on a large number (up to 150 species) of host trees (Francke-Grosmann 1967). Colonization of new tree species occurs fairly quickly. For example, the ambrosia beetle, *Xylosandrus compactus* Eichh., was at first primarily on coffee trees on the Hawaiian Islands, but then spread throughout more than 100 tree species there (Hara and Beardsley 1979).

Symbiotic connections with fungi lead to the formation in ambrosia insects of various structures for the transfer of fungi. These structures are known as mycangia or mycetangia and are situated on the body and in the internal organs. The organs have been studied well enough in bark beetle pinhole borers and have also been found in the attelabid beetles (Schneider 1976, Nakashima 1975, Sawada and Morimoto 1986). The synchronization of insect and fungi development is also of interest. It was discovered in *Corthylus punctatissimus* Zimm. (Scolytidae) that ambrosia fungus, *Amabrosiella xylebori*, reproduces intensively by gemmation in mycangia only prior to wood colonization by beetles (Roeper 1988).

In the European part of the U.S.S.R., the complex of ambrosia insects is represented by the borers *Elateroides dermestoides* L. on deciduous trees and *E. flabellicornis* Sch. (Lymexylonidae) on conifers. Usually they are accompanied by the larvae of *Libnotes* Westw. (Limoniidae). The bark beetles *Xyleborus* Eichh., *Trypodendron* Steph., and *Anisandrus* Ferr. are often found together with the borers (Mamaev 1974b, 1977). *Platypus cylindriformis* Rtt., which is close to the more widely distributed *P. cylindrus* Hbst. (Platypodidae), develops in oak stumps in the Transcaucasus region. The ambrosia insect complex in the forests of the Far East (U.S.S.R.) is the most diverse, however. The most common ambrosia insects are *Platypus severini* Bl. (Platypodidae) and *Sipalinus gigas* Fabr. (Curculionidae), which occupy various tree species: cedar, fir, elm, and lime (Mamaev 1974a).

The ambrosia dipterans complex forms in moist dying or dead wood. It is represented by species of Axymyiidae, Syrphidae (*Temnostoma* St. Farg et Serv.) (Fig. 1a), Stratiomyidae (*Xylopachygaster* Kriv.), and Limoniidae (*Libnotes* Westw.).

Axymyiidae larvae colonize newly felled trunks, where they may exist for several years in the moist conditions. The larvae construct galleries, constantly removing boring dust and fungi. Both larvae and pupae are mobile, the latter having a sclerotized flat cover on the head for clearing galleries (Fig. 1).

A similar life pattern is typical to the species of the genus *Temnostoma* St. Farg. et Serv. (Syrphidae), which occupy the fresh wood of fallen trees. The peculiar keg-like shape of their larvae's bodies helps them to clear galleries (Fig. 1c).

Unfortunately, the composition of the fungi communities in the galleries of *Ambrosia dipterans* and the mechanism of their transfer have not yet been studied. It is very likely that, in addition to ambrosia fungi, yeast is of great importance there. The species of the genera *Libnotes* Westw. (Limoniidae) and *Xylopachygaster* Kriv. (Stratiomyidae) associate only with ambrosia insects and do not take part in fungi transport.

Ambrosia Xylomycetophagous (Phloeomycetophagous) Insects

The ambrosia xylomycetophagous insects are consistently associated with the cup and imperfecti fungi (micromycetes). The latter consume chiefly the contents of the cells and do not destroy cellular walls, though these traits do not strictly define them (Gorshin and Krapivina 1969).

Unlike the ambrosia fungi, the wood-coloring fungi are not closely associated with insects, appearing in the galleries after completion of insect development. Easily cultivated, they can be mistaken for ambrosia fungi because they are often associated with them.

The most typical representatives of this group are the *Ceratocystis*, causing the blue-stain disease of the wood. The spores of the blue-stain fungi are spread by the air flow and by xylobiont insects, particularly when insects transfer sticky secondary spores of the cup fungi (Beliakova 1954, Batra 1985). Wood-coloring fungi infest weakened, drying, and newly felled trees, which are characterized by the high humidity of wood and large amounts of easily assimilated substances.

Close connections between wood-coloring fungi and bark beetles of the genera *Dendroctonus* Er, *Ips* Deg., *Pityogenes* Bed., *Hylastes* Er., and *Hylurgops* Lec. have been established (Mathre 1964, Francke-Grosmann 1967, Barras and Perry 1971, Raffa and Smalley 1988, Furniss et al. 1988, and Bennet and Tattar 1988).

It is possible to observe mutualistic interactions between wood-coloring fungi and bark beetles. The wood infested by blue-stain fungi is the most attractive and accessible to the bark beetles (Goheen et. al. 1985). This can be explained by several facts. The fungi facilitate wood assimilation by the insects and promote xylophage aggressiveness, and fungi activity is known to increase the protein content of the wood (Hodges et al. 1968) and to decrease the water supply (Horntvedt at al. 1983). Together this results in the most favorable conditions for bark beetle development. On the other hand, mutualistic interactions promote special adaptations for fungi transmitting (Barras and Perry 1972, Furniss et al. 1988). The mechanism of fungi transfer is not simple. Secondary spores are fixed not only in mycangia, but directly on the body surface as well (Barras and Perry 1972, Livingston et al. 1983, Paine and Birch 1983).

Some data testify to the complex interactions between the ambrosia fungi and the ambrosia xylomycetophagous insects. The connection between tree colonization by bark beetles and intensive mycelium growth in mycangia was noted by Paine and Birch (1983). The bark beetles inoculate the wood with several *Ceratocystis* species. At the same time, however, the species preventing intensive blue-stain fungi development and favoring beetle breeding are also transferred in mycangia (Bridge and Perry 1985, Wood et al. 1988).

The interactions between bark beetles and wood-coloring fungi are considered by some authors to be facultative (Mamaev 1977, Batra et al. 1985). That supposition is partially confirmed by the peculiarities of the ecology of the fungi--they can develop without interactions with insects--and by

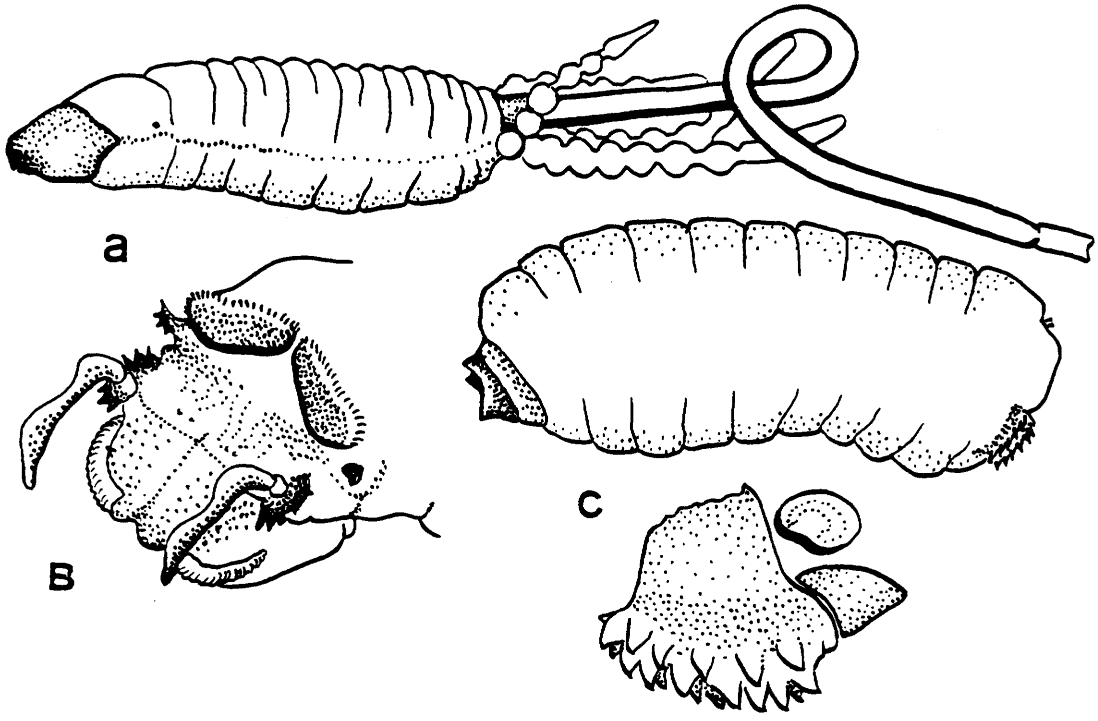

Figure 1. Preimaginal stages of xylobiont dipterans. A - the larvae of *Mesaxymyia kerteszi* Duda (Axymyiidae), B - the fore end of the head of pupa *Mesaxymyia kerteszi* Duda (Axymyiidae), and C - the larvae of *Temnostoma vespiforme* L. (Syrphidae).

features of the ecology of the insects--their capacity for development without symbiotic fungi has been documented (Grosmann 1931, Holst 1937). At the same time, more recent data do not resolve this question definitively. The bark beetles of this community feed on wood infested by fungi. We classify these beetles as xylo- or phloeomycetophages.

Xylophagous Insects Associated with Vascular Mycoses

Vascular mycoses are common among elms (Ulmaceae) and beeches (Fagaceae) and are caused by *Ceratocystis* fungi. The most familiar is Dutch elm disease, caused by the fungus *C. ulmi*. Among its vectors are now considered all the species of *Scolytus* Geoffr., the species of *Pteleobius* Bed., *Hylurgopinus rufipes* Eichn., the weevil *Magdalis armigera* Geoffr. (Curculionidae), and the capricon beetle *Saperda punctata* L. (Cerambycidae) (Pfeffer 1979, Bejer 1979, Covassi 1980, Sengonca and Leisse 1984). The insects infect living trees during their feeding in the crown. Dying of the branches and tree weakening create favorable conditions for occupation of the stems by the insects. A similar disease causing oak mortality is widely distributed throughout Europe and North America. The pathogen of oak mycosis in the U.S.A. is *Ceratocystis fagacearum* (Rexrode and Jones 1970, 1971); in Europe it is the species of *Ceratocystis*, *Diaporte*, and *Fusarium* (Kriukova and Plotnikova 1979, Kuzmichev 1982). The bark beetles *Pseudopityophthorus minutissimus* Zimm., *P. pruinosus* Eichh., and *Scolytus intricatus* Ratz. are considered vectors. In recent years, the role of sap beetles (Nitidulidae) in fungi transmitting has been discussed (Appel et al. 1986). These diseases caused by insect vectors are likely to be distributed widely. Accordingly, the role of *Platypus subgranosus* Schedl. as a *Chalara australis* vector causing the drying wilt of beech myrtle (Fagaceae) has recently been identified (Elliott et al. 1988). Similar interactions have been observed between the sawyer beetle, *Monochamus urussovi* Fisch., and the fungi, *Ceratocystis* spp. (Isaev et al. 1988). Isaev et al. (1988) attach no less importance to these fungi than to the well-known pathogen of Dutch elm disease.

Infection of the beetle by the secondary spores takes place in the pupal chamber, on the walls of which the perithecium develops. Coincidence of the development cycles of both fungus and insect points to the historical connections between these species. Thus Vasechko (1981) and Lindeman (1986) thought this fungi to be an adventive species, against which the trees have not yet developed a pronounced resistance. It is possible, however, that the cause of such wide disease distribution is sufficient pathogen variability; if anything, it is represented now by several strains (Bazzigher 1981).

There are essential differences in the interactions between the fungi and the ambrosia xylomycetophages communities associated with wood-coloring fungi and those of the xylophages associated with vascular mycosis pathogens. In the first case, the bark beetle galleries occur on the trunk sections infected by the blue-stain fungi or in the parts nearby. In the case of vascular mycosis, there is asynchrony of trunk colonization by fungus and insects. With respect to insects, the fungi are a factor of tree weakening. As a result, insect species of this community have neither trophic nor biotopic connections with fungi and are typical phloeoxylophages.

It is important to remember that two ecologically distinct groups of fungi, having qualitatively different connections with insects, exist within the genus *Ceratocystis*.

Destructive Xylomycetophages Occupying Mainly Dead Wood

Wood-destroying fungi affect cellulose and lignin--the main components of the cell walls--causing wood rotting. Various species of fungi are characterized by different selectivity, causing rots distinct in color and structure: corrosive or destructive, brown or light. In the final stages of a tree's decay, the xylophagous insects prefer destructive light and brown rots. The greatest numbers of wood-destroying fungi are among the basidium fungi, but trunk rot is caused by cup and imperfecti fungi as well.

Insects associated with wood-destroying fungi can be placed in three large groups: species-vectors of fungi, which are not trophically related to infected wood; species transferring the fungi spores and preparing the substrate for their brood; species trophically related to fungus infecting the wood, but lacking special structures for fungi transfer. Representatives of the first group, while promoting wood-destroying fungi development, weaken trees and create conditions favorable to xylophage breeding.

Up until now, not enough attention has been paid to the role of insects in the transferring of wood-destroying fungi. The assumption has often been made that the role of the bark beetles is secondary, only associated with wood-destroying fungi (Beaver 1976). In fact, however, much data document bark beetles--*Dendroctonus* Er., *Hylurgops* Lec., *Ips* Deg., *Scolytus ratzeburgi* Jans.--occupying trees infected by tinder or gill fungi (Livingston et al. 1984). At the same time the role of *Dendroctonus* in transferring spores of *Fomitopsis pinicola* has been demonstrated by Harrington et al. (1981). The connection between the bark beetles *D. ponderosae* Hopk. and *Pityogenes fossifrons* Lec. and tree infection by the honey-fungus *Armellaria mellea* was discovered by Kulhavy et al. (1984). Bark beetles and weevils, particularly *Hylobius abietis* L., are thought to be vectors of the pine-fungus *Fomitopsis annoosa* (Nuorteva and Laine 1968). The role of the representatives of the above mentioned group in the tree-fungus-insects system is not simple; they are likely to be both fungi associates and their vectors.

Typical representatives of the second species group, transmitting fungus infection and preparing the substrate for brood development, are the horntails. A connection has been found between horntails and the fungi *Polyporus*, *Daedalia*, *Daldinia*, and others (Stillwell 1960, 1964, Vaartaja and King 1964), the spores of which are transmitted by females during oviposition (Stillwell 1964). A dual effect of horntails on wood has been discovered. The horntails inoculate the tree with a special secretion which causes needle yellowing and weakening of tree resistance to fungi (Coutts 1969). Inoculation by the fungi causes changes in wood properties that facilitate tree occupation by horntails (Sinadsky 1967, Schimitschek 1974). On wood sections, the direct correlation between horntail attacks and fungus mycelium infections is vividly evident.

Strong preference for wood infected by basidium fungi was also found in some Peltidae and Buprestidae species. *Peltis grossum* L. (European-West Siberian species) and *P. giganteum* Rtt. (East Siberian species) are typically found with the brown rots of conifers and *Ostoma ferrugineum* L. with the brown birch rots caused by the fungus *Piptoporus betulinus*. The larvae develop only in the wood infected by mycelium. The possibility of spore transmission by species of Peltidae has not yet been studied.

Direct connections between damage to asian poplars *Populus pruinosa*, *P. ariana*, and other species by the popylore *Inonotus pseudohispidus* and the buprestid beetle *Eurythyrea oxiana* Sem. were recorded in the riparian forests of Middle Asia. Both the fungus and the beetle species are extremely common there. The fungus infects weakened, but visibly vigorous trees. The infected wood takes on a brownish or red color due to pigment accumulation (Sinadsky and Bondarceva 1956). The buprestid larvae occupy only those wood sections infected by the fungus. Conditions for spread of the fungus have not been studied. The spores are thought to penetrate to the wood at various injury sites (Sinadsky and Bondarceva 1956). At the same time, the close connections between the buprestid larvae and the fungus (common area, beetle habitation only in fungus-infected wood zones, initial occupation by both beetle and fungus of the trunk base) testify to the possibility of spore transmission by beetles. It is quite possible that the connections between this insect group and the fungi are not simple and belong to a different category of insect/fungal relationship. This supposition is confirmed by the example of the horntails, for many of which mutualistic, symbiotic relations are evident. Thus *Xeris spectrum* L. (Siricidae) with poorly developed mycetangia injure wood only during the year following occupation by another horntail species (Spradbery 1974), which infect it with fungi.

Species Trophically Associated with Fungus-Infected Wood and Lacking Special Structures for Fungal Transmission

This group includes the destructive xylophages breeding in light and brown wood rots. Wood occupation takes place quite long after fungi inoculation. The imago of this insect group tries to locate tree trunks suitable for colonization (Mamaev 1974c). By wood boring, xylophages promote various microorganisms and fungi activity (Callaham and Shifrine 1960, Mamaev 1960) and favor their penetration of the wood through galleries (Hesterberg et al. 1976).

The capacity of this group to feed on poorly assimilated, less nutritional wood pulp in the absence of ectosymbiotic associations with fungi can be explained by the presence of cellulases in the intestine. So, unlike bark and capricorn beetles feeding on bark and sap-wood and possessing hemicellulase, the capricorns as typical inhabitants of destructive rots have a set of cellulases, promoting cellulose utilization by the insect (Chararas 1983, Chararas and Chipoulet 1983, Kukor and Martin 1986). The high cellulases concentration in the intestine is thought to result from fungi reproducing in the folds of the intestine (Schlottke 1948, Mamaev 1960, 1974c). At the same time, capricorn beetles breeding in weakened trunks on the border of xylem and phloem were discovered to possess an extra set of enzymes and yeast, favoring assimilation of the carbohydrates (Chararas and Pignal 1981).

Brown rots most often form under the influence of the polypore *Fomitopsis pinicola* and are most common to conifers. The typical inhabitants of brown wood rots in the European part of the U.S.S.R. are *Toxotus cursor* L. (Cerambycidae), *Ceruchus chrysomelinus* Hochw., and *Aesalus scarabeoides* Pz. (Lucanidae). In the mountains of the Caucasus, the last of these species is replaced by *Aesallus ulanovskyii* Gglb. (Kosarjevskaya and Mamaev 1962, Mamaev 1977).

The typical destroyers of brown rot wood in the Far East are the cockroach, *Cryptocercus relictus* B. Bien., the beetles *Prostomis mordax* Rtt. (Cucujidae), *Istrisia rufobrunnea* Lew. (Salpingidae), *Nematoplus semenovi* Nik. (Nematoplidae), *Phellopsis amurensis* Heyd. (Zopheridae), and others (Mamaev 1973a, 1973b, 1974b). Among Diptera, the most common inhabitant of brown rots is *Hyperoscelis eximia* Bohem. (Canthyscelidae).

The light rots, usually developing under the influence of the tinder fungus *Fomes fomentarius*, are most typical to leaf-bearing trees. The light rot wood in the European part of the U.S.S.R. are usually destroyed by the larvae of common stag beetles, *Lucanus cervus* L., *Dorcus parallelopipedus* L., and *Sinodendron cylindricum* L. (Lucanidae), and the larvae of dipterans, *Tanyptera atrata* L., *Dictenidia bimaculata* L. (Tipulidae), and *Epiphragma ocellaris* L. (Limoniidae). The main consumers of light rots in the Far East are the stag beetles, *Prismognathus subaeneus* Motsch. and *Eurytrachelus rubrofemoratus* Voll. (Lucanidae), the darkling beetles, *Misolampidius tentyrioides* Sols (Tenebrionidae), and the dipterans, *Phoroctenia vittata* Mg., *Tanyptera nigricornis* Mg. (Tipulidae), *Hesperinus rohdendorfi* Kriv. et Mam. (Hesperinidae), and *Pachyneura oculata* Kriv. et Mam. (Pachyneuridae). In this group one can also find the beetles *Melandrya mongolica* Motsch. (Melandryidae) and *Dentisca serridens* Ter.-Min. (Curculionidae).

Among the ecological groups considered, two groups of destroyers (bark and capricorn beetles) can be classified as xylophages, and the last horntails, peltids, and some buprestids as xylomycetophages, because of their feeding on wood infected by fungus mycelium.

CONCLUSIONS

Vigorous trees have diverse properties for facilitating their resistance against consumers. Moreover, wood is a substance resistant to degradation. Therefore, representatives of the "tree-fungus-insect" system have evolved allowing insects to exploit a vast resource.

My attempt to classify these relations is no doubt far from being complete, partly because the delicate mechanisms of insect-fungi interactions have as yet been insufficiently studied. Nevertheless, the examples presented permit us to conclude that complicated insect-fungi relationships exist at all successional stages of wood degradation (Lindemann 1986).

SUMMARY

Based on the forms of their interrelationships with fungi, we distinguished four groups of insects: 1) ambrosia mycetophagous insects, symbiotically associated with primary ambrosia fungi; 2) ambrosia xylomycetophagous (phloeomycetophagous) insects, symbiotically associated with wood-coloring fungi; 3) xylophagous insects, symbiotically associated with vascular mycosis fungi; and 4) destructive xylo-, mycetophagous insects, associated with wood-destroying fungi. Among the destructive xylo-, mycetophagous insects, three ecological subgroups were identified in terms of their trophic and symbiotic connections with fungi.

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ON THE ROLE OF THE TREE IN RELATION TO COLONIZATION BY IPS TYPOGRAPHUS L.

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INTRODUCTION

For roughly 200 years it was assumed that trap trees attracted the bark beetle *Ips typographus* by means of specific chemical compounds produced by the tree. After the aggregation pheromone was discovered, the importance of tree volatiles was at first more or less totally denied (Vité 1980).

Since Johann succeeded in proving that the combination of pheromone plus tree is, at times, considerably more attractive than the combination of Pheroprax plus plastic trap (Bombosch et al. 1982, Johann 1986a, 1986b), more attention has been paid to the tree even by pheromone supporters (Bakke 1985, Vité and Franke 1985). What follows is a brief synopsis of the findings thus far obtained on this question at our institute.

FLIGHT--A FUNCTION OF ENERGY RESERVES

After leaving their breeding tree or winter quarters, by no means all beetles react immediately to stimuli from trees or pheromones. A large proportion, on the contrary, fly directly from the forest surroundings into the bright sky. According to investigations by Botterweg (1982) and Gries (1985), the proportion of the total population made up of these migrating beetles and the length of the migratory phase of individual beetles depends on the individual beetles' energy reserves. These are determined earlier by the amount of nourishment at the larvae's disposal. The model calculations of De Jong and Saarenmaa (1985) were very successful in showing these shifts in the nutritional condition of individuals in a population.

These findings allow us to see that an *I. typographus* population contains at least two different groups of individuals: one which migrates and one which does not. The proportion of these two groups is not constant since the population density of the larvae, which is determinant here, depends upon the respective breeding trees available.

VERTICAL SILHOUETTES AND VOLATILES

Let us track the course of the migrating beetles. Their flight into the bright light brings about a great dispersion as a result of which, in addition to a high mortality rate, we can find *I. typographus* everywhere in the countryside (Bakke 1985, Sanders 1984, Gossenauer 1988). Their distribution is not

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uniform, however. The lowest densities are to be found in agricultural areas and in very dense young deciduous forest stands; conifer cultures are also less often visited than older deciduous stands. This indicates that both the vertical silhouette of the trees and the scents specific to spruce are important to the beetles after their migratory flight. This behavior leads to a more concentrated occurrence in spruce stands but also to the beetles' marked presence in deciduous stands. For this reason, according to our calculations, it is not possible to reduce population density with the help of traps (Table 1) (Bombosch in press). Gries et al. (1989) maintain that *I. typographus* would have no chance of survival if it were to find its breeding trees only by accident. As a lone insect, furthermore, it is not in a position to successfully colonize healthy spruce trees. This migratory portion of the beetle population, operating on its own, is dependent upon suitable fallen or standing stems. The silhouette and the odoriferous quality of the tree itself probably combine to help the beetles find such stems. All earlier attempts to increase the efficiency of trap trees, as recorded in the textbooks, point in this direction. To date, as far as I know, it has not been possible to analyze the chemical structure of the odoriferous substances produced by the tree. It is very unlikely that α-pinene alone is the attractive substance (Vité 1980) because if that were the case all conifers would be colonized. After the beetles have penetrated the bark, the attractiveness of the trees attacked is intensified by the secretion of pheromone. Genuine pioneer beetles initiate this process; every additional beetle that is attracted and produces pheromone in its turn increases the allure of the potential breeding place. In tests with the method developed by Dedek and Pape (1988a, 1988b) of applying methamidophos as an insecticide that takes effect only in the bark, it was noted that the beetle infestation on standing trees was concentrated at a few meters surrounding the pheromone dispenser, whereas beetles appear to colonize the entire length of fallen trees. After landing, then, these beetles seem to spread more intensively in a horizontal direction than vertically.

Numerous other species besides *I. typographus* colonize fallen spruce stems. According to Vité and Franke (1985), the range of species on these trees is determined by the types of change that occur in the bark. A dry change leads to colonization by *I. typographus*, *I. amitinus*, *P. chalcographus*. A wet change, whereby ethanol is released, is responsible for colonization by *Xylosandrus germanus* and *Trypodendron* sp. etc. Within these groups, diverging pheromones are suspected (Vité and Franke 1985) of causing the delimitation of the individual species' territories. In spring 1989 *I. typographus*, *I. amitinus*, *P. chalcographus*, and *P. polygraphus*, and also *T. lineatum* were found in very close proximity to each other on 3-m-long lower stem sections in the Solling hills.

TEMPERATURE EFFECTS ON FLIGHT

The demands, at least of the teetotallers, seem therefore to cover a very large range, and the importance of the deflecting pheromones is not exactly paramount. In my opinion, when trying to find out the causes for the different species' distribution on the stem, more attention should be directed to the temperature necessary for setting them into flight than has hitherto been paid. In 1987 we were able initially to observe a strong flight of *I. amitinus* in two low mountain ranges. When *I. typographus* flew 3 weeks later after a sudden onset of cold weather, it was able to colonize only those places that had been left open by its predecessor. It is thus quite conceivable that an exact spatial separation of the individual species occurs according to temperature thresholds when the temperatures rise slowly in spring, but that the commingling described above occurs when the temperature suddenly turns hot, using all species' thresholds.

Table 1. Calculation of the reduction of the population of *Ips typographus* by different success of trapping

Parameter	Spruce clearcuts 10 ha	Spruce stands 90 ha	Total population	Reduction rate %
Distribution (Johann, Gossenauer)	20%	80%		
Assumed population/ha	200	800		
Total	2,000	72,000	74,000	
Reduction on clearcuts				
Johann, Beuke (-17%)	-340	72,000	73,680	0.4
Weslien (-30%)	-600	72,000	73,400	0.8
Hypothetical (-50%)	-1,000	72,000	73,000	1.3
Assumed population (Bakke)	6,000	68,000	74,000	
Reduction on clearcuts				
Johann, Bueke (-17%)	-1,020	68,000	72,980	1.4
Weslien (-30%)	-1,800	68,000	72,200	2.4
Hypothetical (-50%)	-3,000	68,000	71,000	4.0
Hypothetical (-100%)	-6,000	68,000	68,000	8.1

TEMPERATURE AND LIGHT EFFECTS ON PIONEERS

In contrast to fallen trees, healthy, standing stems cannot be colonized by single beetles since for that a simultaneous attack by many individuals is necessary. Aggregation is supposed to materialize as single, pioneer beetles land on the tree and then attract more and more beetles by the production of contact pheromone, until finally the number of insects necessary for a successful attack is present (Vité 1980). This hypothesis assumes that beetles, having once landed, do not fly away again, and leaves open the question by which criteria the first beetles choose their landing place and what it is that triggers the mass attack.

Our observations suggest that pioneer beetles do not play a part in the colonization of standing trees. On standing spruce trees we have never as yet found increasing congregations before the beetles' penetration. On the contrary, in the spring of 1989 we found, apart from numerous stem sections on the ground that had been attacked, single standing trees exhibiting "Spechtspiegel" on the lower part of their stems. Spechtspiegel are small pale patches appearing on the bark where the squamae have been removed by woodpeckers or other birds in search of xylophages. We also found one tree with ten, and three trees each with one, unsuccessful boring attempt. This indicates that the bulk of the insects in the *I. typographus* population we observed was searching for wood lying on the ground, but that a few individual insects reacted to standing trees and attempted to attack them (e.g. the Spechtspiegel). An attack on standing trees does not, therefore, require presence of many beetles reacting in the same way. It was also evident that Spechtspiegel and boring attempts did not occur at random around the stems, but always faced south to southwest. This observation accords with the long known fact that when standing trees are attacked, mass propagation in a beetle "nest" is usually to be found where the sun shines in the afternoon. As the triggering stimulus for beetles in search of suitable standing wood, differences in the trees' warmth may be of more decisive importance than their scents. The number of beetles attacking, however would not depend on the strength of the allurement, but on the number of beetles reacting to particular degrees of warmth of the trees. These may represent the nonmigratory portion of the population mentioned earlier. The fact that an attack on a standing tree always occurs in the immediate vicinity of an earlier attack in a beetle nest speaks in favor of this hypothesis. It can also be observed that the infestation of wood lying on the ground subsides in the course of a gradation (Bombosch 1954). This may be the result of a deterioration in the larvae's nutrition due to increasing population density together with a simultaneous reduction of breeding possibilities causing a continuous reduction in the number of migrating individuals. Since the relationship between the number of beetles and suitable breeding places is not constant, the question why each blowdown that is colonized by *I. typographus* does not endanger neighboring stems can still be answered. But the question to what extent this part of the beetle population reacts to pheromone traps still remains completely open. The investigations begun by Sahota and Peet (1988), whose objective is to characterize the quality of bark beetle populations, should contribute to considerable progress in the elucidation of this complex of questions.

SUMMARY

When assessing *I. typographus* populations, one should differentiate between the proportion of migratory and nonmigratory individuals. The reason for this difference may be found in changes in the larvae's nutrition. Individuals in the migratory proportion set off alone and are dependent on finding suitable stems. They search for them purposefully, probably because of the silhouette and primary attractive substances of these trees. The first to colonize intensify the tree's allurement by pheromone secretion. They are genuine pioneer beetles.

With respect to breeding suitability of the tree, the beetles' requirements do not seem to be as restrictive as has hitherto been assumed, since *I. typographus* and *T. lineatum* can be found next to each other on the same stem. As for spatial distribution of the individual species on the stem, not only deflecting pheromones but also the temperature conditions and differences in the beginning of the flying period of the individual species should be considered. In beetle nests, the attack of standing trees may be caused by the nonmigratory portion of the beetle population. Temperature differences between the trees may function as directing stimuli. A mass attack would not be determined by intensity of the allurement, but by the number of nonmigratory beetles in the given population.

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INTERSPECIFIC OLFACTORY COMMUNICATION IN THE SOUTHERN PINE BARK BEETLE GUILD[1]

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INTRODUCTION

The southern pine bark beetle guild consists of many species, the most economically significant of which are the five scolytid species, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). All five species co-exist in pine forests across the southern and southeastern United States. When the species cohabit in the same host tree each usually occupies a distinct niche. However, the area occupied by one species generally overlaps with that occupied by another (Fig. 1) (Birch and Svihra 1979, Dixon and Payne 1979, Birch et al. 1980, Svihra et al. 1980, Paine et al. 1981, Wagner et al. 1985.

Host selection, aggregation and colonization by all the various species involves a complex chemical communication system composed of compounds produced both by the beetles and by the host tree. Electrophysiological investigations have shown that each species has antennal olfactory receptors capable of detecting semiochemicals produced by itself and by the other species in the guild (Payne 1970, 1971, 1974, 1975, Payne and Dickens 1976, Dickens and Payne 1977, Payne et al. 1982, 1987, 1988, Smith et al. 1988). Behavioral investigations of some of the species have shown that they respond to intra- and interspecific semiochemicals, as well as to volatiles from beetle-infested host materials (Renwick and Vité 1969, Werner 1972, Hedden et al. 1976, Payne et al. 1978, Richerson and Payne 1979, Dixon and Payne 1980, Billings 1985, Siegfried et al. 1986, Payne et al. 1987, Payne et al. 1988, and Phillips et al. 1989). Investigations have also shown the response patterns of the species to

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trees or logs containing the various members of the guild (Vité et al. 1964, Godbee and Franklin 1976, Birch et al. 1980, Svihra et al. 1980, Svihra 1982, Phillips et al. 1989). In this paper, using both new findings and previously published information, we survey the interspecific olfactory receptor sensitivity of the species for specific pheromones and explore the behavioral responses of the most significant species in the southern pine bark beetle guild to the pheromonal blends of the species.

EXPERIMENTAL METHODS

Antennal olfactory responses were measured using the electroantennogram (EAG) and single-cell techniques (Schneider 1957; Boeckh 1962, Payne 1975, Dickens and Payne 1977). EAGs were recorded with glass capillary, Ag-AgCl microelectrodes filled with 3M KCl. The recording electrode was inserted in the antennal club, and the indifferent electrode was inserted in the beetle's head capsule or mouth. Single-cell recordings (SCR) were made using tungsten electrodes with electrolytically polished tips of < 2 u. The recording electrode was inserted at the base of a sensillum in the sensory bands of the antenna; the indifferent electrode was inserted in the mouth. Responses were recorded on magnetic tape and polaroid film. The compounds tested, their source, and their purity are given in Table 1. Test stimuli were delivered as 5 ul aliquots onto a piece of filter paper in a glass cartridge via a 1 L/min airflow. Serial dilutions of the stimuli were presented in order from the lowest to the highest concentration. Dosage-response curves plotted from mean responses to each stimuli were used to determine the relative sensitivity of the olfactory receptors to each compound. The threshold of response, the minimal stimulus concentration at which an EAG was detectable above background, was considered an indication of olfactory receptor sensitivity to a compound.

Table 1. Beetle- and host-tree-produced compounds tested

Compound	Source of supply	Purity (%)
Frontalin		
(+,-)	Chem. Samp. Co.	99
(+)	K. Mori	98
(-)	K. Mori	98
Verbenone		
(+,-)	Chem. Samp. Co.	98
(+)	Chem. Samp. Co.	98
(-)	Chem. Samp. Co.	98
endo-brevicomin	Chem. Samp. Co.	99
Ipsdienol	Borregaard Industries	81
Ipsenol	Borregaard Industries	89
cis-verbenol	Borregaard Industries	95
trans-verbenol	Borregaard Industries	95
α-pinene	Aldrich Chem. Co.	97

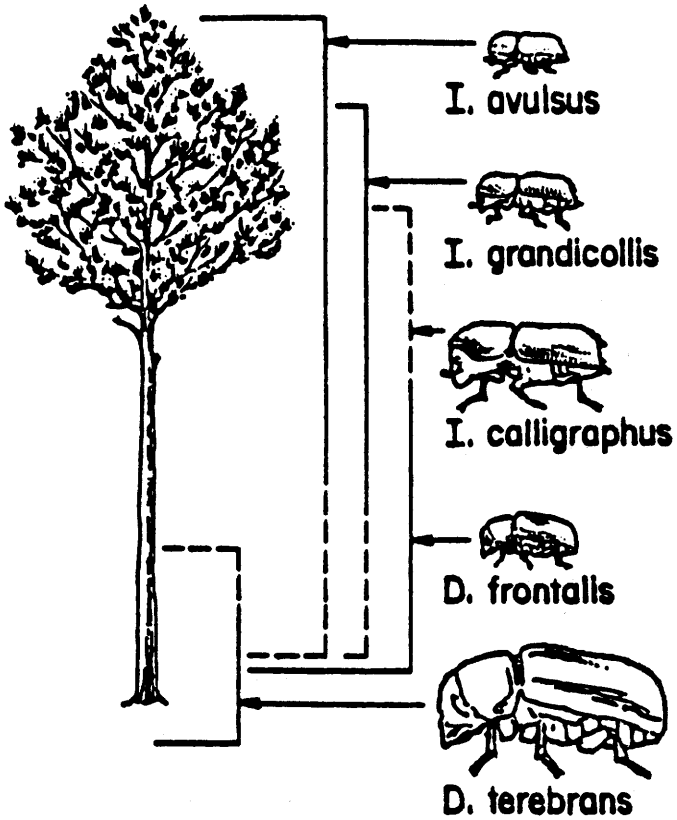

Figure 1. Primary species of the southern pine bark beetle guild and their generalized spatial distribution on the host tree. (From Flamm et al. 1988.)

Our field studies were conducted in the east Texas pine forest during the summer of 1987. To minimize possible effects of host tree odors on beetle response, the studies were carried out in a 2-year-old clear-cut. The surrounding forest was mostly loblolly pine, *Pinus taeda*, and, to the best of our knowledge, no bark beetle infestations were present within ca. a 50-mile radius. At the time, beetle populations in Texas were considered to be at an endemic level. As a result, the number of beetles trapped during the study was low.

Test Compounds

Pheromonal blends for the guild members were determined from published and unpublished reports of pheromone production and were individually formulated and tested. In addition, specific enantiomers of the major pheromonal components were evaluated for *D. frontalis* and the *Ips* spp., since previous research had demonstrated differential production and/or responsiveness based on enantiomeric composition (see references, Table 2). To determine the presence and relative abundance of flying beetles of each species in the test area, a *Dendroctonus* standard composed of frontalin and turpentine and an *Ips* standard composed of ipsdienol, ipsenol, and *cis*-verbenol (Billings 1985) were included as separate treatments in the experiments. A trap baited only with turpentine and a blank trap were included as controls for response to host odor and trap configuration, respectively.

Table 2. Beetle-produced pheromonal blends tested

Species	[1] Sex	[2] Chemical compounds	Compound ratios	Elution rate (mg/24 h)	[3] Reference
D. frontalis	F	(-)-F:(+)-F:TV:V	21.25:3.75:750:6	0.85:0.15:30:0.24	1,2
D. frontalis	M	(+)-ENB:(-)-ENB:EXB:V:TV	0.94:0.03:0.03:800:9	0.94:0.03:L0.03:800:9	2,3
D. terebrans	F	F:TV:V	1:500:50	1:500:50	2,4
	M	EXB:TV:V	1:15:1.1	1:15:1.1	2,4
I. calligraphus	M	(R)-(-)-,(S)-(+)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	5,6
	M	(R)-(-)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	6
	M	(S)-(+)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	6
I. calligraphus	F	TV:CV	5.5:1	4.4:0.8	5
I. avulsus	M	(R)-(-)-,(S)-(+)-IPSD:TV:CV	45:1:1	0.2:0.0044	5,6
	M	(R)-(-)-IPSD:TV:CV	45:1:1	0.2:0.0044	6
	M	(S)-(+)-IPSD:TV:CV	45:1:1	0.2:0.0044	6
I. grandicollis	M	(S)-(-)-,(R)-(+)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	5,7
		(S)-(-)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	7
		(R)-(+)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	7

[1] Sex: F = female; M = male.

[2] CV = *cis*-verbenol, ENB = *endo*-brevicomin, EXB = *exo*-brevicomin, F = frontalin, IPSD = ipsdienol, IPSE = ipsenol, TV = *trans*-verbenol, and V = verbenone.

[3] 1) Stewart et al. 1977, 2) Payne, West, Silverstein (unpubl.), 3) Redlich et al. 1987, 4) Payne et al. 1987, 5) Vité et al. 1972, 6) Vité et al. 1978, and 7) Vité et al. 1976.

Elution Devices and Rates

Based on weight loss/24 h, elution devices were developed and rates determined for each compound tested (Table 2). Glass capillaries and vials of various sizes provided the desired elution rates.

Experimental Design

The multiple funnel trap was used to monitor the beetles' response to the different pheromonal blends (Lindgren 1983). Traps were placed ca. 45 m apart in a single, straight row running through the center of the clear-cut. Initially, treatments were assigned positions randomly. Thereafter, treatments were advanced one position each subsequent day in order to minimize positional effects and disproportionate trap catches caused by any nonrandom distribution of beetles. Thus each treatment occupied each position during the 20-day experiment. Every 24 h, trapped beetles were removed and placed in labeled vials for subsequent counting and sexing. Chi Square and/or Fisher's exact tests were used to analyze the data, followed by a binomial test for paired comparisons, when appropriate (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

Olfactory Perception

Electroantennogram analyses of the species have consistently shown that each species possesses more receptors with lower thresholds for compounds produced by conspecifics and to which they are behaviorally most responsive (Payne 1970, 1971, 1974, Dickens and Payne 1977, Payne et al. 1982, 1988, Smith et al. 1988). For examples, see Figs. 2 and 3.

More detailed investigations of the peripheral olfactory receptor systems have been made using single cell recording (SCR) techniques (Fig. 4).

Both general and chiral-specific acceptors have been identified, as well as a wide variety of olfactory cell types with different degrees of receptor specificities which range along a continuum from cells narrowly tuned to a single compound to cells broadly tuned to a number of different compounds (Figs. 5-7).

Compounds which attract and/or arrest, enhance attraction or reduce attraction, may be perceived by a common neuron and acceptor. These overlapping acceptor specificities may provide the beetles with the genetic plasticity needed to code both qualitative and quantitative information about several behaviorally significant odors present in the insects' environment.

Behavioral Response

The responses of *D. frontalis*, *D. terebrans*, *I. calligraphus*, *I. avulsus*, and *I. grandicollis* to the *Dendroctonus* and *Ips* standards (treatments 17 and 18) verified that the species were present throughout the test area for the duration of the experiment, even though, due to their endemic population levels, the number of beetles trapped was low.

D. frontalis

As expected, both male and female *D. frontalis* were attracted to the pheromonal blends of female *D. frontalis* and, to a lesser extent, female *D. terebrans* (treatments 1 and 4) (Fig. 8). Attraction to both blends can be attributed to the presence of frontalin and *trans*-verbenol. *D. frontalis* has been

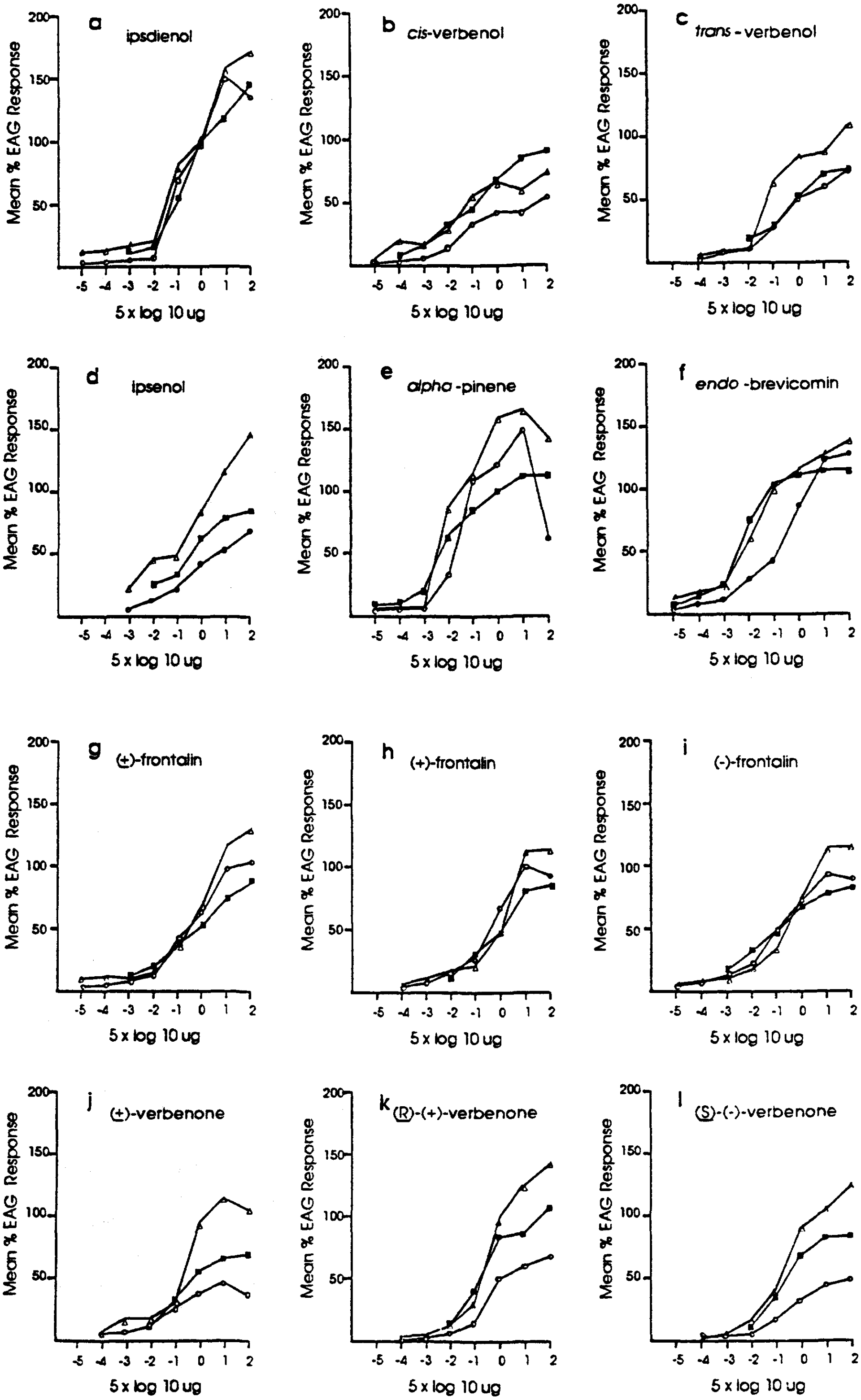

Figure 2. Mean percentage response of *I. avulsus*, *I. calligraphus*, and *I. grandicollis* to behavioral chemicals. Means are percentage of EAG to the standard ipsdienol. O = *I. avulsus*; ■ = *I. calligraphus*; Δ = *I. grandicollis*. (From Smith et al. 1988.)

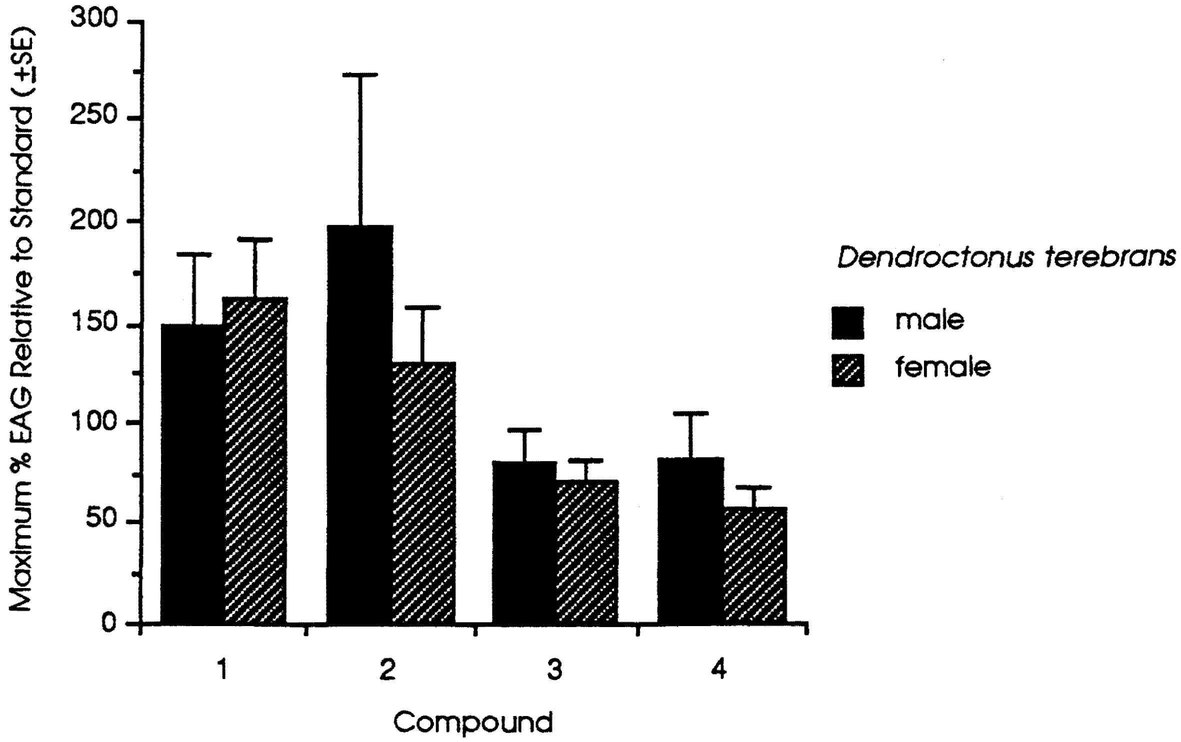

Figure 3. Maximal percentage of EAGs to behavioral chemicals recorded from male and female *Dendroctonus terebrans* N = 5; vertical bars represent ± $\bar{x}$ SE. Standard = 5 ug frontalin. 1 = Frontalin, 2 = *endo*-brevicomin, 3 = *trans*-verbenol, 4 = turpentine. (From Payne et al. 1987.)

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reported to be attracted to frontalin and frontalin plus *trans*-verbenol (Renwick 1969, Renwick and Vité 1969, 1970, Payne et al. 1978, Billings 1985). *Trans*-verbenol has been reported significantly to enhance the attraction of *D. frontalis* to frontalin (Renwick 1969, Renwick and Vité 1970, Payne et al. 1978).

Male and female *D. frontalis* were not attracted to the pheromonal blends of male *D. frontalis* (treatment 2) or male *D. terebrans* (treatment 5). Responses of both sexes of *D. frontalis* to the pheromonal blend of female *D. frontalis* was significantly ($P < 0.05$) reduced by the simultaneous presence of the male *D. frontalis* blend (treatment 3). In part, these results can be attributed to the relatively high proportion of verbenone eluted from the blends of both male *D. frontalis* and male *D. terebrans*. Eluted at relatively high rates, verbenone has been reported to reduce *D. frontalis* attraction to frontalin plus α-pinene and/or *trans*-verbenol and frontalin plus turpentine (Renwick and Vité 1969, Payne et al. 1978). The results can also be attributed to the presence of *exo*-brevicomin, eluted from the blend of male *D. terebrans*, and *exo*-brevicomin plus *endo*-brevicomin, eluted from the blend of male *D. frontalis*. The brevicomins reduce *D. frontalis* attraction to frontalin plus α-pinene (Vité and Renwick 1971a, Payne et al. 1978). *D. frontalis* attraction to frontalin plus turpentine, with and without *trans*-verbenol, has also been reported to be reduced by *endo*-brevicomin (Payne et al. 1978). More specifically, Vité et al. (1985) reported that (-)-*endo*-brevicomin significantly reduced *D. frontalis* attraction to frontalure (1:2 ratio of frontalin and α-pinene) plus turpentine.

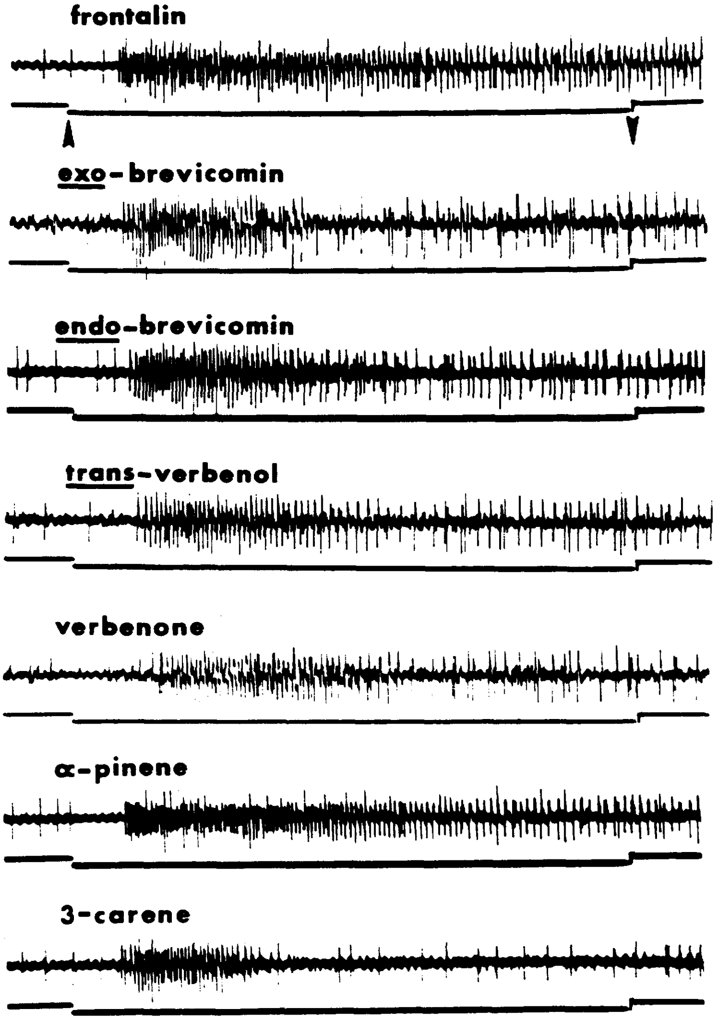

Figure 4. Single-cell response from a sensillum basiconicum of a *D. frontalis* female to pheromones and host tree terpenes. Displaced horizontal bar (indicated by arrows) represents 1 sec stimulation. Delay from stimulus onset to spike initiation was due to an artifact in delivery system. (From Dickens and Payne 1978.)

None of the pheromonal blends of the *Ips* species was attractive to *D. frontalis* (treatments 7-16). The results correspond to the report by Billings (1985) of the lack of attraction of *D. frontalis* to an *Ips* pheromone blend, a mixture of 2 percent *cis*-verbenol, 2 percent ipsenol, and 2 percent ipsdienol in a vaseline-based paste, with and without turpentine. In addition, studies using beetle-infested pine bolts provided no evidence for the attraction of *D. frontalis* to bolts infested with *I. calligraphus*, *I. avulsus*, or *I. grandicollis* (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

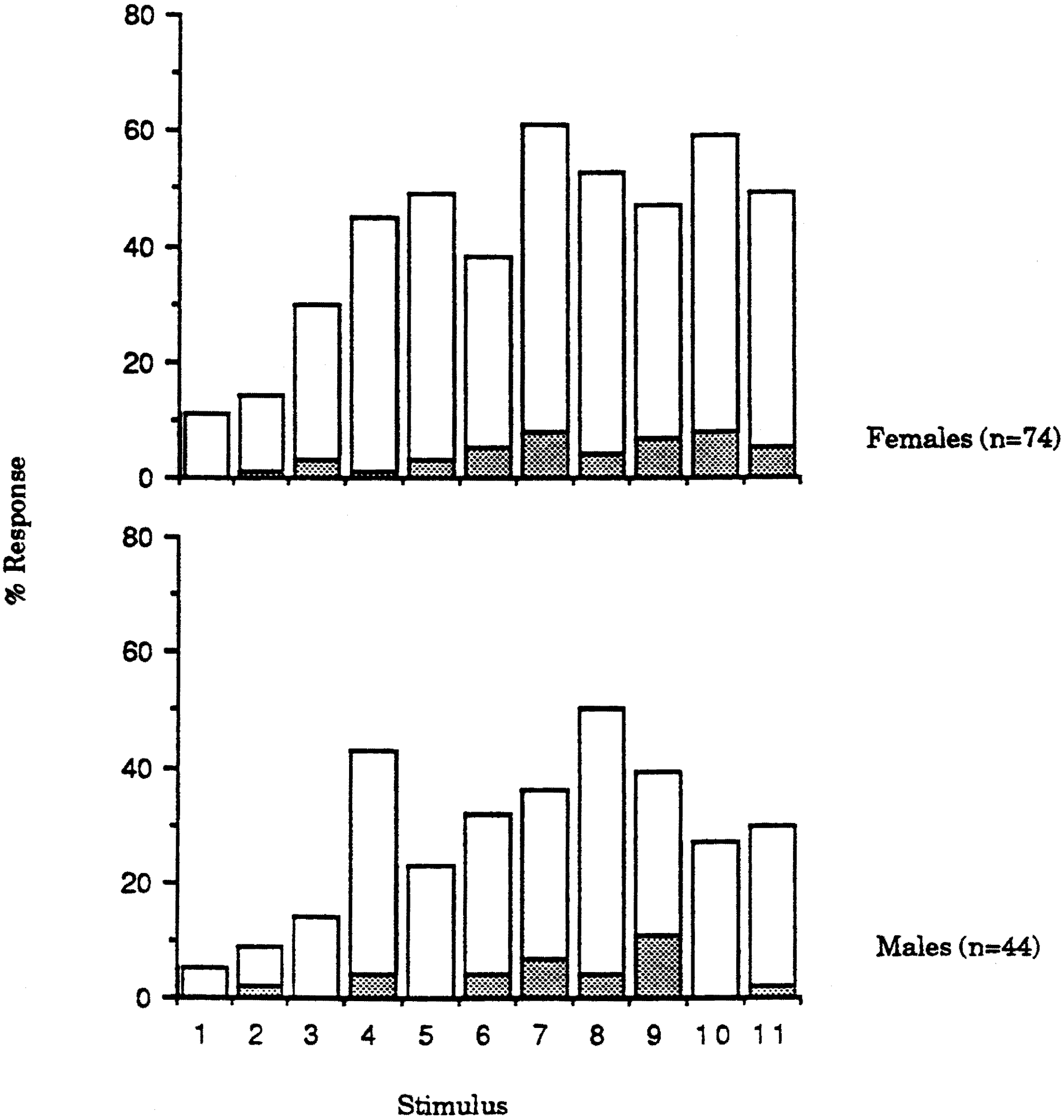

Figure 5. Percentage of *Ips grandicollis* olfactory cells which responded to stimuli. Shaded area equals percentage of cells which responded to only one compound. 1) spontaneous activity, 2) air, 3) pentane, 4) α-pinene, 5) frontalin, 6) *endo*-brevicomin, 7) *trans*-verbenol, 8) *cis*-verbenol, 9) verbenone, 10) ipsdienol, and 11) ipsenol.

D. terebrans

D. terebrans were trapped in such low numbers that analysis of their cross-attraction was not possible (Fig. 9). It should be noted, however, that the lack of response of *D. terebrans* to frontalin, frontalure, and *trans*-verbenol, separately, has been reported (Payne et al. 1987, Phillips et al. 1989). In combination with a high elution rate of turpentine, the pheromones were significantly attractive to

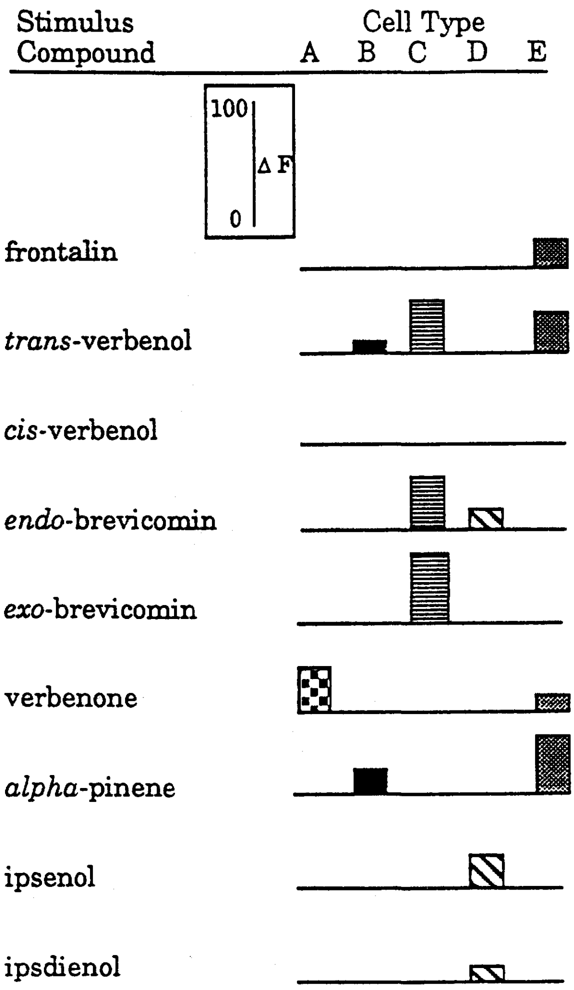

Figure 6. Relative frequency of nerve spikes from *D. frontalis* olfactory cells in response to semiochemicals.

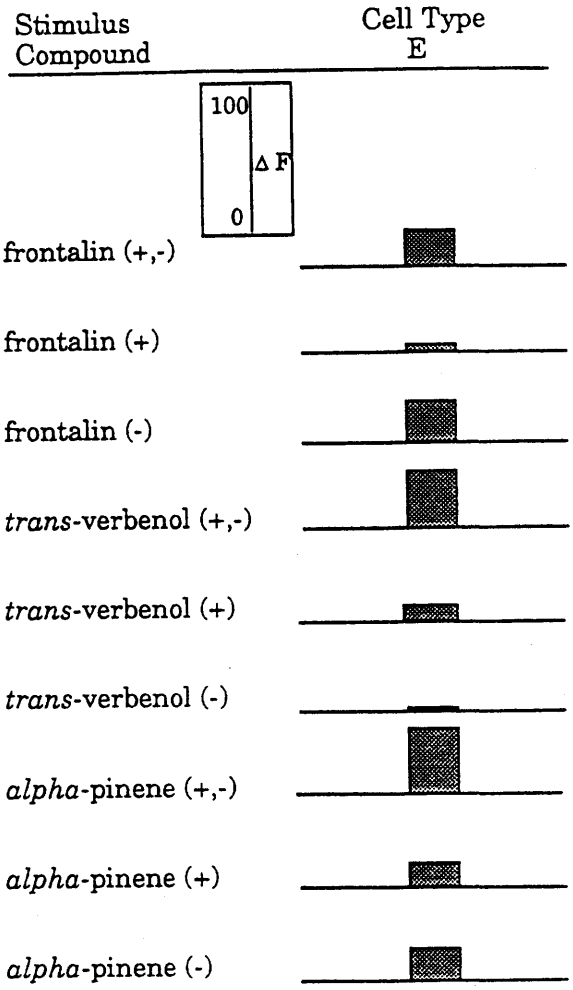

Figure 7. Relative frequency of nerve spikes from a single *D. frontalis* olfactory cell in response to semiochemicals and enantiomers.

D. terebrans, which indicates the presence of pheromonal-based interspecific communication between *D. terebrans* and *D. frontalis*, as reported earlier (Payne et al. 1987).

I. calligraphus

Male and female *I. calligraphus* were attracted to the pheromonal blends of male *I. calligraphus* and *I. avulsus* containing either racemic ipsdienol (treatments 7 and 11) or (R)-(-)-ipsdienol (treatments 8 and 12) (Fig. 10). More *I. calligraphus* ($P > 0.05$) were attracted to the male *I. calligraphus* blend containing racemic ipsdienol (treatment 7) than to the blend containing (R)-(-)-ipsdienol (treatment 8). But *I. calligraphus* were not attracted to the blends of male *I. calligraphus* or male *I. avulsus* containing (S)-(+)-ipsdienol (treatments 9 and 13). Our results agree with earlier reports of the attraction of *I. calligraphus* to ipsdienol plus *cis*-verbenol and ipsdienol plus *trans*-verbenol (Renwick and Vité 1972).

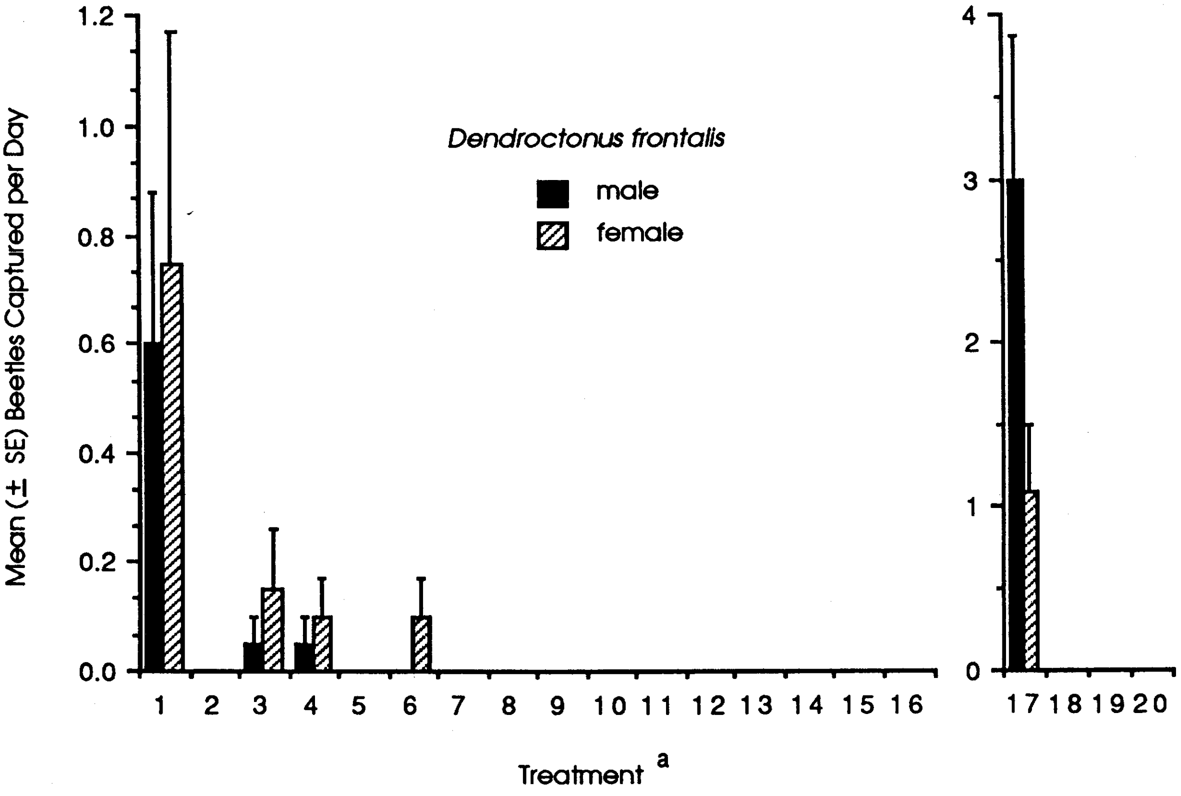

Figure 8. Mean number of *Dendroctonus frontalis* trapped in response to pheromonal compounds eluted at varying rates. [a]See Table 2. Vertical bars represent standard errors of means.
1) (-)-F:(+)-F:TV:V, 2) (+)-ENB:(-)-ENB:EXB:V:TV, 3) 1+2, 4) F:TV:V, 5) EXB:TV:V, 6) 4+5, 7) (R)-(-)-,(S)-(+)-IPSD:TV:CV, 8) (R)-(-)-IPSD:TV:CV, 9) (S)-(+)-IPSD:TV:CV, 10) TV:CV, 11) (R)-(-)-,(S)-(+)-IPSD:TV:CV, 12) (R)-(-)-IPSD:TV:CV, 13) (S)-(+)-IPSD:TV:CV, 14) (S)-(-)-,(R)-(+)-IPSE:TV:CV, 15) (S)-(-)-IPSE:TV:CV, 16) (R)-(+)-IPSE:TV:CV, 17) *Dendroctonus* standard, 18) *Ips* standard, 19) turpentine standard, and 20) unbaited blank trap.

More specifically, the results are in agreement with the report that for *I. calligraphus* (R)-(-)-ipsdienol plus *cis*-verbenol was attractive, whereas (S)-(+)-ipsdienol plus *cis*-verbenol was not (Vité et al. 1978). However, the results reported here are not consistent with the report by Vité et al. (1978) that (S)-(+)-ipsdienol significantly reduced the attraction of *I. calligraphus* to (R)-(-)-ipsdienol plus *cis*-verbenol.

The pheromonal blends of male *I. grandicollis* were not attractive to *I. calligraphus* (treatments 14-16). Although there are no reported analyses of the behavioral response of *I. calligraphus* to the *I. grandicollis* pheromone, ipsenol, when tested alone, the results presented here could be attributed to the lack of attraction of *I. calligraphus* to ipsenol. By contrast, Birch et al. (1980) showed attraction of *I. calligraphus* to *I. grandicollis*-infested bolts; however, other researchers reported the lack of such attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982).

The *D. frontalis* blends were not attractive to *I. calligraphus*; for *D. terebrans* only the female blend exerted an attraction and that was slight. Dixon and Payne (1980) also reported the lack of

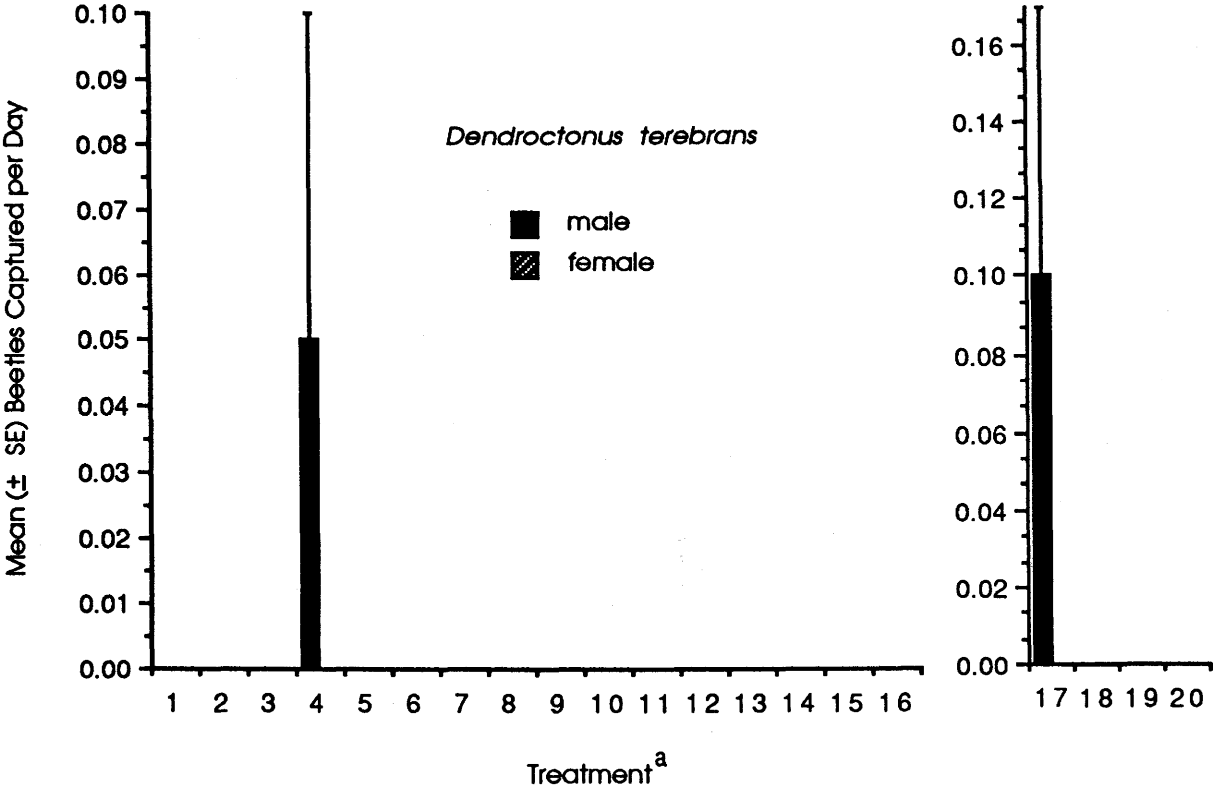

Figure 9. Mean number of *Dendroctonus terebrans* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

attraction of *I. calligraphus* to frontalin, *trans*-verbenol, *endo*-brevicomin, *exo*-brevicomin, verbenone, and turpentine, when tested individually or in various combinations. Further, *I. calligraphus* was reported to be unresponsive to *D. frontalis*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Dixon and Payne (1980), however, found that *I. calligraphus* was attracted to bolts infested with female *D. frontalis*.

I. avulsus

The pheromonal blends of male *I. calligraphus* (treatments 7-9) and male *I. avulsus* (treatments 11-13) attracted both male and female *I. avulsus* (Fig. 11). The blends of male *I. calligraphus* containing racemic ipsdienol or (R)-(-)-ipsdienol (treatments 7 and 8) attracted significantly ($P > 0.05$) more *I. avulsus* than the blend containing (S)-(+)-ipsdienol (treatment 9). Also, significantly ($P > 0.05$) more *I. avulsus* were attracted to the blend of male *I. avulsus* containing (R)-(-)-ipsdienol (treatment 12) than to the blend containing racemic ipsdienol (treatment 11). The blend of male *I. avulsus* containing (R)-(-)-ipsdienol (treatment 12) was significantly ($P > 0.05$) more attractive to female than to male *I. avulsus*. Our results are in agreement with those reported for the attraction of *I. avulsus* to racemic ipsdienol and (R)-(-)-ipsdienol plus (S)-(-)-ipsenol (Hedden et al. 1976, Vité et al. 1978). Furthermore, the results support reports of the attraction of *I. avulsus* to male *I. avulsus*--and to male *I. calligraphus*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

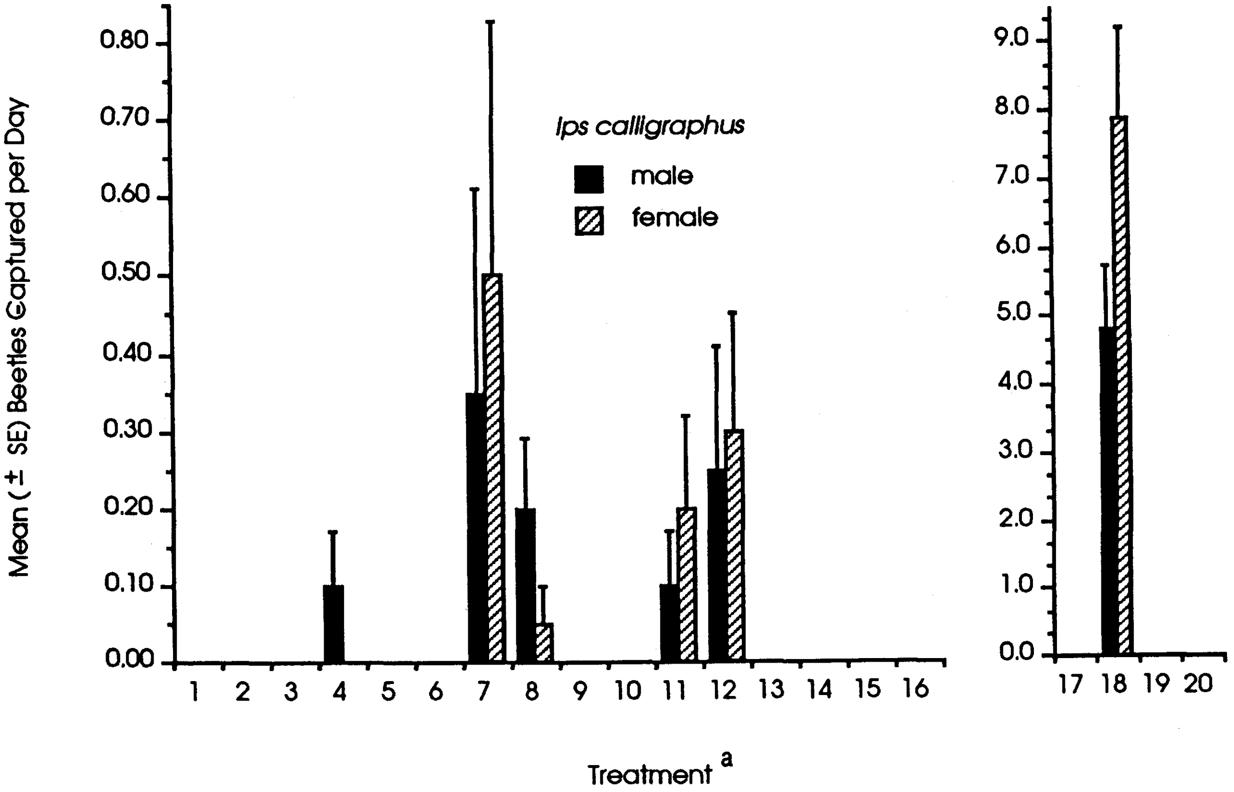

Figure 10. Mean number of *Ips calligraphus* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

Few male *I. avulsus* were attracted to the pheromone blend of male *I. grandicollis* containing racemic ipsenol; females were not attracted. The results are supported by the reported attraction of *I. avulsus* males over females to ipsenol (Hedden et al. 1976) and the attraction of *I. avulsus* to male *I. grandicollis*-infested pine bolts (Birch et al. 1980). Though not significant, *I. avulsus* also showed some attraction to the blends of female and male plus female *D. frontalis* and *D. terebrans* (treatments 1 and 3-6). While some studies have reported the lack of attraction of *I. avulsus* to *D. frontalis*-infested bolts (Birch et al. 1980, Svihra 1982), others have demonstrated attraction (Vité et al. 1964, Svihra et al. 1980). It is apparent, however, that *I. avulsus* is not strongly attracted to *Dendroctonus* pheromonal blends.

I. grandicollis

Both sexes of *I. grandicollis* were attracted to the pheromonal blend of male *I. grandicollis* containing (S)-(-)-ipsenol (treatment 15) (Fig. 12). The results support earlier reports that ipsenol (Vité and Renwick 1971b, Vité et al. 1976) and, more specifically, (S)-(-)-ipsenol (Vité et al. 1976) are attractive to *I. grandicollis*. The pheromone probably accounts in part for the attraction of *I. grandicollis* to male *I. grandicollis*-infested bolts, as reported earlier (Vité et al. 1964, Vité and Renwick 1971b, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982). (R)-(+)-ipsenol was not attractive by itself (treatment 16), and significantly ($P > 0.05$) reduced attraction of *I. grandicollis* to the male *I. grandicollis* blend containing (S)-(-)ipsenol (treatment 14). The results agree with previous reports that (R)-(+)-ipsenol significantly reduced the attraction of *I. grandicollis* to (S)-(-)-ipsenol (Vité et al. 1976). The blends of male *I. grandicollis* containing (S)-(-)-ipsenol attracted significantly ($P > 0.05$) more female than male *I. grandicollis* (treatment 15).

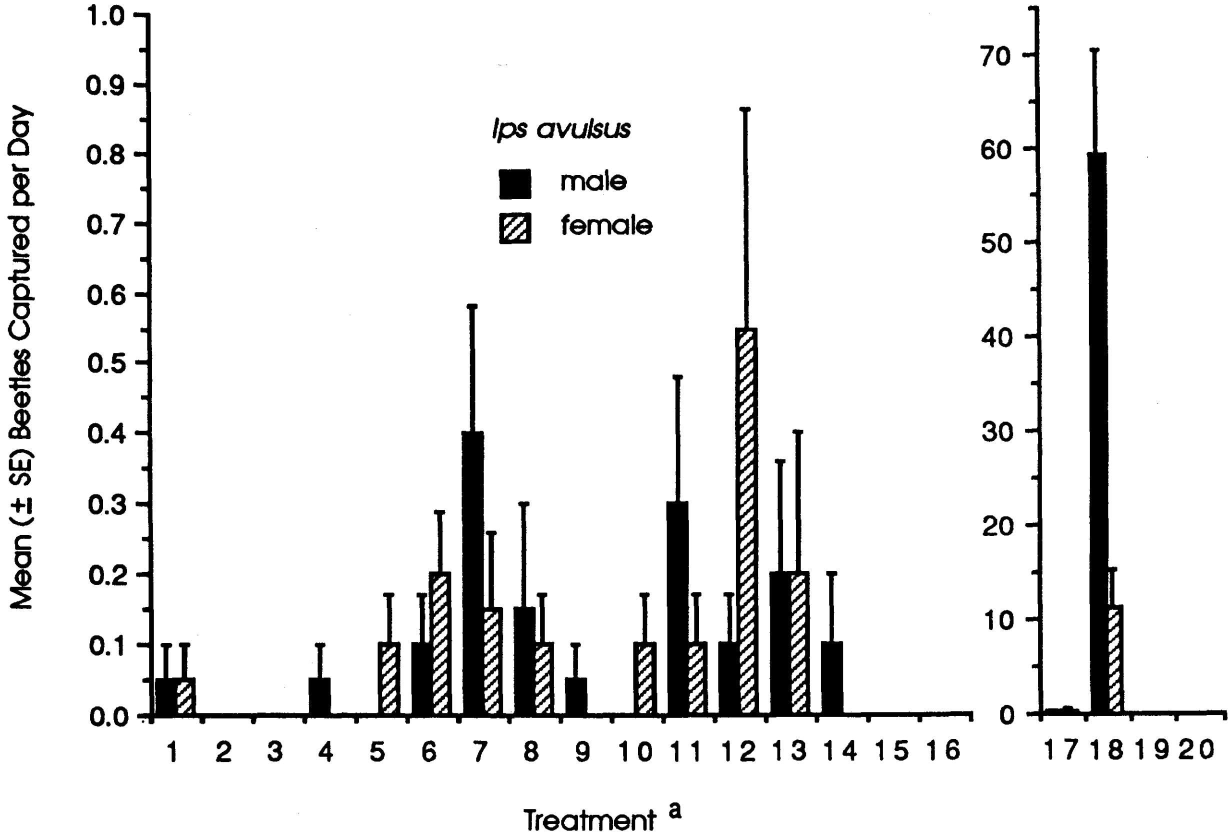

Figure 11. Mean number of *Ips avulsus* trapped in response to pheromonal compounds eluted at varying rates. ^{a}See Figure 8.

Most of the blends of *I. calligraphus* (treatments 7-10) and *I. avulsus* (treatments 11-13) attracted *I. grandicollis*, but at low levels. Vité et al. (1976) reported the lack of attraction of *I. grandicollis* to ipsdienol alone, which indicates the importance of the blends to interspecific communication. However, while some research has shown the attraction of *I. grandicollis* to bolts infested with *I. calligraphus* (Vité et al. 1964, Birch et al. 1980, Svihra 1982) and *I. avulsus* (Birch et al. 1980), other research has shown a lack of attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Without analysis of the volatiles from the bolts, of course, the blend of pheromones released in those studies cannot be determined.

The blends of male and female *D. frontalis* (treatments 1-3) and *D. terebrans* (treatments 4-6) attracted *I. grandicollis*. Significantly more ($P > 0.05$) *I. grandicollis* were attracted to a combination of male and female *D. frontalis* blends (treatment 3) than to either blend alone (treatments 1 and 2). By comparison, significantly more ($P > 0.05$) *I. grandicollis* were attracted to the blend of female *D. terebrans* (treatment 4) than to the blends of male *D. terebrans* (treatment 5) or male plus female *D. terebrans* (treatment 6). The attraction of *I. grandicollis* to the pheromonal blends of both *Dendroctonus* species supports previous reports of the attraction of *I. grandicollis* to frontalin plus *trans*-verbenol (Dixon and Payne 1980), as well as to *D. frontalis*-infested bolts (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Dixon and Payne 1980, Svihra et al. 1980).

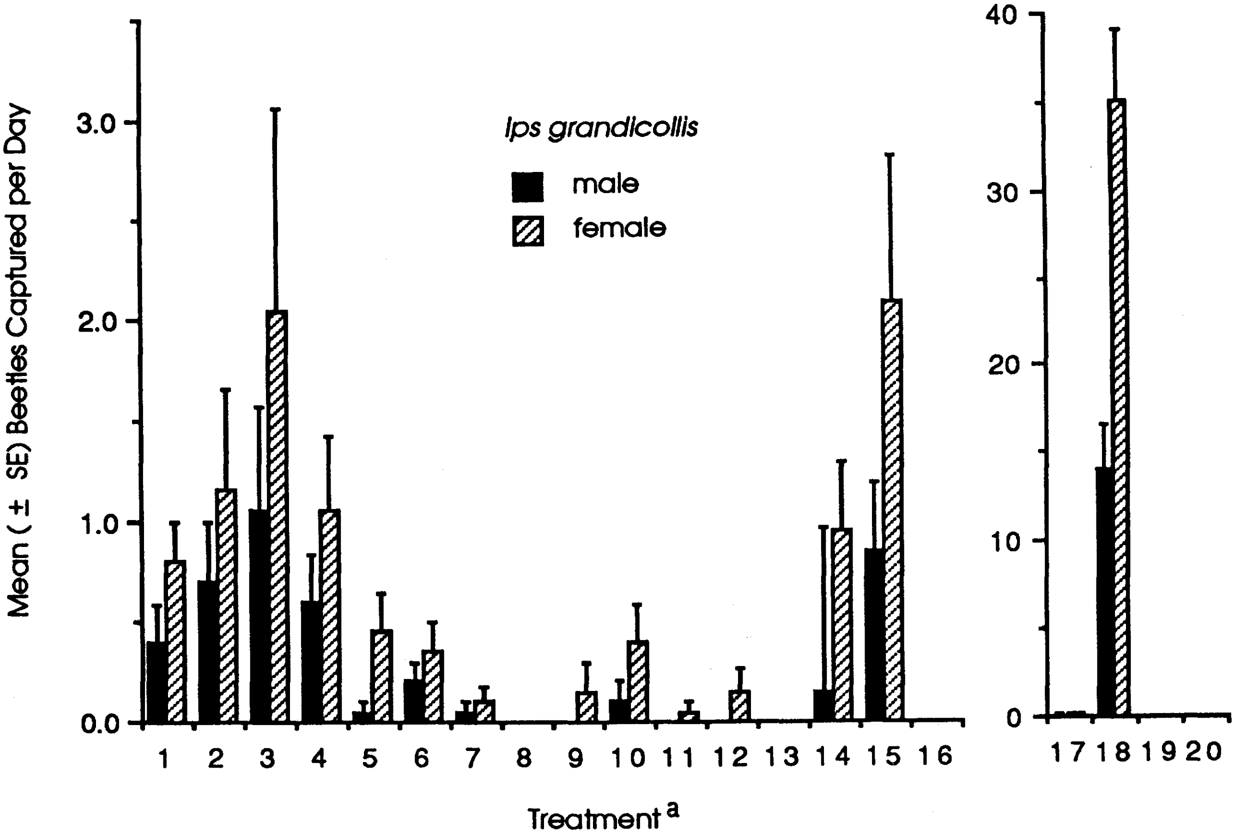

Figure 12. Mean number of *Ips grandicollis* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

As represented by turpentine alone (treatment 19), host odor did not provide an adequate stimulus to attract any of the scolytid species. It should be emphasized, however, that the release rate used was probably far less than that provided by a stressed tree in nature. In addition, the vertical silhouette alone (treatment 20), as provided by the unbaited trap, did not attract any of the five scolytid species. Thus the results verify that response by the beetles to the pheromone-baited traps was probably due to the pheromones and blends and not simply to host odor or to a visual stimulus alone.

CONCLUSIONS AND INDICATIONS

Detection of both *Ips* and *Dendroctonus* pheromonal compounds by the cohabiting species shows a sensory basis for their interspecific olfactory communication and interaction. The fact that differences in both threshold responses and relative numbers of receptors for the various behavioral chemicals do occur suggests differences in specific behavioral roles for each compound.

The field tests showed variation in behavioral response among the species in interspecific olfactory communication. *D. frontalis*, the pioneering species of the group (Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980), apparently does not utilize *Ips* pheromones in host selection. Cross-attraction of *I. calligraphus* to male *I. avulsus*, as of *I. avulsus* to male *I. calligraphus*, was verified. However, given our results and the mixed results of the other reports cited, the attraction of *I. calligraphus* and *I. avulsus* to *I. grandicollis* or *D. frontalis* still remains in question. *I. grandicollis* was the least specific in its responsiveness, displaying the greatest degree of cross-attraction among the cohabiting species.

Although cross-attraction ranged from none for *D. frontalis* in response to the pheromonal blends of *Ips* to extensive for *I. grandicollis*, it is probable that all five species benefit from the olfactory-based behavioral interactions. The interactions are probably most important when population levels are endemic, particularly for the less aggressive species, i.e. *I. grandicollis*, when the joint efforts of the group members are essential for overtaking the defenses of the host trees. Certainly this would increase the probability of the successful colonization of a resistant host by each species.

SUMMARY

Interspecific olfactory response was investigated in the five primary scolytid species of the southern pine bark beetle guild, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). Antennal olfactory response was measured with the electroantennogram and single-cell techniques and showed that each species possesses receptors most sensitive to their own pheromones, but also responsive to the pheromones of the other species. Behavioral responses were measured with field trap catch data and showed that each species was attracted mostly to the pheromonal blend produced by conspecifics. Interspecifically, *D. frontalis* showed no cross-attractancy to *Ips* pheromonal blends, but was attracted to the pheromonal blend of female *D. terebrans*. All three *Ips* species showed some level of cross-attraction as well as attraction to the *Dendroctonus* pheromonal blends. Specifically, *I. calligraphus* was attracted to *I. avulsus* and slightly so to the male *D. terebrans* pheromonal blend. *I. avulsus* was more cross-attractive than *I. calligraphus* and showed attraction to the pheromonal blends of female *D. frontalis*, male and female *D. terebrans*, male *I. calligraphus*, and male *I. grandicollis*. *I. grandicollis* showed the greatest cross-attraction, particularly to the pheromonal blends of *Dendroctonus*.

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USING PHEROMONES IN THE MANAGEMENT OF BARK BEETLE OUTBREAKS

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INTRODUCTION

Identification of aggregation pheromones and field experiments using synthetic components have given scientists a better understanding of the behavior of many bark beetles. They have also yielded more effective weapons with which to control outbreaks of aggressive pest species. Synthetic pheromone components are commercially available for control of many species (Borden 1985) and are used in forestry practice in several areas of the world (Vité and Francke 1985). The pheromone may be used as part of an integrated pest management program: for mass trapping, for monitoring of beetle populations, and for inhibition/disruption of beetle infestation.

During the last 10 years we acquired valuable knowledge about the potential of pheromones for practical use. This paper summarizes some of the experience we have gained in our work with the spruce bark beetle, *Ips typographus*.

THE PHEROMONE SYSTEM OF *IPS TYPOGRAPHUS*

The spruce bark beetle, *I. typographus*, is one of the most aggressive and serious pests of Norway spruce in Eurasia. There are two main reasons for their capacity to attack and kill healthy trees. First, they carry a pathogenic blue-stain fungi that invades the sapwood of the tree, induces water stress, and renders the tree susceptible to colonization by the beetles (Horntvedt et al. 1983). Second, they have developed an effective chemical signal system by which to coordinate the attack and to aggregate in masses on selected trees (Bakke et al. 1977, Schlyter et al. 1987).

When the male beetle initiates the boring in the bark of trees, he produces a pheromone which attracts female beetles and other males. The two major components of the aggregation pheromone are (S) chaos-verbenol and 2-methyl-3-buten-2-ol. Ipsdienol, common in many Ips species, is also present, but seems to play only a minor role. Two components occur when the females have entered the gallery. These are ipsenol and verbenone, which inhibit response to the aggregation pheromone and act as an antiaggregation pheromone (Bakke 1981).

MASS TRAPPING

Mass trapping of bark beetles to suppress the population is a control measure that has been employed in Europe for more than 200 years. Until 1979 the trap used was a mature fresh tree which was felled in spring and left in the forest during the main flight period of the beetle. When the trunk had been colonized by the beetles it was removed from the forest while they were still breeding in the

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BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

bark. After development of the synthetic pheromone and a trapping technology, the trap tree was replaced by the pheromone-baited trap (Bakke et al. 1983, Vité and Francke 1985).

The Epidemic in Scandinavia in 1970-80

Parts of southern Norway and Sweden suffered from an extensive beetle outbreak in the 1970s. In Norway, trees equivalent to 5 million cubic meters of timber were attacked and killed in an area of 140,000 km^2, which is equal to the area of East Germany.

Extensive windthrow and severe summer drought combined to cause the outbreaks (Worrell 1983, Bakke 1983). At the same time, many forest areas contained an abundance of overmature trees susceptible to beetle attack.

Methods of the Control Program

The pheromone of *I. typographus* was identified in a research program conducted to search for methods to control the outbreak. Syntheses for commercial production of the pheromone were developed, and a method was devised by which to use the pheromones as bait in traps. A simple trap was designed to replace the trap trees (Bakke et al. 1983).

In 1979, 600,000 drainpipe traps (Fig. 1) were produced and distributed in the outbreak area in Norway. Guidelines were developed for location of the traps. During 1979, 1980, and 1981 several billion beetles were trapped (Table 1).

It must be emphasized that the use of traps alone was not recommended. Traps must be included in an integrated management program. In Norway several measures, both short-term and long-term, were undertaken during the outbreak period. Government funds were available for support of road construction in areas containing overmature stands and for logging in steep terrains. A forest practices law was amended to prohibit storage of unbarked logs in the forest during summer and to require cleanup after storm damage and logging. Besides the mass trapping, felling and removal of beetle-infested trees comprised the main short-term measure. Trapping was not recommended for saving old stands with extensive beetle infestation or stands severely weakened by drought. Only clear-felling was recommended for such stands (Nou 1979).

The Trap Catches

Average catches per trap varied widely between areas and years. In 1980, 10,000-12,000 beetles were the average catches per trap in districts with extensive beetle damage. Traps located at clearcuts from recent winter had the highest catches. During 1979-81 several billion beetles were trapped (Table 1).

More than 99 percent of the insects caught in the traps were beetles of the genus *I. typographus*, but a few percent of those caught in certain localities were *I. duplicatus* which respond to ipsdienol. The clerids, *Thanasimus formicarius* and *T. femoralis,* are attracted by the pheromone (Bakke and Kvamme 1981) and were caught in some number even when the trap had been constructed to prevent them from entering through the holes. The average number of clerids per trap was 1.6 per thousand *Ips* in 1979 and 1.4 in 1980. A new trap model (1980 model) giving *Thanasimus* possibilities of escape retained only 0.5 clerids per thousand *Ips*.

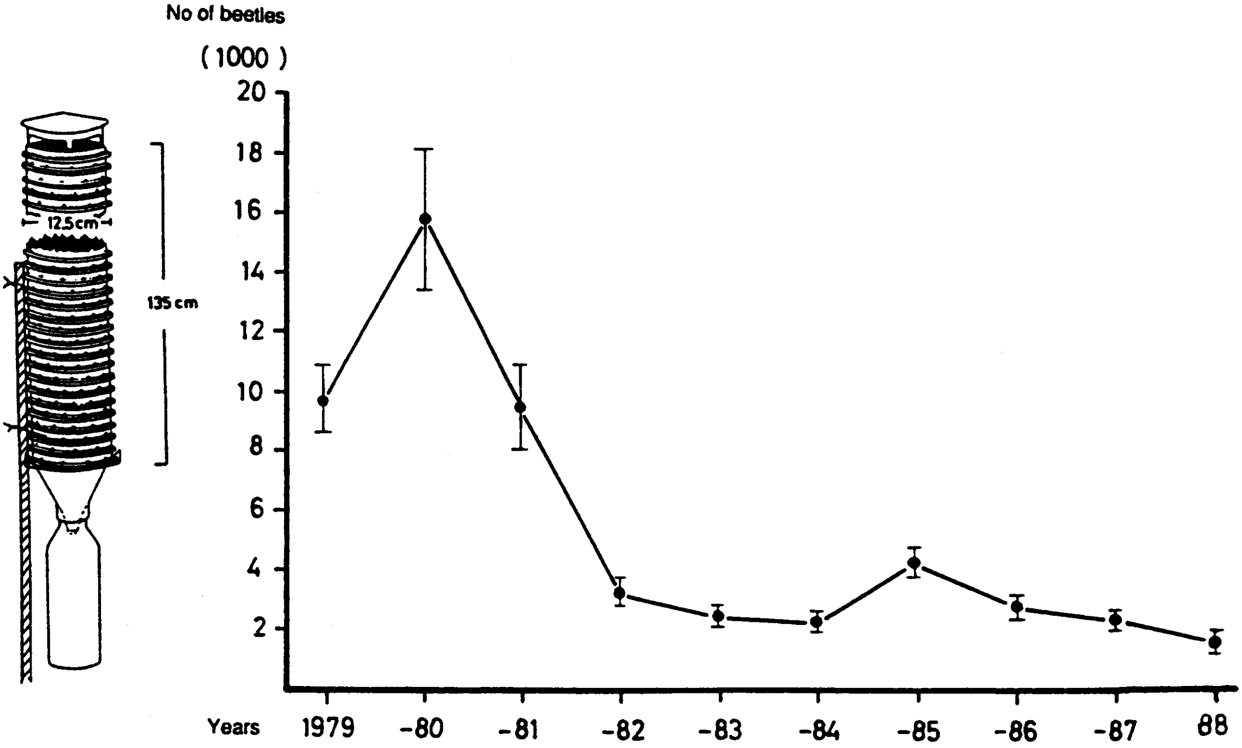

Figure 1. Average catches of *Ips typographus* per trap on fresh clearcuts in districts of southeast Norway during 1979 to 1988. The drainpipe trap is to the left.

Socio-Economic Aspects

A control campaign involving 80-100,000 private forest owners and people employed in forestry, covering the whole spruce area of South Norway and operating on government funds would have to confront problems in the areas of technology, economics, administration, and information dissemination.

Technological Problems

Trapping technology is, of course, an important part of a mass trapping program. The trap model must catch effectively, and pheromone release and composition must be optimal for the trap model. In addition, trap location and trap spacing must be evaluated, and traps must be inexpensive and easy to manage. Later studies (Bakke et al. 1983) have shown that we had good luck with the selection of our trap model, even though it had some weaknesses. Design of the dispenser and composition of the pheromone components had also been successfully estimated (Schlyter et al. 1987).

Economics

During the period from 1978 to 1982 the control program was supported by government funds totaling 90 million Norwegian Kroner, equivalent to 13 million 1988 U.S. dollars. Input from private forest owners came to at least that amount. The government paid 2/3 of the trap costs and about 1.5 U.S. dollars per pheromone dispenser to the producers who had donated them to the project. A rough estimate of the total trapping cost incurred is 6 million U.S. dollars.

Table 1. Number of traps and estimated number of beetles caught in southern Norway in the years 1979-81

Year	Number of traps	Estimated number of trapped beetles
1979	600,000	2,900,000,000
1980	590,000	4,500,000,000
1981	530,000	2,100,000,000

Administration

The Civil Forest Administration was involved in the campaign in the counties and in every municipality. Committees were appointed on every administrative level. The local committee, headed by the district forest officer, coordinated the measures taken; decided on the number of traps each forest owner should deploy, and organized the search for infested trees, often by means of airplanes. The district officer also administered the government grant supporting the measures and provided the information to the local newspapers, television, and radio.

Information

Information about the control program was directed to the general public as well as the forest owners. Information was disseminated by means of leaflets, meetings and conferences, and newspaper articles. The drainpipe trap was used as the symbol of the program and had a great impact on public awareness. Seeing the thousands of beetles trapped in their forest, most forest owners in particular became aware of the hazard of retaining overmature trees.

The general public had to be informed about the pipe traps they would encounter on their hikes in the forest. The function of the traps was explained in newspaper advertising campaigns and on radio and television. The information reached nearly everyone. The beetles even got their own pop song, "Bark-beetle Boogie," which placed on "top of the hits" in Norway for several weeks.

The Decline of the Epidemic

The epidemic began to decline after 1980, and in 1982 it was difficult to find trees killed by the beetle. The decline may have been caused by several factors, probably by a combination of factors (Bakke 1983). Cool and wet summer weather may have restored the resistance of the trees and limited the flight activity of the beetle. Though it is difficult to prove, we believe that the mass trapping campaign also had a significant impact on the beetle population.

For a couple of reasons, the program is not easy to evaluate scientifically. We can estimate the number of trapped beetles, but we are unable to determine the size of the natural population. It is evident from several studies that the beetle disperses over large distances. Traps may be able to attract and catch most of the beetles within a certain area, but new beetles will quickly move in from surrounding areas to fill the vacated space. Actually to reduce the overall population, a larger area must be covered by a trapping program. Our experience further indicates that the most promising results are obtained with a low-density beetle population and in forests which are not too weak.

Today programs using pheromone-baited traps to maintain a low population of *I. typographus* are established in several countries in Central Europe, among them the German Federal Republic, Poland, and Czechoslovakia (Zumr 1987). There, too, traps have replaced trap trees.

MONITORING

Aggressive bark beetles are a threat to the forest only when the population is above a certain threshold. The flying population must be high enough to overcome the resistance of a healthy tree. Knowledge of the population level is therefore of great importance, particularly when external conditions, such as long-lasting drought or stormfelling, favor population increase. Traps baited with pheromones may be useful in monitoring populations and in assessing the risk for damage caused by bark beetle.

Research data for development of a monitoring system for *I. typographus* have been gathered in Scandinavia in recent years. Different sites for deploying pheromone-baited traps have been studied and evaluated. The trapping period required to obtain a good estimate has also been studied (Bakke 1985).

A recently completed Scandinavian collaboration (Weslien et al. 1989) indicates that pheromone-baited traps as well as selected trees baited with pheromones have potential use in assessing the risk for damage caused by *I. typographus*.

The threat of damage to spruce forests in Central Europe as a result of air pollution, intensifies the need to monitor populations of other bark beetles as well (Vité 1984). Germany is using a system which combines monitoring with mass trapping to suppress beetle populations. In Norway, a monitoring system has continued since the great outbreak in the late 1970s. The mean catches per drainpipe traps during the years 1979-88 are given in Fig. 1.

INHIBITION

Pheromone components acting as inhibitors, lowering the attraction to the aggregation pheromone, are known in several bark beetle species. Best known is the MCH from *I. dendroctonus*, which has been applied to windblown trees to prevent beetles from infesting the trunk (Furniss et al. 1977). In addition, pine oil, a by-product derived from pulp mills, shows a semiochemical effect in bark beetle when sprayed on the bark surface of logs and trees (Nijholt 1980).

In *I. typographus* two pheromone components produced from the beetle have shown antiaggregative effect: ipsenol and verbenone. They are also known to inhibit attraction in other bark beetles (Bakke 1981). Combination of the two components produced the best inhibition effect when used together with the aggregation pheromone as bait in traps.

Logs are stored for short or longer periods in the forest, often because in Scandinavia the snow-melting period in spring makes it difficult to use trucks in the forest. To prevent the logs from being infested by bark beetle and used for reproduction, the logs are often sprayed with insecticides. In Norway a field experiment was conducted during a 3-year period to determine whether any of the semiochemicals, when used in controlled release formulation on logs, are able to influence the colonization process of *I. typographus* (Bakke 1987, Schlyter et al. 1989).

All experiments showed that treatments with a combination of verbenone and ipsenol released from laminated structure dispensers significantly reduced the attack density of *I. typographus*, whereas turpentine treatment had no effect on the rate of beetle infestation.

As applied in these experiments, with a rather high dosage of pheromones, antiaggregative semiochemicals may reduce beetle infestation in logs, but do not prevent logs from being attacked. As a consequence of reduction in population density, moreover, the survival rate of the brood may increase due to a more sufficient supply of food for the larvae. This would be very significant because overpopulation is a primary factor in mortality. On the other hand, the ipsenol acts as a kairomone (Bakke and Kvamme 1981) and may attract a larger number of the predator *Thanasimus*, which may eliminate a larger portion of the beetle and its brood.

In my opinion, the pheromone will be an important part of the integrated management of several forest pests in the future.

SUMMARY

Bark beetle pheromone may be used in integrated pest management for mass trapping, monitoring of beetle population, and inhibition/disruption of beetle infestation. This paper reviews our experience in using both the aggregation pheromone and the antiaggregation pheromone for controlling *I. typographus* in Norway. Drainpipe traps baited with synthetic aggregation pheromone components were used for mass trapping as part of an integrated control program during an epidemic. In 1980, 4,500,000,000 beetles were trapped in 590,000 traps distributed in spruce forests in Norway. A monitoring program was developed using traps deployed on recent winter clearcuts. Application of antiaggregation pheromones to spruce logs stored in the forest during summer significantly reduced the attack density of spruce beetles, but the effect was not sufficiently great to make widespread implementation economically feasible.

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EFFECTS OF LARCH DEFENSES ON XYLOPHAGOUS INSECT GUILDS

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INTRODUCTION

One of the best studies of a xylophage consortium is the case of larch insects by Isaev and Girs (1975). In their book, a basic theory was presented about host responses to xylophagous insects injury. According to their concept of "sliding resistance," different trunk-infesting insect species have different reactions to the tree's defenses and invade the tree successively depending on the stage of its decline or dieback. With regard to the general tree status, groups of invaders were identified by the authors: 1) primary species invading living trees whose resistance may increase back to the initial level; 2) secondary species colonizing living trees with fatally disturbed metabolism, and 3) necrophagous species living only in dead trees.

However, owing to its general nature, this classification cannot provide a detailed coverage of all the complexities arising when analyzing the ecological niche of xylophages. In particular, the potential increase in xylophage subcortical penetration rate was related mostly to the defense system of an individual tree without consideration of the environmental conditions (Sukachev 1967, Smagin et al. 1980, Polikarpov et al. 1986).

STAND FACTORS AFFECT XYLOPHAGES

Certain groups of forest types have differential stress resistance and pronounced peculiarities in composition and structure of their xylophagous insect complexes (Yanovsky 1987). Thus, analyzing entomofauna within the framework of forest type classifications allows examination of both the peculiarities of the interaction between host tree and insects and interspecific relationships between insects: within ecologically homogenous insect groups (i.e. xylophages or phyllophages), between different insect groups (e.g. between xylophages and phyllophages) and also between phytophages and entomophages. Specific habitat conditions, plant defensive responses, both composition and structure peculiarities of a given biocenosis, as well as the insect "aggressiveness" determine outbreak probability and insect dispersal. All the above factors influence the rate of decline of individual trees and the total stand, and, thus, indicate the level probability for epidemics by the invading xylophage species (Yanovsky and Korotkov 1984).

Deadwood load and distribution throughout the stand varies with forest type. So, food availability for sparse xylophagous insect populations and their dispersal patterns vary accordingly. At the same time, variations in the forest type response to the insect invasion and, consequently, tree dieback rate are responsible for the xylophage epidemic level.

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INTERACTIONS AMONG XYLOPHAGES

Important also is the detailed analysis of xylophage interspecific relationships, with special regard to the primary infesting species located within a microstation (tree). Isaev and Girs (1975) divided the insect species into two groups based on their potential to overcome host defenses, disregarding the insect population density. Now we know that the aggressiveness of some insects varies with their abundance. Within the primary trunk infesting insect species two groups can be identified: 1) xylophages capable of inhabiting the nonfatally declining trees, regardless of their population density, and 2) xylophages which can invade weakened trees only by means of severe, high density attacks. In the absence of severe stand damage, the first group dominates during the early stages of tree decline. These trees are inaccessible to the species of the second group so long as they remain at low population density.

In case of a nonfatal tree declines, i.e. after surface fires, the species of the first group dominate xylophage complexes. They provide the conditions required for the attack of the second insect group, particularly if population density of the latter is low. This results in a sharp increase in the population density of insects of the second group, which the allows them to independently inhabit resistant trees.

Burned Versus Defoliated Larch Forests

These conclusions are consistent with the results of a study of xylophage outbreaks in the larch forests of middle Siberia, affected by fires (burned areas) and the siberian moth, *Dendrolimus superans sibiricus* Tschetv. In these stands the beetle, *Tetropium gracillicorne* Rtt. and the larch buprestid, *Phaenops guttulata* Gebl. are representative of the primary insect species, capable of inhabiting non-fatally declining trees. On the other hand, the big larch bark beetle, *Ips subelongatus* Motsch., which is notorious for its violent population fluctuations, is incapable of invading trees with only slight metabolic disturbance unless it attacks en masse.

Observations on the invading insect species groups at the early stage of stand decline show in defoliated stands, that the non-fatally declining larch trees are extensively attacked by the buprestids and *Tetropium* beetles that can overcome the host defense system and inhabit the trees with weakly disturbed metabolism (Table 1). Therefore, immediately after hatching, the nutrient status in the phloem is sufficient for larval feeding. The phloem physiological properties responsible for the oxidation processes do not differ noticeably from those of the control (Table 2). However, the free carbohydrate concentration in the phloem, that is vitally important for protein biosynthesis, is insufficient for the larval feeding due to the tree's low photosynthesis level.

The bark beetles only inhabit the most weakened trees (Table 1 and 2). A few small populations of these insects were able to colonize trees with non-fatal metabolic disturbance, but the subsequent larval development was interrupted by pronounced resinosis (Isaev and Girs 1975). The bark beetle's ecological niche consists of slightly weakened larch trees with nonfatal metabolic disturbances. In this period a sharp increase in oxidation processes is observed, but enough carbohydrates are retained in the host phloem for the bark beetle larval feeding.

The rate of stand decline determines the specific composition of the xylophagous insect group. In the burned areas, where the stands are severely damaged by fires, the bark beetles dominate these groups immediately during the year of the fire (Table 1). It is noteworthy, that the trees infested with the bark beetles exhibit all the signs of total decline. The needles of these larches regenerating from dormant buds are pathological (too long and with water excess) and do not contribute much to tree recovery. But short-term physiological imbalance of trees does not allow bark beetle invasion. Under these conditions, hosts in early stages of decline are inhabited by buprestids. However, a lot of dead trees scattered throughout the burned area favor bark beetle buildups (Isaev and Girs 1975). For this

Table 1. Numbers of different xylophagous insects per sq dm of trunk in burned and defoliated larch stands over time

Years after xylophage outbreaks	Mode of tree decline	Attacked part of trunk	Insect population density[1]		
			Phaenops guttulata	*Tetropium gracillicorne*	*Ips subelongatus*
Burned area					
First	Fatal	Base	0.06	0.14	0.36
		Middle	0.02	-	0.86
		Top	-	-	1.04
Second	Fatal	Base	-	0.09	1.09
		Middle	0.01	-	1.29
		Top	0.07	-	0.41
Third	Nonfatal	Base	-	-	3.78
Moth defoliated area					
First	Nonfatal	Base	1.97	2.04	-
		Middle	1.85	1.04	-
		Top	1.36	0.18	-
Second	Fatal	Base	1.97	1.18	0.29
		Middle	2.39	0.15	0.25
		Top	1.77	0.05	0.05
Third	Fatal	Base	0.42	0.45	2.00
		Middle	0.63	0.52	1.52
		Top	0.25	-	0.22
Fourth	Nonfatal	Base	-	-	2.80

[1] Number of larvae (*Tetropium* beetles and buprestids) or galleries (bark beetles) per 1 sq decimeter of trunk.

reason, at the maximum xylophage population level (the second year after outbreak initiation) the primary insect group consists only of this one species (Table 1).

Trunk Temperature Effects

The bark beetle outbreaks are also likely to occur in the stands previously damaged by the phyllophagous insects, but in this case the bark beetles are competitively displaced by the buprestids and *Tetropium* beetles. Invasion and spread of buprestids in the moth-affected larch forests is retarded by the fact that the adults lay eggs on one and the same trunk part. Usually, the eggs are concentrated on the most weakened trunk part, arranged in strips on the southern side where phloem decline is facilitated by warming (Table 3). (See also Bombosch, this volume.)

Increase in phloem surface temperature stimulates the general metabolic activity, which, in case of unstable metabolism, leads to the increase in oxidation and hydrolysis, protein decomposition, and

Table 2. Variations in tree phloem properties associated with invasion by various xylophagous species expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

State of insect colonization	Phloem property: Moisture content (% fwt)		Respiration rate (mg CO2/g)		Reducing capability (ml 0.01 N J/g)		Total sol. carbohydrate (% dwt)		Starch (% dwt)	
	AV	%	AV	%	AV	%	AV	%	AV	%
Phaenops guttulata and *Tetropium gracillicorne*										
Preinvasion	63.6	112	0.40	95	5.2	100	5.2	85	5.8	85
Eggs	61.4	115	0.51	100	6.6	143	5.5	125	4.8	60
Eclosion	63.4	106	0.58	232	4.4	100	6.6	129	4.9	45
Larvae in phloem	31.5	58	0.25	61	1.1	24	2.8	42	4.2	24
Ips subelongatus										
Oviposition	60.5	102	0.84	162	4.0	78	2.2	43	2.5	35

Table 3. Variation in phloem properties on the north and south sides of infested trunks expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

Side of trunk	Phloem properties: Temperature in day time (°C)	Moisture content (% fwt)		Total sol. carbohydrate (% dwt)		Starch (% dwt)	
		AV	%	AV	%	AV	%
North (shaded side)	21.9	53.8	80	7.5	59	3.2	32
South (sunny side)	25.7	48.6	73	3.0	24	1.1	11

decreases in tree defenses. The net result is that host phloem nutrient status is maintained high enough for the buprestid larval development. The phloem on the northern trunk part is wetter and richer in carbohydrates and starch. Here the insect penetration is time-delayed. Trees in similar conditions that fortuitously go uncolonized renew their needle next year and do not thereafter usually suffer from insect attacks. In trees with minimally disturbed metabolism, early subcortical penetration by the larch buprestids and *Tetropium* beetles is considerably interrupted by defensive biochemical and anatomical responses. The first instar larvae attempting to inhabit the phloem and adjacent wood layer are affected by a pronounced resinosis, followed by encapsulation of the larval galleries by the corked phloem cells. (See Herms and Mattson, this volume.) As the larvae grow in size their capsules grow longer and are oriented along the trunk (total length is 0.5 to 0.7 cm). The capsule cavities are filled with resinous woody frass. This slow down the larval development rate, and increases mortality of the larvae in this period of time is up to 70 percent. The period of development of encapsulated buprestids and *Tetropium* larvae is considerably long. If the tree was inhabited late in summer, the larvae are expected to come out of the capsules in June next year. By this time the larvae are 2 to 3 mm long and their most rapid development is observed in July (Table 4). Doubtless, the larval development is most rapid on the warmest (southern) side of the trunk. Here, the larval galleries are wide and meandering as can be seen from the gallery length and area measurements (Table 4). Quite in contrast, on the northern side of the host tree the larval galleries are narrower and run straight up and down.

Due to this vertical direction of the larval galleries, the resin channels on the shaded side of the host plant are less damaged and, therefore, the larval mortality from resinosis is low. After being attacked by the *Tetropium* and buprestid beetles, the target trees exhibit a gradual decrease in resistance induced by the larval development. During the colonizing period and while larvae are encapsulated, the weakened trees do not differ greatly from the healthy ones in their physiological properties (Table 2). After this time the tree decline is obvious from the decrease in crown assimilation capability caused by the declining needle biomass followed by decreases in the phloem carbohydrate. The host plants show the first signs of decline by the time the larval emergence from capsules is over. This can be attributed to the general decrease in host viability manifested by reduced resin flow from the phloem resin channels. This, in turn, allows the larvae to extensively locate the intact zones of the phloem. On the other hand, the phloem destruction caused by the larval galleries leads to wound hyperoxidation which is evident from a sudden increase in respiratory rate, decrease in reduction capability, and gradual exhaustion of assimilant inflow which leads to decrease in carbohydrate concentration. These trees become attractive for the bark beetles. During the period of the young larval feeding, the host phloem suffers from a considerable water shortage.

Table 4. Development of larch buprestid larvae

Development variables	Side of trunk	Date of observation in July						
		4	8	14	17	22	27	31
Length of larvae (mm)	South	5.2	0.7	9.3	12.0	12.7	18.0	21.3
	North	3.8	4.2	4.2	4.7	7.5	9.0	9.0
Length of gallery (cm)	South	1.9	2.9	3.6	4.3	4.5	-*	-*
	North	0.9	1.4	1.5	2.1	2.8	2.8	4.6
Gallery area (cm^2)	South	0.51	1.12	1.99	2.21	3.21	-*	-*
	North	0.17	0.18	0.35	0.67	0.79	0.80	1.47

*Galleries join, making individual measurements impossible

Table 5. Variation in the larch phloem parameters in relation to bark beetle invasion expressed as the actual values (AV) and as a percentage of the "control" host phloem (%)

State of bark beetle colonization	Phloem property									
	Moisture content (% fwt)		Respiration rate (mg CO2/g)		Reducing capability (ml 0.01 N J/g)		Total sol. carbohydrate (% dwt)		Starch (% dwt)	
	AV	%	AV	%	AV	%	AV	%	AV	%
Initial attack	62.5	104	0.40	91	3.8	80	2.2	43	4.9	76
Oviposition	58.4	99	1.08	179	4.2	75	2.4	38	5.2	66
Eggs and larvae	44.1	75	0.52	210	3.0	47	2.1	28	3.7	21
Larvae	50.7	88	0.67	110	5.1	78	2.3	30	3.7	21
Larvae and pupae	42.0	77	0.30	56	1.1	27	2.8	20	3.8	22
Larvae to callow adults	35.0	62	0.32	74	0.6	14	0.3	3	0	0

Bark Beetle Invasion of Trees

The buprestids and the *Tetropium* beetles weaken the tree to the level suitable for the bark beetle survival. Distinguished by its high reproductive potential, that is being capable to produce much more generations per unit time in comparison with other insects, the bark beetle populations rapidly grow, competitively displace the buprestid and *Tetropium* beetles and become the dominant consumer. A significant difference between the bark beetles and other insects of interest lies in the way bark beetles injure the trees at high population density level. Symptoms of the declining host resistance become visible in the period of the bark beetle subcortical penetration and gallery construction. This period is characterized by the phloem hyperoxidation and total carbohydrate decline (Table 5). By the time the galleries are made the phloem tissues appear to be significantly damaged by the bark beetles. Crown isolation from the root system as well as the decrease of downward assimilant flow contribute to the host gradual dieback. During construction of larval galleries, the phloem moisture content, and the carbohydrate and starch concentration are reduced and the phloem turns brown owing to irreversible oxidation of many tissues (Table 5). The adult bark beetles are very capable of overcoming the host defense system, hence, they are largely responsible for the tree's defensive decline. A sharp decrease in the host defenses is observed during the mass larval hatching. At this stage of development the larval mortality is no more than 30 percent. Now the larval growth is no longer interrupted by the phloem defensive response. However, the phloem carbohydrate concentration remains comparatively high providing suitable conditions for the larval feeding and development.

It can be concluded that examination of xylophage group composition at the time of an outbreak allows one to predict the extent of decline both the individual tree and total stand. Sparse populations of the *Tetropium* and buprestid beetles located on resistant trees indicate that reduction of tree defenses below a critical level may allow bark beetle infestation to follow. On the other hand, the subcortical penetration of the low density bark beetle populations predict an ominous future for the stand.

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EFFECTS OF FIR SAWYER BEETLE ON SPATIAL STRUCTURE OF SIBERIAN FIR STANDS

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INTRODUCTION

Insects not only use plants for food and habitat; they also change plant populations by influencing their structure and dynamics. This influence is evidenced in the alteration of the spatial structure of a stand.

The fir sawyer, *Monochamus urussovi* Fisch. (Coleoptera: Cerambycidae), is the most abundant xylophagous insect injuring siberian fir, *Abies sibirica* Ledeb. It dominates both in outbreak and non-outbreak areas. The beetles influence the structure and dynamics of fir stands by damaging tree crowns during adult feeding. At high population density this damage eventually determines the spatial structure of the fir stands.

METHODS

We sampled plots on a western slope in the taiga zone of the Western Sayan mountains, South Siberia, U.S.S.R. In this habitat, siberian fir is a climax species that successfully reproduces under its own canopy.

To estimate the spatial pattern of fir stands, we used two sample plots (1 and 1.5 ha), with 1,000 and 2,000 fir trees, respectively. The first plot was an all-aged fir stand with an age distribution described by a rather smooth, inverse J-shaped curve. The second plot was an uneven-aged fir stand with a bimodal curve of age distribution. The first plot was inhabited by sparse populations of *M. urussovi* and the second by a very dense population.

We obtained coordinates of all fir trunks within the plots as well as their parameters and used the radial distribution function to interpret the data statistically. We used a version of the technique and computer programs modified by Dr. O.P. Sekretenko (Buzykin et al. 1985). Radial function of distribution G(r) characterizes probability in order to find a point at a distance from r to r + dr away from a randomly chosen point on a plot map. A simple modification of G(r) allows us to study mutual arrangement of trees classified into two groups. This technique is known as partial radial distribution function. This function characterizes the probability of detecting an object of one class at a distance from r to r + dr away from a randomly chosen object of the other class.

We have obtained the partial radial function of distribution of 40- to 60-year-old fir trees in relation to dead, standing trees damaged by the fir sawyer and vigorous trees of the crown layer. The radial distribution function of the young trees over the plots has also been calculated.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

RESULTS AND DISCUSSION

To date no direct observations have been made of the behavior of adult fir sawyers during colonization of a forest stand. We have assumed that adults normally fly a short distance away from the place of emergence.

In the stands we examined, the fir sawyer damages mature, but not young trees. This critical feature of host selection allows a self-replacement process in the fir population. The pattern of establishment and growth of seedlings and the mortality of mature trees determine the structure of a fir stand. In the all-aged fir population a low asynchronous mortality is observed. Under these conditions, the micropopulations of the sawyer colonizing the dying trees appear to be spatially separated. Hence tree crowns neighboring the infested ones are damaged rather lightly and the trees are not weakened sufficiently to allow for egg laying. Since the fir sawyer attacks only the naturally dying trees or occasionally those weakened by other factors, sparse populations of fir sawyer are maintained.

In the second fir stand, old trees predominate, which results in increased mortality of mature fir trees and a higher density of fir sawyer population. There is some evidence of beetle concentration on weakened trees and of localized insect distribution for adult feeding and oviposition (Vetrova 1986, 1987). Intensive crown damage (5 to 9 grazing wounds per 1 m of first-order branches) resulted in irreversible tree weakening. The damaged trees were then attacked by ovipositing females. High colonization density (up to 7 eggs per 1 sq dm) is observed. We believe that beetle activity explains the patchy distribution of infested fir trees that we observed (Fig. 1).

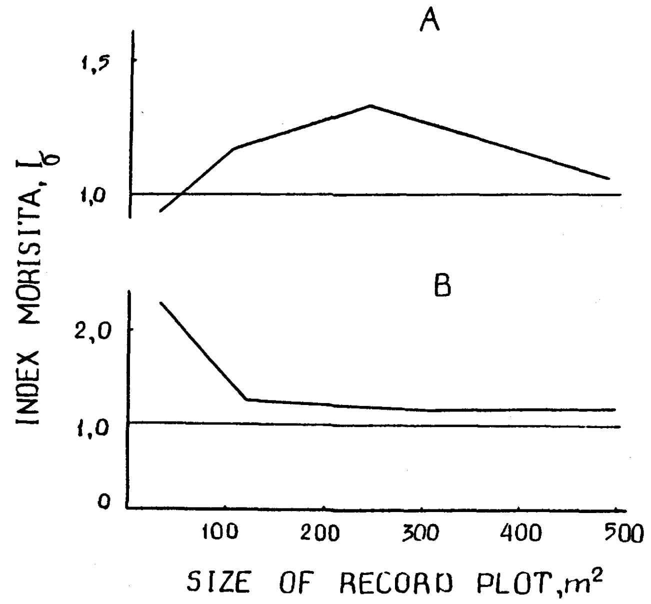

Figure 1. Spatial distribution of infested trees on the sample plots. $I_\delta = q\left[\frac{\Sigma n_i\,(n_i - 1)}{N\,(N - 1)}\right]$, where q = number of record plots, n_i = number of trees on a record plot, N = number of all trees on a sample plot, A and B = habitats of the beetle populations (A = dense population, B = sparse one).

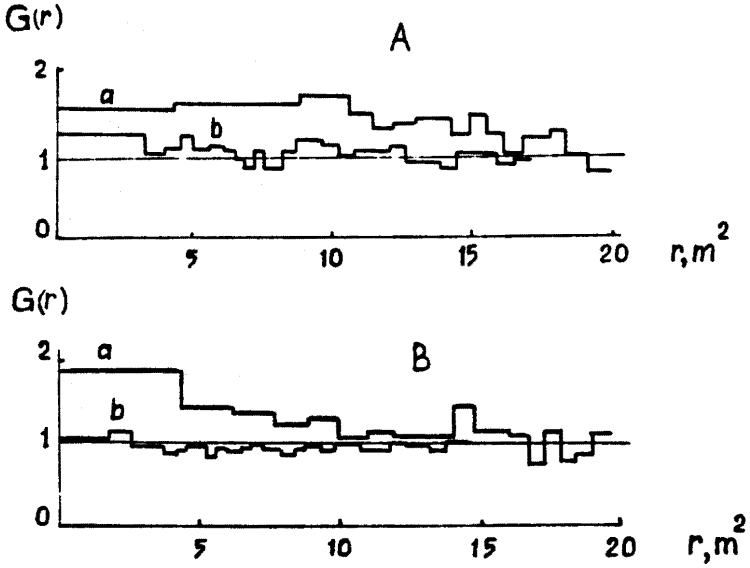

Figure 2. Spatial distribution of young fir trees in relation to standing dead trees (a) and undamaged old ones (b). G (r) - radial function of distribution (see text), r - radius of a record plot, A and B - quantities shown in Fig. 1.

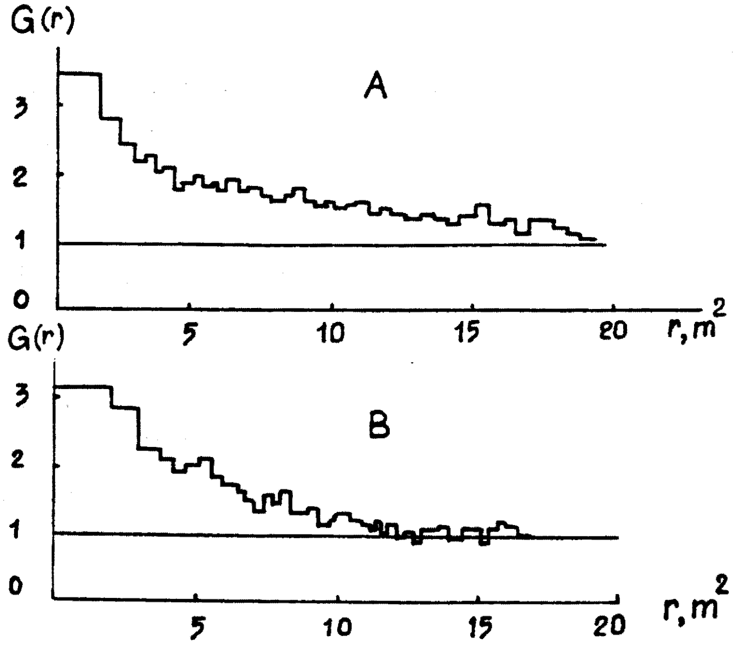

Figure 3. Histograms of radial function of distribution of young fir trees. G(r) - radial function of distribution (see text); other symbol codes as in Figs. 1 and 2.

A relation between the distribution of young (40- to 60-year-old) trees and standing dead trees exists such that the partial radial function of distribution shows a positive correlation in relative mutual arrangement of these two groups (Fig. 2). If so, we should expect different parameters of spatial distribution of young fir trees in the stands we examined. In fact, we observed more clustered distribution of young trees in the fir stand of the second type, as can be shown in Fig. 3.

In the habitat of the sparse sawyer population, the tree mortality pattern of mature trees results in rather small patches of young trees (not more than 50 sq m). Large patches of dying trees occur when the fir sawyer population are high and consequently cause larger patches of young tree (up to 200 sq m).

From the reports of other authors on the ecology of *M. urussovi*, it is clear that the case of outbreak populations of the beetle sharply differs from the above (Isaev et al. 1985, 1988). Usually, outbreak populations cause a constantly high mortality rate of mature trees. Spatial dynamics of fir stand damage look like the spreading of a single wave, comparable sometimes to that of fire.

CONCLUSION

M. urussovi F. is an important factor in the spatial and age dynamics of *A. sibirica* stands. Sparse beetle populations do not disturb the asynchronous, all-aged pattern of fir stand structure and do not prevent the fir population from achieving stability. On the other hand, high-density populations of the fir sawyer, accelerate the mortality rate of mature trees, giving rise to relatively widespread, local synchronization of fir tree development and decrease the stability of the whole system.

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FIR SAWYER BEETLE-SIBERIAN FIR INTERACTION MODELING: RESISTANCE OF FIR STANDS TO INSECT OUTBREAKS

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INTRODUCTION

Entomological monitoring is part of a total ecological monitoring system. Its purpose is the identification, prognosis, and estimation of forest ecosystem impacts induced by insects. The entomological monitoring of a forest is based on a clear understanding of the role played by insects in forest ecosystems. The patterns of insect population dynamics in space and time have to be discovered. Mathematical models can be used to make a prognosis and determine the components and parameters of a given system.

SAWYER BEETLE BIOLOGY

After monitoring fir forests in the northeastern part of the U.S.S.R., we present here a mathematical model describing an outbreak of *Monochamus urussovi* Fisch. (Cerambycidae: Coleoptera). It is known that food availability is the major factor determining population density of this sawyer beetle and other xylophages. Sawyer beetles generally colonize only weak and dying trees, where the larvae of this species develop. The adult insects feed in the crowns on the thin bark of branches, and in so doing causes branches to dry out. When the feeding damage is considerable, the tree weakens and becomes suitable for oviposition and larval feeding. In a resistant forest ecosystem, the variations in sawyer beetle populations are determined by the variations in availability of weakened trees for infestation. Population density is regulated by the negative feedback principle. The population was in a stable state at the time of our study. During a sawyer beetle outbreak the high beetle numbers decrease the resistance of normally vigorous trees, and this positive feedback results in expansion of the outbreak area. If the process of forest destruction is stabilizing, the sawyer beetle population achieves a hyperstable state.

MODELING BEETLE-STAND INTERACTIONS

Our simulation model of the "stand-beetle" system takes into account patterns of interaction between sawyer beetles and separate fir trees at different stages of damage. The system variables are: number of imagos (N), food supply (F) for imago, and food supply for larvae (D). A system of three discrete equations describes the interaction of insects with separate trees. The beetles colonize the most attractive trees surrounding the one from which they have emerged. The attractiveness of a tree is a function of the extent of damage to the tree by the beetles and is determined from the

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experimental data. The parameters of the system are 1) the dimensions and condition of the tree, 2) the time when the tree is suitable as a food resource, 3) survival during ontogenesis, 4) fecundity, 5) sex ratio, 6) time of pre-imago development, and 7) migration characteristics.

The model is solved through a set of computer programs. Simulation experiments allow us to study the dynamics of a system in space and time. The system may be in one of two states: stable or hyperstable. Transition from one state to another is related to the transition of the parameter values from below to over threshold values. We have shown that the stable state of a system is achieved as a result of natural random dying of trees. The hyperstable state takes on the form of running waves of sawyer beetle densities and food resources. Threshold values exist for the initial imago density, annual rate of food consumption per one beetle (Ro), initial food resources, and some others. Crossing of a threshold transforms a system from a stable state into a hyperstable one.

We have found that a metastable state can occur only in stands with a certain defined structure. A tree is suitable for colonizing when the ratio of damage by beetles to the crown during adult feeding is greater than a critical ratio. This critical ratio depends on the values of N, F, and Ro. The greater the ratio between imago density and food supply in the crown, the greater the probability of positive feedback in the system, and, consequently, of an outbreak.

In the hyperstable state, the number of emerged imago at some selected part of the forest is determined by the total identifiable food supply for larvae. This number was obtained from the experimental data on the relationship between the number of emerging imagos and tree diameter (d) and is equal to $\sum_{i=1}^{n} k_i(d)$, where $k_i(d)$ is the number of imago emerging from the tree with diameter, d, and n is the number of trees in the given part of the forest. The food supply for imago in the same part of the forest is equal to $\sum_{i=1}^{n} F_i(d,P)$, where F(d,P) is the food supply in the crown of a tree with diameter, d, and P is the stand density. We have introduced the parameter, $\eta = \Sigma k_i / \Sigma F_i$, to characterize fir stand resistance to sawyer beetle damage. Classifications of stable and unstable stands are made using this parameter. Increase in the mean diameter and density of a stand indicates an increase in the probability of an outbreak.

CONIFER DEFENSES AND XYLOPHAGOUS INSECTS

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INTRODUCTION

The resistance of woody plants to phytophage damage consists of a universal system of mechanisms: 1) repellent chemicals, 2) defensive reactions both mechanical and chemical, 3) retention of viability under disturbed metabolism and low biomass accumulation, and 4) recuperative capacity.

Siberian coniferous tree species, with the exception of *Larix*, are less resistant to phytophage damage than deciduous ones. Evergreen conifers evolved toward constitutive antibiosis by improving their chemical mechanisms of defense, i.e. terpenoid repellents and toxins. In deciduous species, there was evolution of defenses in the direction of an increase in tolerance and recovery (especially after damage or loss of assimilation organs). The universality of the protective mechanisms of woody plants is manifested in the nonspecificity and the relative uniformity of their responses to the different agents of injury (biotic, chemical, or mechanical).

We have tried to correlate the main stages of tree decline with tree metabolic and resistance changes (Fig. 1). The number of eliciting damage sources could be extended to include drought or disturbances in soil conditions, but the five categories of tree conditions shown in Fig. 1 were determined to be adequately representative of the processes involved.

STAGES OF TREE DECLINE

Each successive stage of decline in tree resistance is characterized by certain biochemical transformations. During the first stages of injury, under excited but not reduced metabolism, the levels of resins, a number of mono- and sesquiterpene hydrocarbons, quinic and shikimic acids, polyphenols, tannins, some amino acids (e.g. proline), increase in the inner bark. For a while, the increase in these substances stimulates the protective system to a level exceeding its initial level. Even the most aggressive xylophages fail to colonize such trees.

The prolonged defensive responses result in a decrease in biomass synthesis and hence in insufficient repair of the photosynthesizing, conducting, and storage systems. In such a weakened tree with reduced metabolism, the synthesis of protective toxins begins to decrease. In the majority of cases, a decrease of delta-3-carene and an increase of α-pinene takes place. The diminution of the resin "barrier" in conifers colonized by xylophages can be accounted for mainly by the overall content of resinous substances in the inner bark and the involvement of their neutral fraction. The concentrations of specific toxic components of the essential oils are also significant.

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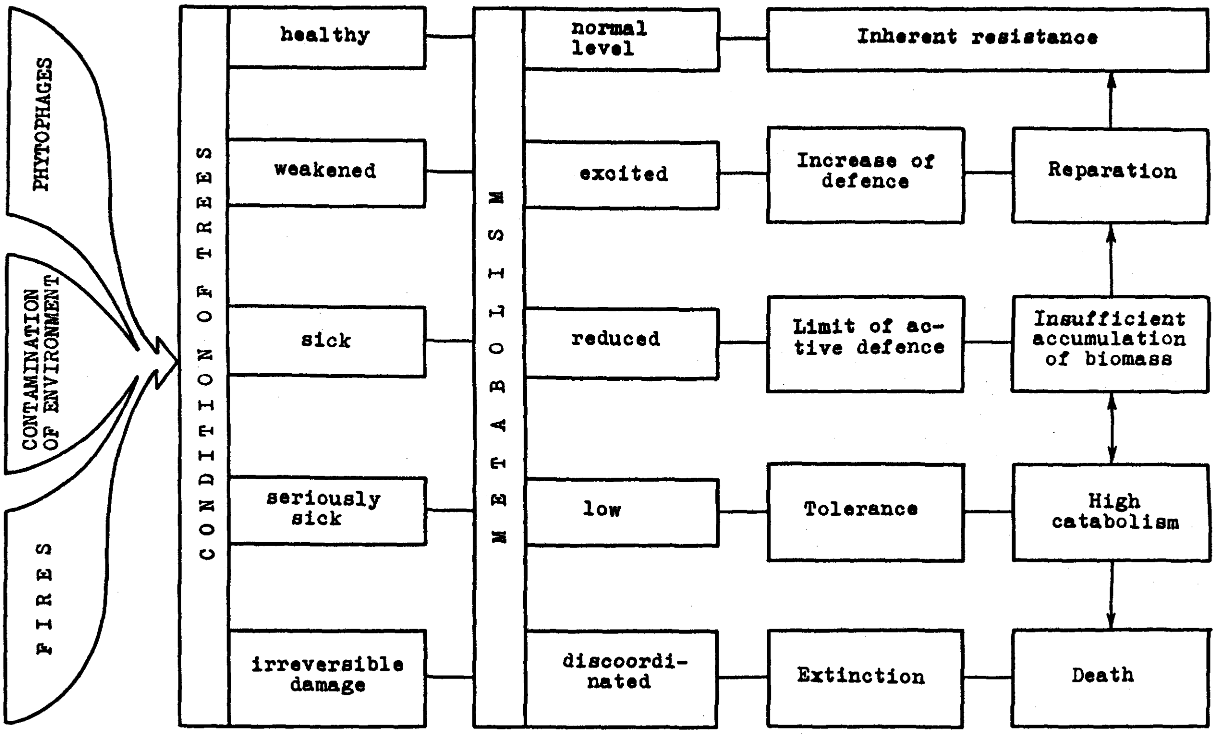

Figure 1. Correlation of tree decline stages with changes in tree metabolism and resistance.

The severely weakened tree is accessible to attack both by aggressive xylophage species and by species otherwise susceptible to its defenses (mainly conifer oligophages). In many cases, this stage of tree damage culminates in irreversible disturbance of the tree's metabolic processes without any additional damage by insects to the trunk tissue. This state of irreversible damage is characterized by a very low level of resins and resin activity. Larch, pine, and fir trees become nonviable when their resin level has fallen to 1 to 2 percent, 3 to 4 percent, and 4 to 5 percent, respectively.

ATTRACTION OF SOME SCOLYTIDS AND ASSOCIATED BEETLES TO THE HOST VOLATILES α-PINENE AND ETHANOL

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INTRODUCTION

Several scolytid species are known to use host volatiles such as monoterpenes and the degradation product, ethanol, when searching for suitable host material. The release rates of terpenes and ethanol and the proportions in which they are released can be expected to differ depending on the breeding substrate preferences of the various scolytid species.

The aim of this study was to compare the attraction of various scolytid species and associated beetles to combinations of α-pinene and ethanol in proportions of approximately 1:1 and 1:10 when released at three different rates. α-Pinene was chosen because it is one of the major monoterpenes in both Scots pine, *Pinus sylvestris* L., and Norway spruce, *Picea abies* (L.) Karst., the two dominant conifers in Scandinavia. Ethanol was chosen because it is one of the major degradation volatiles which are produced as a result of deterioration processes in dead or dying trees. Both substances have previously been demonstrated to attract several wood- and bark-living beetle species.

EXPERIMENTAL METHODS

The attraction of beetles to the different compounds or combinations of compounds was estimated using baited flight-barrier traps (40 x 40 cm transparent plastic sheets). The chemicals used were (-)-α-pinene (Fluka 97 percent) and 95 percent ethanol (5 percent water). The substances were released at different rates from polyethylene vials with different-sized openings. After combinations of α-pinene and ethanol had been tested, the two substances were released from separate vials. To minimize release of oxidized substances during the experiment, new vials containing fresh compounds were exchanged for old ones on each day of the experiment. A randomized block experimental design was used in the arrangement of the experiment. There were 10 blocks, and each block consisted of 14 treatments (traps). The following types of treatments were used: unbaited control, three release rates of α-pinene (0.1, 1, 10 mg/hr), four release rates of ethanol (0.1, 1, 10, 130 mg/hr), and the 1:1 and 1:10 combinations of α-pinene and ethanol at the three α-pinene release rates.

RESULTS

With the exception of *Anisandrus dispar* (F.), all scolytid species involved in the study breed in conifers. *A. dispar*, which breeds in dead or dying trees of several hardwood species, was the only species that was repelled by the conifer monoterpene, α-pinene. *A. dispar* was strongly attracted to ethanol alone.

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In contrast to the other scolytids in this study, *Tomicus piniperda* (L.) generally breeds in relatively fresh material, e.g. newly windbroken or windthrown trees and winter- or spring-cut logs. Since such material has only just begun to deteriorate, the release of ethanol should be rather low, while high amounts of terpenes may be released from resin exuding from damaged parts. Accordingly, *T. piniperda* was the species most strongly attracted by α-pinene alone. Ethanol also attracted this species, but to a much lesser degree than α-pinene. *T. piniperda* was synergistically attracted to combinations of α-pinene and ethanol at the two lowest release rates of α-pinene. At the highest release rate of α-pinene, the combinations caught lower numbers of *T. piniperda* than did α-pinene. Evidently, attraction cannot be increased further by adding ethanol to α-pinene at this high release rate.

The scolytids *Hylurgops palliatus* (Gyll.) and *Trypodendron lineatum* (Oliv.) generally reproduce in dead or dying trees. They prefer logs cut during autumn of the previous year over newly cut logs. This type of stored breeding material may release relatively high amounts of ethanol produced in deteriorating tree tissue, while monoterpenes are probably released in lower amounts compared with the amounts released from newly felled or broken trees. As expected, neither *H. palliatus* nor *T. lineatum* was attracted as strongly to α-pinene alone as was *T. piniperda*. The ambrosia beetle *T. lineatum* was not attracted at all by α-pinene, but was strongly attracted by ethanol which exerted a weaker attraction on *H. palliatus*. Both species were synergistically attracted to combinations of α-pinene and ethanol. The synergism was strongest when the release rate of ethanol was 10 times higher than that of α-pinene.

Adults of the clerid *Thanasimus formicarius* (L.) prey on adults of several species of bark beetles, and their larvae feed on bark beetle progeny. The wide range of prey species, which in their turn are attracted to different kinds of breeding material, may explain the fact that *T. formicarius* was as strongly attracted to α-pinene alone as to combinations of α-pinene and ethanol.

The nitidulid beetles *Glischrochilus quadripunctatus* (L.) and *Epuraea* spp. were significantly attracted to α-pinene and ethanol alone, but much higher numbers of beetles of these species were attracted to the combinations, especially when the ethanol was released at a higher rate than the α-pinene. *G. quadripunctatus* and *Epuraea* spp. are species associated with bark- and wood-living beetles. Adults and the progeny of these species inhabit scolytid galleries. In this kind of substrate, deterioration processes should result in a gradual increase in the production of ethanol, released together with host terpenes. This may explain the strong synergistic effect of combinations of α-pinene and ethanol on attraction in these species.

CONCLUSIONS

The present study demonstrates great differences between beetle species in their response to α-pinene, ethanol, and combinations of the two. These probably reflect the dissimilarities in the release of volatiles among the various types of breeding material to which the different species are adapted. Both the absolute release rates and the ratios at which the two substances were released influenced the response of the beetles to the combinations.

A more detailed presentation of the experiments and the results is given in Schroeder (1988) and Schroeder and Lindelöw (1989).

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INFLUENCE OF PREDATORS AND PARISITOIDS ON BARK BEETLE PRODUCTIVITY

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In an earlier field experiment, natural enemies of the bark beetle, *Ips typographus* (L.) were estimated to have reduced bark beetle productivity by more than 80 percent. To test this hypothesis, spruce logs (*Picea abies*) were placed in the forest in the spring, prior to commencement of flight by *I. typographus*. The logs were screened at different times following onset of bark beetle attack. The screens prevented further colonization by bark beetles and associated insects. The insects were subsequently collected as they emerged from the logs the following autumn or the following spring. The treatments used were as follows:

C = Control, screening prior to attack, bark beetles released on logs under the screen
E.S. = Early screening, 1 week after first bark beetle attack
I.S. = Intermediate screening, 4 weeks after first attack
L.S. = Late screening, 8 weeks after first attack.

The earlier the screening was done, the more bark beetles emerged from the logs. The mean number of juvenile imagos of *I. typographus* emerging was 2800/m^2 from the control logs, 2300/m^2 from the E.S. logs, 1200/m^2 from the I.S. logs, and only 460/m^2 from the L.S. logs. Mean attack densities were similar for all treatments: 230-240 nuptial chambers/m^2. Therefore, the differences in bark beetle emergence between the treatments cannot be explained by varying degrees of intraspecific competition.

Virtually no predators and parasitoids emerged from the control logs and very few from the E.S. logs. Overall, the later the screening was done, the more predators and parasitoids emerged.

The most important predator was *Medetera* spp. (Diptera: Dolichopodidae), which emerged at a mean rate of about 170 imagos/m^2 from both I.S. and L.S. logs. The most important parasitoids were *Roptrocerus* spp. and *Rhopalicus* spp. (Hymenoptera: Pteromalidae), which together emerged at a mean rate of about 50 imagos/m^2 from the I.S. logs and about 340 imagos/m^2 from the L.S. logs.

Other insects which emerged were *Thanasimus* spp. (Coleoptera: Cleridae), eight larvae/m^2 emerging from I.S. logs and 18 larvae/m^2 from L.S. logs; small staphilinid larvae--mostly *Phloeonomus* spp. and *Placusa* spp.--(Coleoptera: Staphilinidae)--60 larvae/m^2 emerging from I.S. logs and 150 larvae/m^2 from L.S. logs; and *Lonchaea* spp. (Diptera: Lonchaeidae), 55 imagos/m^2 emerging from L.S. logs.

In contrast to other insects emerging, *Epuraea* spp. (Coleoptera: Nitidulidae) were abundant in E.S. logs, about 380 larvae/m^2, but scarce in logs screened later. This may indicate that late-arriving insects preyed also on *Epuraea* larvae.

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SEASONAL AND SPATIAL CHANGES IN THE STRUCTURE OF THE SUBCORTICAL INSECT COMMUNITY IN PINE FORESTS

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INTRODUCTION

More than 30 species of beetles have been identified/documented as pine borers in Japan, the majority of them belonging to the Curculionidae, Cerambycidae, and Scolytidae. The density of their populations is controlled primarily by food supply. Although most of them are secondary pests which cannot attack healthy trees, an epidemic of pine wilt disease caused by the pine wood nematode, *Bursaphelenchus xylophilus*, has guaranteed them a continuously sufficient food supply. This paper discusses the results of an experiment to study seasonal and spatial changes in the structure of the subcortical insect community in pine forests.

EXPERIMENTAL METHODS

The study was conducted in pine forests along the ridge of a group of hills extending 8 km inland from the seashore (Fig. 1). Traps made of black vinyl chloride and baited with α-pinene and ethyl alcohol were used to attract flying adult beetles. Eight traps were set up in 1985 and seven traps were added the following year. The traps were placed 1.5 m above ground to facilitate evaporation of the attractants, α-pinene and ethyl alcohol. the dominant species of pine in the area under study shifts from *Pinus thunbergii* in the coastal region to *P. densiflora* in the inland area.

RESULTS AND DISCUSSION

Fauna

More than 1,300 specimens of Cerambycid beetles were captured during three seasons. They were classified into 36 species and 28 genera. The dominant three species, *Monochamus alternatus*, *Spondylis buprestoides*, and *Arhopalus coreanus*, accounted for about 65 percent of the total catch.

Weevils were classified into 59 species and 42 genera belonging to four families, Curculionidae, Rhynchophoridae, Anthribidae, and Apionidae. Fifteen species, representing 95 percent of the total catch, can attack pine trees (Shikoku Branch Gov. For. Exp. Stn. 1962). About 85 percent of these specimens belonged to the genus *Shirahoshizo*, which includes *Sh. insidiosus*, *Sh. pini*, and *Sh. rufescens*. The ratio among the number of these three species was 53:28:19.

Scolytidae and Platypodidae were classified into 52 species and 14 genera. About one half of them (14 out of 29 identified species) belonged to the group of ambrosia beetles. Eleven species can

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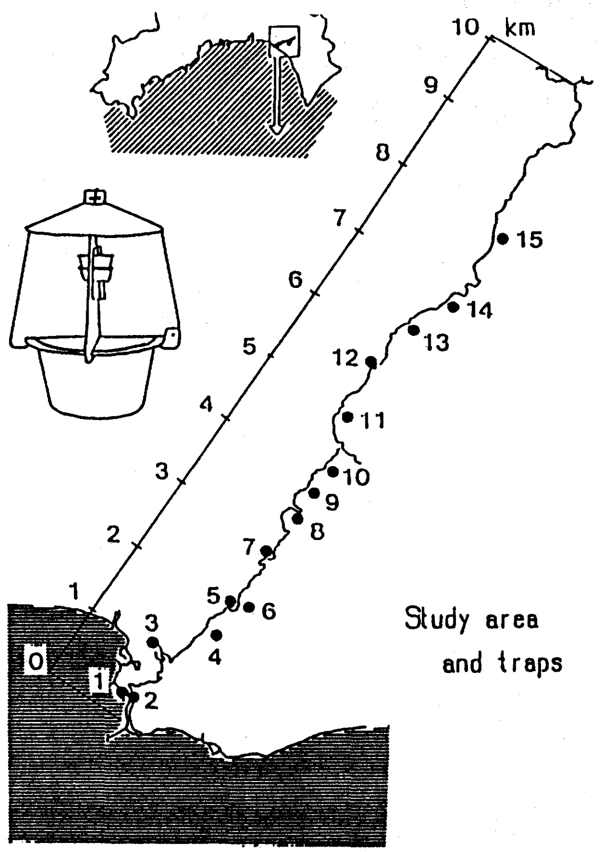

Figure 1. Trap and trapping sites along an 8 km ridge.

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feed on pine trees (Yasunaga 1964, Nobuchi 1966, Hayashi et al. 1984). *Taenioglyptes fulvus*, *Tomicus piniperda*, and *Xylosandrus crassiusculus* were the main pests and they accounted for 89 percent of the total catch.

Although α-pinene is the principal attractant for *M. alternatus*, almost all other species were attracted to α-pinene. Thus α-pinene appears to be an effective tool for investigating the subcortical insect community.

Changes in Abundance

Temporal and spatial niche segregations were observed among the dominant species of the three groups--the cerambycids, the weevils, and the scolytids.

Seasonal Changes

In the cerambycid community, *M. alternatus* and *Sp. buprestoides* were the first to commence flight (Fig. 2A). As the flight period of *Sp. buprestoides* was not long, the ratio of this species decreased in August, as that of *A. coreanus* increased. In September, *A. coreanus* amounted to about 60 percent of the total catch.

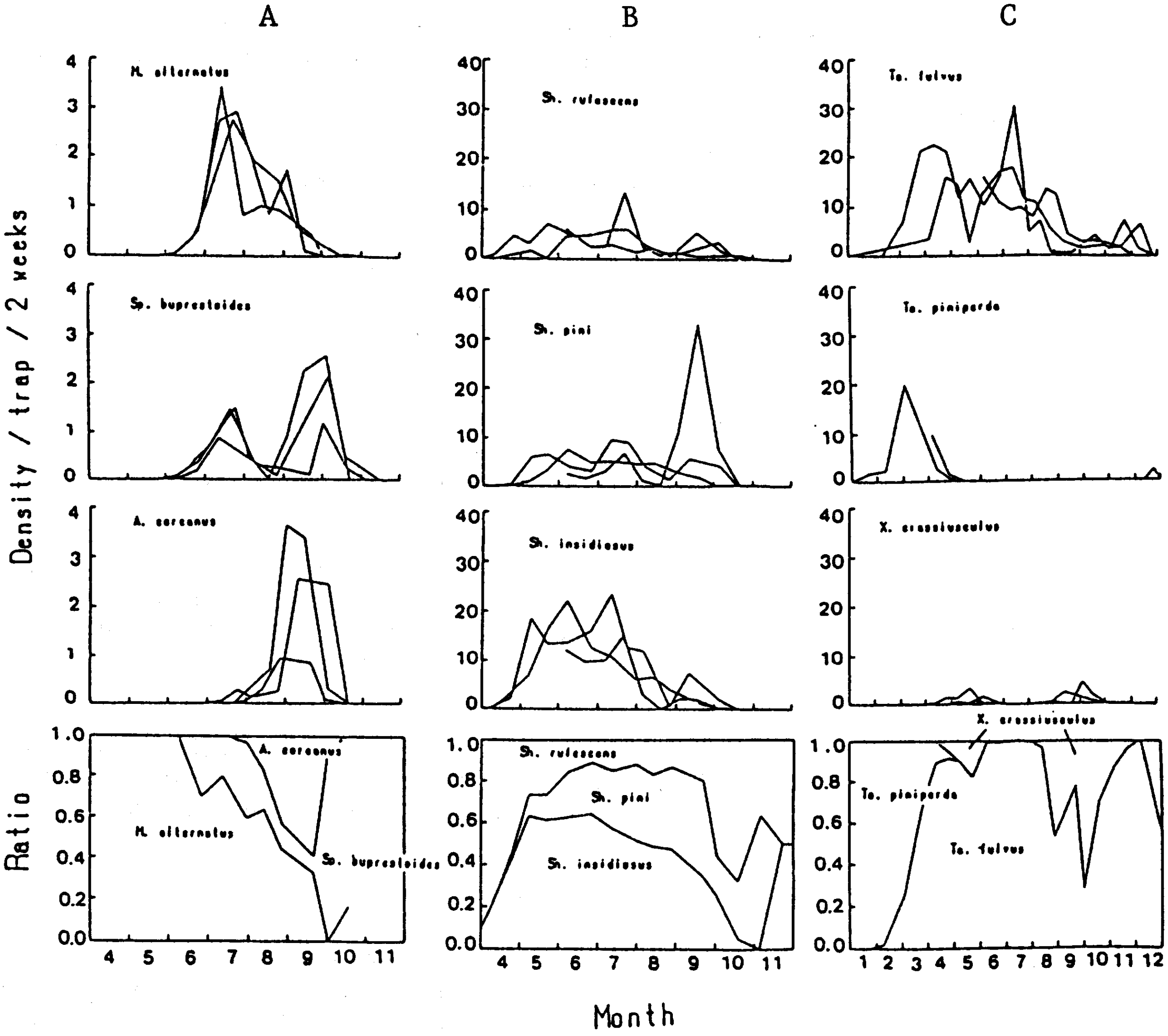

Figure 2. Seasonal trapping density (upper three diagrams in each column) and relative proportion of catch (lower diagram in each column) in three separate years for (A) the cerambycids: *Monochamus alternatus*, *Spondylis buprestoides*, and *Arhopalus coreanus*, (B) the weevils: *Shirahoshizo rufescens*, *S. pini*, and *S. insidiosus*, and (C) the scolytids: *Taenioglyptis fulvus*, *Tomicus piniperda*, and *Xylosandrus crassiusculus*.

Sh. rufescens was the first species to appear in the spring (Fig. 2B). The main season for *Sh. insidiosus* extended from May to July and showed several peaks during the flight period.

Ta. fulvus was attracted to the α-pinene traps throughout the year (Fig. 2C). This species was able to repeat one or two generations under field conditions (Oda 1970). *To. piniperda* characteristically appeared in early spring, showing peaks from March to April. *X. crassiusculus* showed two peaks, one from May to June and a second from September to October.

Local Changes

The distribution of *M. alternatus* was concentrated in an area between 1 and 3 km from the seashore, and that of *A. coreanus* in the inland portion of the ridge. *Sp. buprestoides* appeared both in coastal and inland areas.

The number of *Sh. pini* increased with the distance from the seashore and attained maximal numbers at a point 6 to 8 km inland. Neither *Sh. insidiosus* nor *Sh. rufescens* showed such a regular/uniform/consistent increase.

In the coastal region, *Ta. fulvus* was the dominant scolytid species. The ratio of *Ta. fulvus* exceeded 95 percent at the seashore, and that of *To. piniperda* increased with distance from the seashore. The main distribution area of *X. crassiusculus* was 3 to 4 km from the seashore.

Community Structure

By the seasonal changes in diversity index (H'), local differences in community structure were analyzed.

For the cerambycid beetle community, the study area was divided into the coastal portion and the inland portion at a point about 4 km from the seashore. For the weevil community, traps were divided into two groups by a borderline drawn at a point 2 to 3 km from the seashore. Traps were also grouped into two clusters for the scolytid beetle community and the boundary between the two groups was drawn at a point 3 to 4 km from the seashore.

Points where the community structure of subcortical insects changed were found to overlap with alterations in elements of the pine stand structure such as tree height and species composition. Thus the structure of pine forests appears to affect the community structures of subcortical insects.

SUMMARY

In Japanese pine forests, 36, 59 and 52 species of cerambycid beetles, weevils, and scolytid beetles, respectively, were attracted to/by traps baited with α-pinene and ethyl alcohol over a period of 3 years. For each group of insects, seasonal and spatial changes of dominant species were investigated.

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Twenty-five full-length papers and 19 poster papers on the interactions of different forest insect guilds with their host plants are presented in this proceedings, which is the result of an International Union of Forestry Research Organization Symposium that took place in Abakan, Siberia, U.S.S.R. in August 1989.

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