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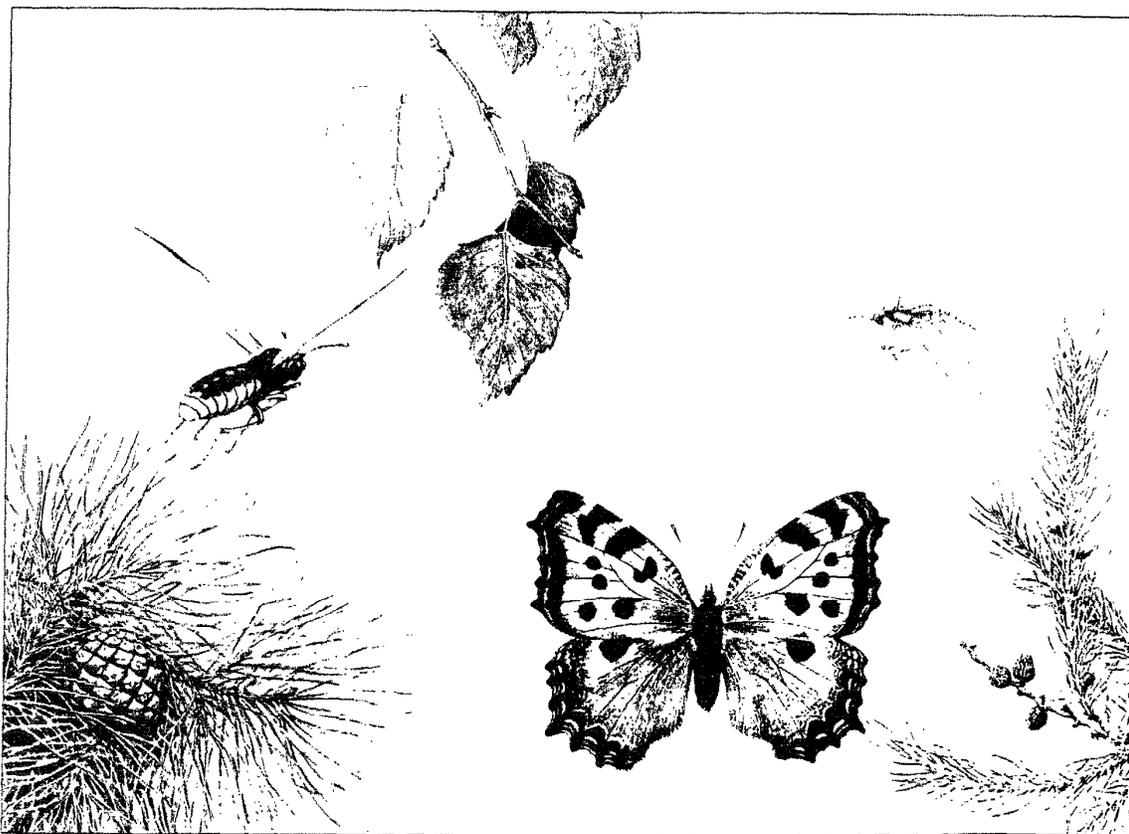


# FOREST INSECT GUILDS: PATTERNS OF INTERACTION WITH HOST TREES

Edited by:

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



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## 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.

**FOREST INSECT GUILDS:  
PATTERNS OF INTERACTION WITH HOST TREES**

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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

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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. Birt, 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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# 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.

## 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, Edelman-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 re-leaf 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, *Pseudotsuga 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 pseudotsugata* and 28-year-cycles of *C. occidentalis* on *P. menzeisii* in British Columbia (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
<i>Acleris gloverana</i>	2-3	<i>Heterocampa manteeo</i>	2
<i>Acleris variana</i>	2	<i>Lambdina fiscellaria lugubrosa</i>	3
<i>Archips argyrospila</i>	5	<i>Malacosoma americanum</i>	2-3
<i>Archips semififeranus</i>	2	<i>Malacosoma disstria</i> <sup>1</sup>	3
<i>Bucculatrix candensisella</i>	2-3	<i>Malacosoma californicum</i>	3-5
<i>Choristoneura conflictana</i>	2-3	<i>Melanolophia imitata</i>	2
<i>Choristoneura fumiferana</i>	5-8	<i>Neodiprion pratti banksianae</i>	2-3
<i>Choristoneura occidentalis</i>	3-6	<i>Neodiprion swainei</i>	3-4
<i>Choristoneura pinus</i>	2-4	<i>Nymphalis californicum</i>	1-2
<i>Coleotechnites milleri</i>	10-20	<i>Orgyia pseudotsugata</i>	1-3
<i>Coleotechnites starki</i>	10-20	<i>Paraclemensia acerifoliella</i>	3-6
<i>Coloradia pandora</i>	6-8	<i>Parorgyia griseifecta</i>	3
<i>Datana integerrima</i>	2	<i>Pristiphora erichsonii</i>	3-20
<i>Dryocampa rubicunda</i>	2	<i>Rheumaptera hastata</i>	2
<i>Heterocampa guttivita</i>	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 <sup>2</sup>	Low shade tolerance <sup>2</sup>	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.

<sup>1</sup>*M. disstria* in aspen forests.

<sup>2</sup>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 through 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 wind-throw 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<sup>3</sup> 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	Tol. med. <sup>4</sup>	Tol. med.	Tol. low
	Con. low	Con. med.	Con. med.	Con. high
	RIR weak	RIR weak	RIR strong	RIR med.
	DIR weak	DIR weak	DIR strong	DIR med.
High stress adapted	Tol. low	Tol. low	Tol. v. low	Tol. v. low
	Con. high	Con. v. high	Con. v. high	Con. v. high
	RIR weak	RIR none	RIR weak	RIR none
	DIR med.	DIR none	DIR med.	DIR none

<sup>3</sup>Tol. = tolerance capacity, Con. = constitutive defense level, RIR and DIR = rapid inducible and delayed inducible resistance, respectively.

<sup>4</sup>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
<i>Acleris</i>	<i>gloverana</i>	Tortricidae	<i>Tsuga heterophylla</i>
	<i>variana</i>	Tortricidae	<i>Abies balsamea</i>
<i>Alsophila</i>	<i>pometaria</i>	Geometridae	<i>Quercus</i> spp.
<i>Anacamptodes</i>	<i>ephyraria</i>	Geometridae	<i>Taxodium distichum</i>
<i>Anisota</i>	<i>senatoria</i>	Saturniidae	<i>Quercus</i> spp.
<i>Archips</i>	<i>argyrospilus</i>	Tortricidae	<i>Quercus</i> spp.
	<i>argyrospilus</i>		<i>Taxodium distichum</i>
	<i>semiferanus</i>		<i>Quercus ellipsoidalis</i>
<i>Argyresthia</i>	<i>thuiella</i>	Argyresthiidae	<i>Thuja occidentalis</i>
<i>Argyrotaenia</i>	<i>tubulana</i>	Tortricidae	<i>Pinus contorta</i>
<i>Bucculatrix</i>	<i>canadensisella</i>	Lyonetiidae	<i>Betula papyrifera</i>
<i>Caliroa</i>	spp.	Tenthredinidae	<i>Quercus</i> spp.
<i>Choristoneura</i>	<i>biennis</i>	Tortricidae	<i>Abies lasiocarpa</i>
	<i>conflictana</i>		<i>Populus tremuloides</i>
	<i>fumiferana</i>		<i>Abies balsamea</i>
	<i>lambertiana</i>		<i>Pinus contorta</i>
	<i>occidentalis</i>		<i>Pseudotsuga menziesii</i>
	<i>orae</i>		<i>Abies amabilis</i>
	<i>pinus</i>		<i>Pinus banksiana</i>
	<i>retiniana</i>		<i>Abies concolor</i>
	<i>viridis</i>		<i>Abies concolor</i>
<i>Coleophora</i>	<i>laricella</i>	Coleophoridae	<i>Larix laricina</i>
	<i>serratella</i>		<i>Betula papyrifera</i>
<i>Coleotechnites</i>	<i>milleri</i>	Gelechiidae	<i>Pinus contorta</i>
	<i>starki</i>		<i>Pinus contorta</i>
<i>Coloradia</i>	<i>pandora</i>	Sphingidae	<i>Pinus contorta</i>
	<i>pandora</i>		<i>Pinus jeffreyii</i>
	<i>pandora</i>		<i>Pinus ponderosa</i>
<i>Dasychira</i>	<i>pinicola</i>	Lymantriidae	<i>Pinus banksiana</i>
<i>Datana</i>	<i>integerrima</i>	Notodontidae	<i>Carya illinoensis</i>
<i>Diapheromera</i>	<i>femorata</i>	Phasmatidae	<i>Quercus rubra</i>
<i>Diprion</i>	<i>similis</i>	Diprionidae	<i>Pinus strobus</i>
<i>Dryocampa</i>	<i>rubicunda</i>	Saturniidae	<i>Acer</i> spp.
<i>Ectropis</i>	<i>crepuscularia</i>	Geometridae	<i>Tsuga heterophylla</i>
<i>Ennomos</i>	<i>subsignarius</i>	Geometridae	<i>Carya</i> spp.
<i>Epinotia</i>	<i>meritana</i>	Olethreutidae	<i>Abies concolor</i>
	<i>solandriana</i>		<i>Betula papyrifera</i>
	<i>tsugana</i>		<i>Tsuga heterophylla</i>
<i>Epirrita</i>	<i>autumnata omissa</i>	Geometridae	<i>Tsuga heterophylla</i>
<i>Erannis</i>	<i>tiliaria</i>	Geometridae	<i>Acer saccharum</i>
<i>Fenusa</i>	<i>pusilla</i>	Tenthredinidae	<i>Betula papyrifera</i>
<i>Galenaria</i>	<i>consimilis</i>	Geometridae	<i>Pseudotsuga menziesii</i>
<i>Halisidota</i>	<i>argentata</i>	Arctiidae	<i>Tsuga heterophylla</i>

## APPENDIX 1 continued

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

APPENDIX 1 continued

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

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

<sup>5</sup>Infestation areas summed over the entire United States and divided by frequency (yrs).

<sup>6</sup>Average area x frequency ÷ 28.

## APPENDIX 2 continued

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

APPENDIX 2 continued

Outbreak insect species	Average area/episode	Maximum area	Frequency (yrs)	Average area/year
<i>Zeiraphera improbana</i>	17,465	61,134	4	2,495
<i>Zeiraphera ratzeburgiana</i>	34,818	34,818	1	1,243
<i>Zelleria haimbachi</i>	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 the dominant plant species. Shade tolerance and growth rate classifications,<sup>7</sup> typical age of mortality from Loehle (1988), and percent host domination of system from various sources, primarily Folwells (1965).

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

<sup>7</sup>Classes range from 1 to 5, low to high, respectively.

APPENDIX 3 continued

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

## APPENDIX 3 continued

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

APPENDIX 3 continued

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

# 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. alexiaries* 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. alexiaries* survive beyond the first instar. Magnoliaceae are typically lethal to all *P. glaucus* taxa except *P. glaucus* and *P. alexiaries*.

### *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<sub>1</sub> 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.

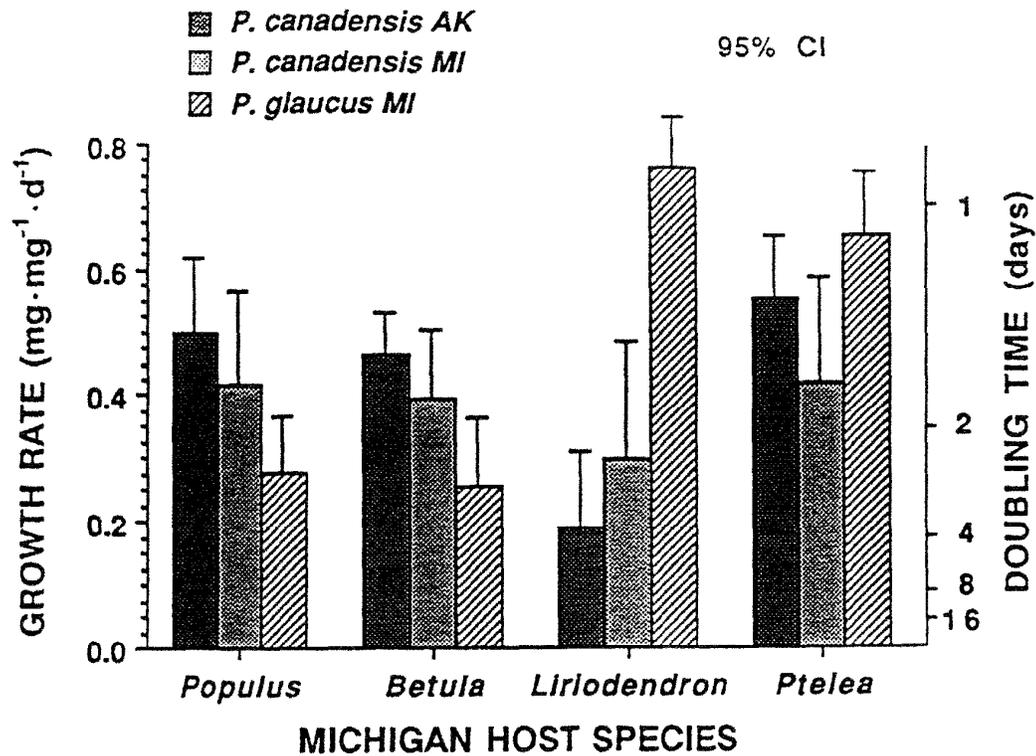


Figure 1. Relative growth rate of first instar larvae from three insect populations tested on four Michigan host species. Right hand axis shows the time required for larvae to double their weight at the corresponding growth rate. The insect populations are *P. canadensis* from Alaska, *P. canadensis* 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 ( $T_1$ ) 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  $(\ln(W_F) - \ln(W_1))/T$ , where  $W_F$  equals the final weight,  $W_1$  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 mg·mg<sup>-1</sup>·d<sup>-1</sup> on *Betula nigra* to 0.20 mg·mg<sup>-1</sup>·d<sup>-1</sup> 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 mg·mg<sup>-1</sup>·d<sup>-1</sup> 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 mg·mg<sup>-1</sup>·d<sup>-1</sup> 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.

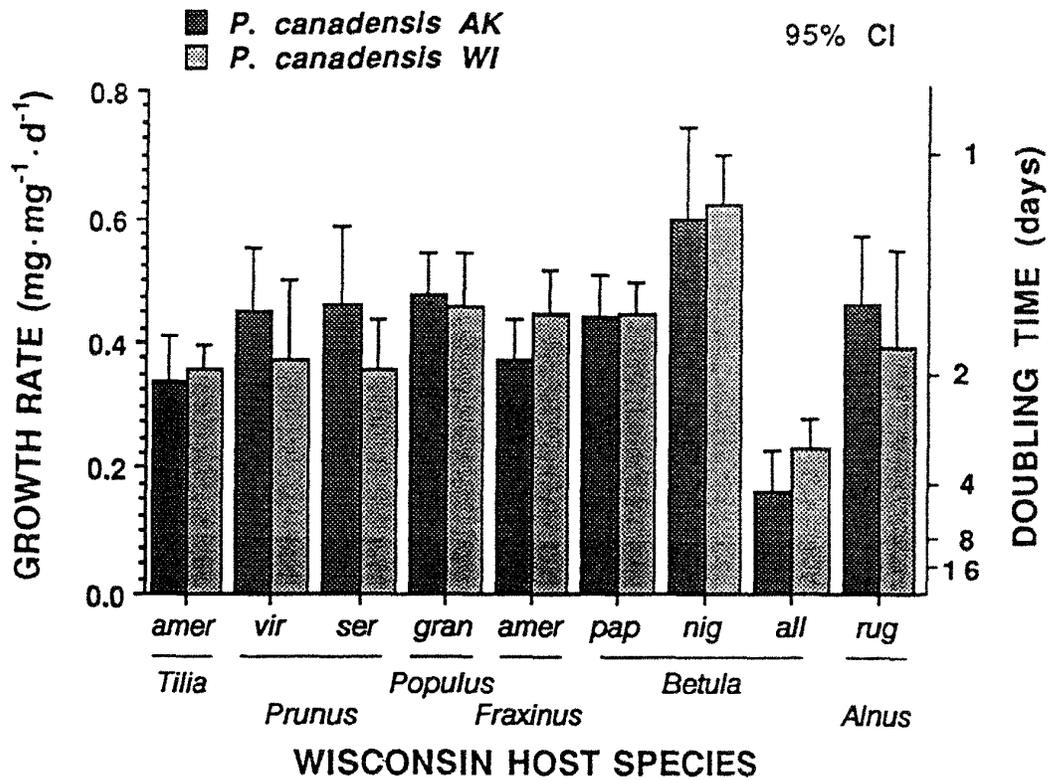


Figure 2. Relative growth rate of first instar *P. canadensis* from Alaska and Wisconsin on nine Wisconsin host species. The host species, from left to right, are *Tilia americana* (basswood), *Prunus virginiana* (chokecherry), *Prunus serotina* (black cherry), *Populus grandidentata* (bigtooth aspen), *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

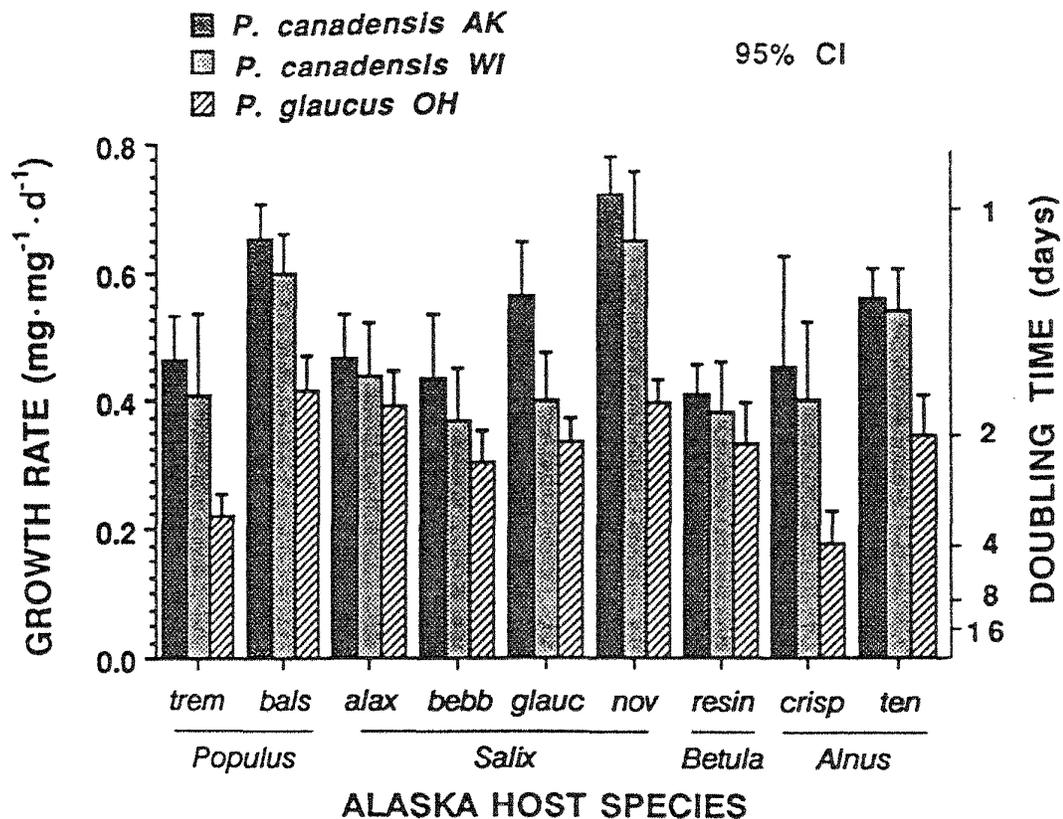


Figure 3. Relative growth rate of first instar larvae from three insect populations tested on nine Alaska host species. The insect populations are *P. canadensis* from Alaska, *P. canadensis* from Wisconsin, and *P. glaucus* from Ohio. The host species, from left to right, are *Populus tremuloides* (quaking 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.

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.).

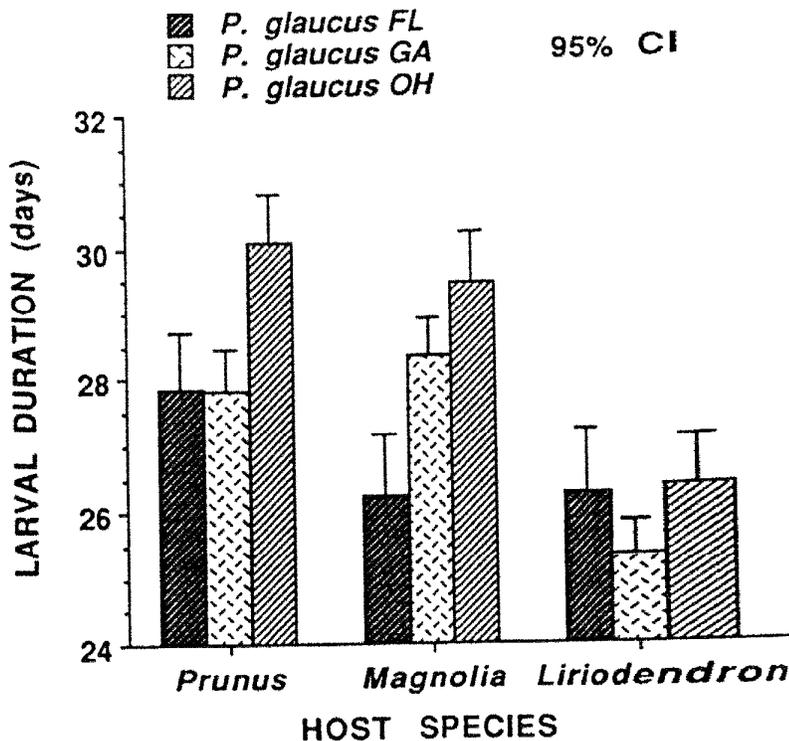


Figure 4. Larval duration of *P. glaucus* populations from Florida, Georgia, and Ohio tested on *Prunus serotina* (black cherry), *Magnolia virginiana* (sweetbay), and *Liriodendron tulipifera* (tuliptree). Measurements were made during May, August, and September 1988 for Florida, Ohio, and Georgia populations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

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#### 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 <sup>a</sup>	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			

<sup>a</sup> 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<sub>100/100</sub> genotypes tended to be fast growers on *Liriodendron* and heterozygous GPI<sub>100/-104</sub> genotypes tended to be fast growers on *Magnolia* (Bossart in prep.). Moreover, the frequency of the GPI<sub>-104</sub> 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.

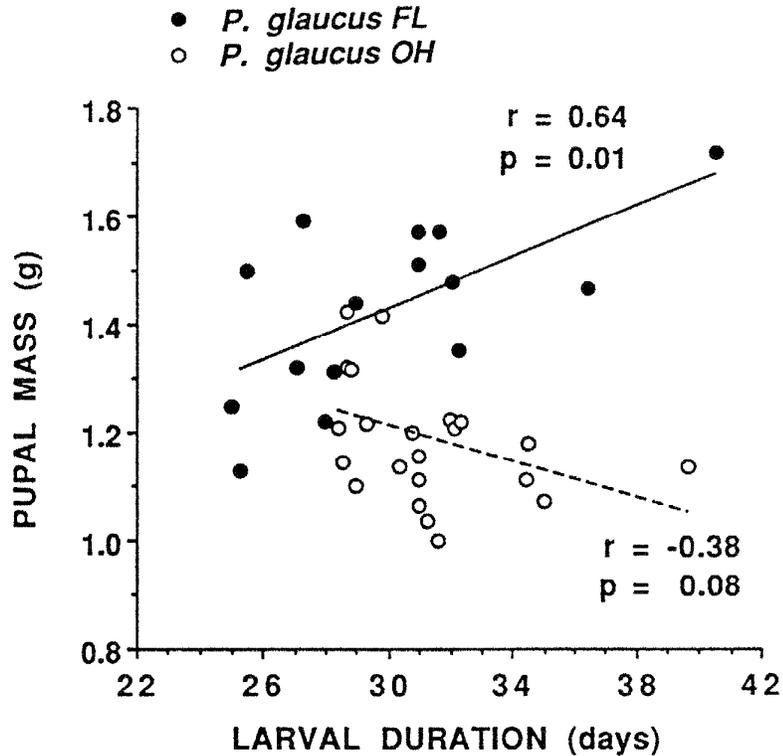


Figure 5. Relationship between larval duration and pupal mass of *P. glaucus* from Florida and Ohio reared on *Magnolia virginiana*. Each point represents the mean of 3 to 30 full-siblings. Figure includes data from 1988 and 1989.

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

	<i>Liriodendron</i>		<i>Magnolia</i>	
	GPI <sub>100/100</sub>	GPI <sub>100/-104</sub>	GPI <sub>100/100</sub>	GPI <sub>100/-104</sub>
Florida	22.36 $\pm$ 0.45 (11)	26.75 $\pm$ 0.75 (8)	26.06 $\pm$ 0.45 (18)	24.86 $\pm$ 0.67 (7)
Ohio	23.88 $\pm$ 0.44 (16)	27.55 $\pm$ 1.14 (11)	29.64 $\pm$ 0.95 (11)	28.50 $\pm$ 0.50 (2)

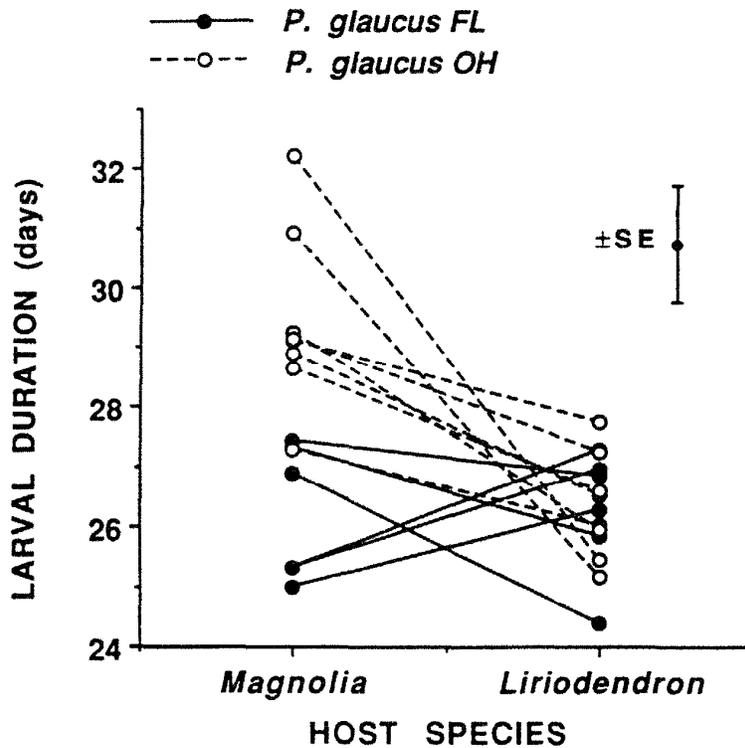


Figure 6. Larval duration of *P. glaucus* families from Florida and Ohio tested on *Liriodendron tulipifera* and *Magnolia virginiana*. Each point represents the mean of 6 to 10 full-siblings. Lines show family reaction norms. Standard error associated with family means is indicated ( $SE^2 = MS_{\text{Error}}/N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

#### 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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<sup>1</sup>Order of authorship determined by tossing a coin.

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 virididorsata* (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

Scots pine		
Species	Family	Larval period
<i>Neodiprion sertifer</i>	Diprionidae	May-July
<i>Diprion pini</i>	Diprionidae	July-September
<i>Gilpinia pallida</i>	Diprionidae	June-August
<i>Microdiprion pallipes</i>	Diprionidae	June-August
<i>Bupalus piniarius</i>	Geometridae	June-August
Birches		
<i>Epirrita autumnata</i>	Geometridae	May-July
<i>Operopthera</i> spp.	Geometridae	May-July
<i>Erannis defoliaria</i>	Geometridae	May-July
<i>Dineura virididorsata</i>	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*
<b>Scots pine needles</b>				
<b>RIR</b>				
<i>Neodiprion sertifer</i>	+	0	+	1
<i>Gilpinia virens</i>	0	0	0	1
<i>Microdiprion pallipes</i>	0	0	-	1
<i>Diprion pini</i>	0	0	0	1
<b>DIR</b>				
<i>Neodiprion sertifer</i>	0	0	0	1
<i>Diprion pini</i>	0	+/0	-/0	10
<b>Birch foliage</b>				
<b>RIR</b>				
<i>Epirrita autumnata</i>	-	-	0	2,3,4
<i>Dineura virididorsataa</i>	0	0	0	3,5
<b>DIR</b>				
<i>Epirrita autumnata</i>	-	-	-	6,7,8
<i>Dineura virididorsataa</i>	+	?	?	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<sup>2</sup>) on *Betula pubescens* ssp. *tortuosa* trees in the field experiment at Labytnangi

Types of damage <sup>a</sup>	Leaf damage (%) and consumption (mm <sup>2</sup> )	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

<sup>a</sup>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 ( $1.81 \pm 0.09$ ) of four leaves available in Petri dishes, as a rule, inflicting four ( $\bar{x} = 4.18 \pm 0.40$ ) holes. *Phyllobius* specimens often damaged all four leaves available ( $\bar{x} = 3.21 \pm 0.09$ ), inflicting about nine ( $\bar{x} = 9.88 \pm 0.47$  holes).

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

Types of damage	Leaf damage (%) and consumption ( $\text{mm}^2$ )	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 ( $\text{mm}^2$ ) of damaged and intact *Betula* leaves by *Epirrita* larvae

Tree number	Replicates	Days after treatment	Damaged leaves ( $\text{mm}^2$ )	Intact leaves ( $\text{mm}^2$ )	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	180.85	191.97	n.s.

Table 4. Consumption ( $\text{mm}^2$ ) of damaged and intact *Betula* leaves by *Phyllobius* weevils

Tree number	Replicates	Days after treatment	Damaged leaves ( $\text{mm}^2$ )	Intact leaves ( $\text{mm}^2$ )	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* Bonzd. (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 Hanhimäki 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.

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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.

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  $-90^{\circ}\text{C}$  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:

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

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 <sup>a</sup> (units)	Douglas-fir foliar chemistry <sup>b</sup>		Artificial diet experiment optimum <sup>c</sup>	
	P <sup>d</sup>	Resistant		Susceptible
N (%)				
$\bar{x}$	<0.001	1.14	0.93	-- <sup>e</sup>
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 <sup>a</sup> (units)	Douglas-fir foliar chemistry <sup>b</sup>		Artificial diet experiment optimum <sup>c</sup>
	P <sup>d</sup>	Resistant	
Ca/N ratio (x 10)			
$\bar{x}$	0.069	2.49	2.93
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
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
SE		0.026	0.039
Range		0.68-0.98	0.79-1.17
Zn ( $\mu$ /g)			
$\bar{x}$	0.631	27.8	27.3
SE		0.90	0.53
Range		24-36	24-30
Zn/N ratio (x 1,000)			
$\bar{x}$	< 0.001	2.44	2.95
SE		0.052	0.084
Range		2.24-2.75	2.43-3.30

<sup>a</sup>All concentrations are based on the dry mass of the foliage or diet.

<sup>b</sup>Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

<sup>c</sup>The concentration that produced the best budworm survival and reproduction when larvae were reared on the diet for three consecutive generations.

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

<sup>e</sup>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<sup>a</sup>

Response variable	Douglas-fir foliage <sup>b</sup>		
	<i>p</i> <sup>c</sup>	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	Douglas-fir foliage <sup>b</sup>		
	<i>P</i> <sup>c</sup>	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

<sup>a</sup>Concentrations of six monoterpenes (tricyclene,  $\alpha$ -pinene, camphene,  $\beta$ -pinene, myrcene, menthene-1) and one oxygenated monoterpene (bornyl acetate), the principal components of the oleoresin of these trees, are presented. Additional monoterpenes ( $\alpha$ -phellandrene,  $\Delta$ -3-carene,  $\ell$ -limonene, terpinolene) and oxygenated monoterpenes (*cis*- $\beta$ -terpineol,  $\ell$ -borneol) that were minor components of the oleoresin were included when calculating terpene totals.

<sup>b</sup>Current-year needles collected in late June 1988, when western spruce budworms were in the late-instar feeding period.

<sup>c</sup>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 (Picne 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 (*Orgyia 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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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.

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.

# NITROGEN (% dwt)

Foliage    
  Frass

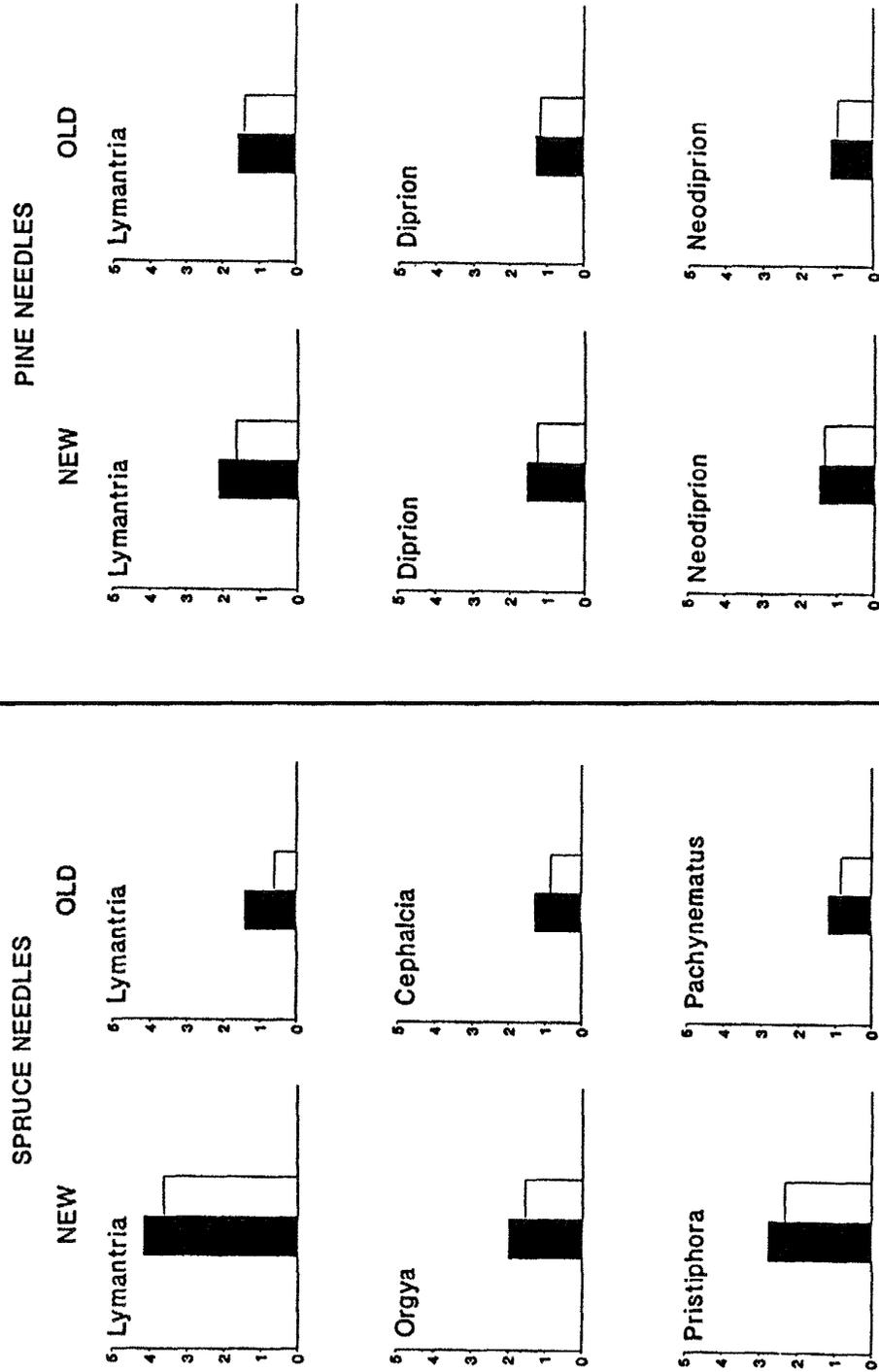


Figure 1. Concentrations of total nitrogen in new and old needles of spruce and pine, and in frass of insect herbivores.

# CARBOHYDRATES (nmoles/g dwt)

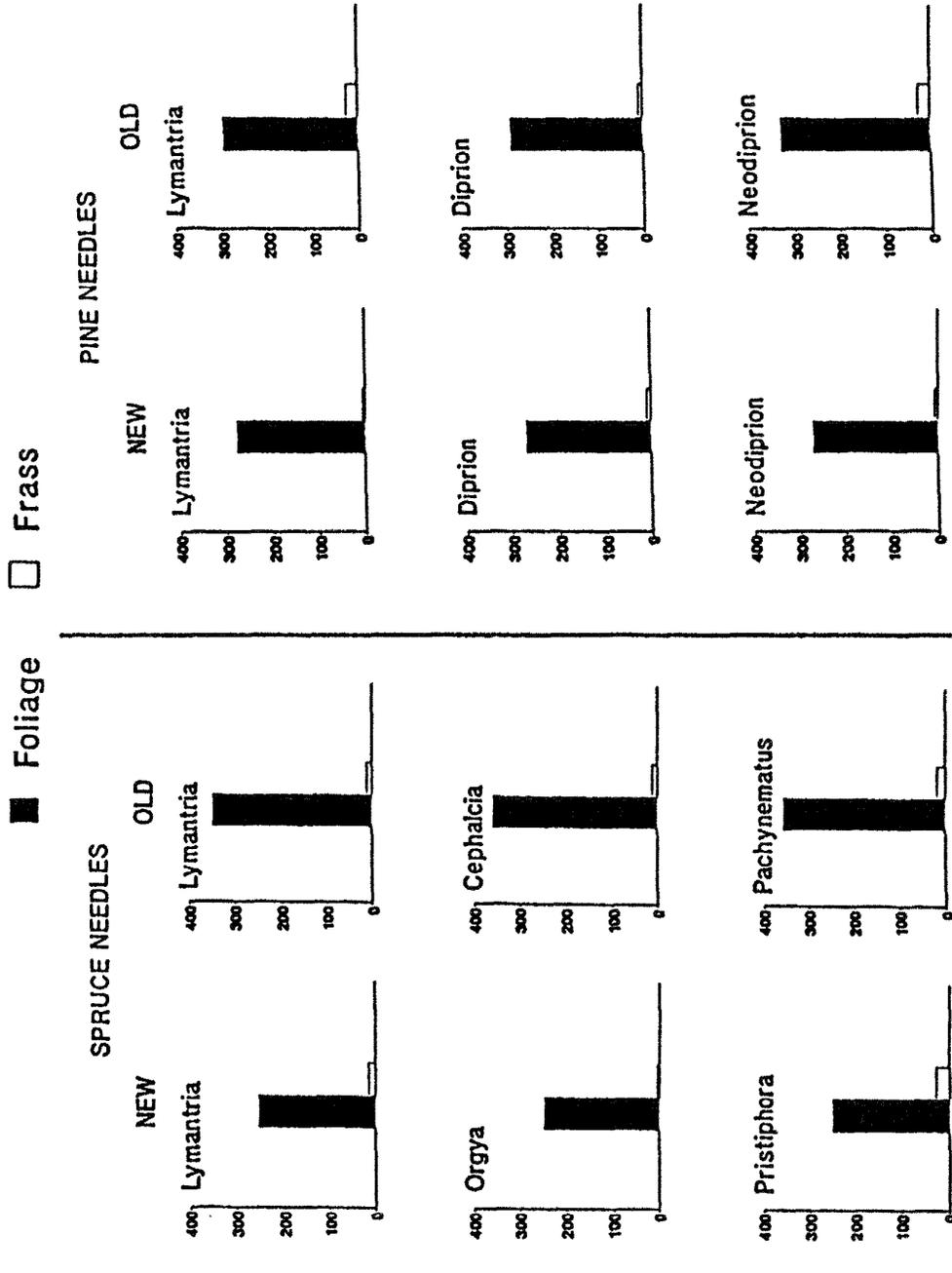


Figure 2. Concentrations of carbohydrates (hexose-equivalents of sucrose, fructose, and glucose) in new and old needles of spruce and pine, and in frass of insect herbivores.

## 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, *Orgyia 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).

# CYCLITES (nmoles/g dwt)

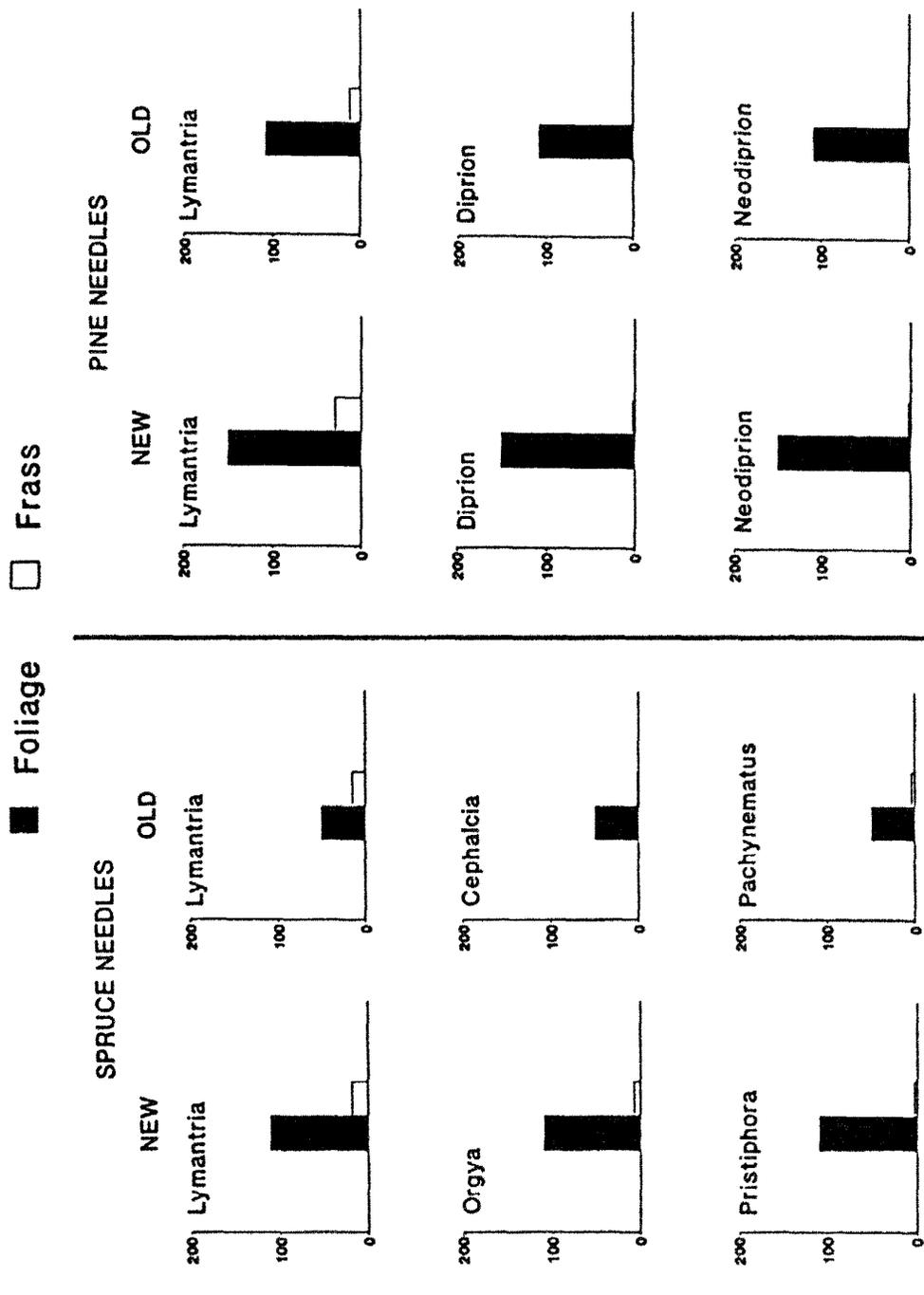


Figure 3. Concentrations of the cyclite, pinitol, in conifer needles and in herbivore frass.

# QUINIC ACID (nmoles/g dwt)

■ Foliage □ Frass

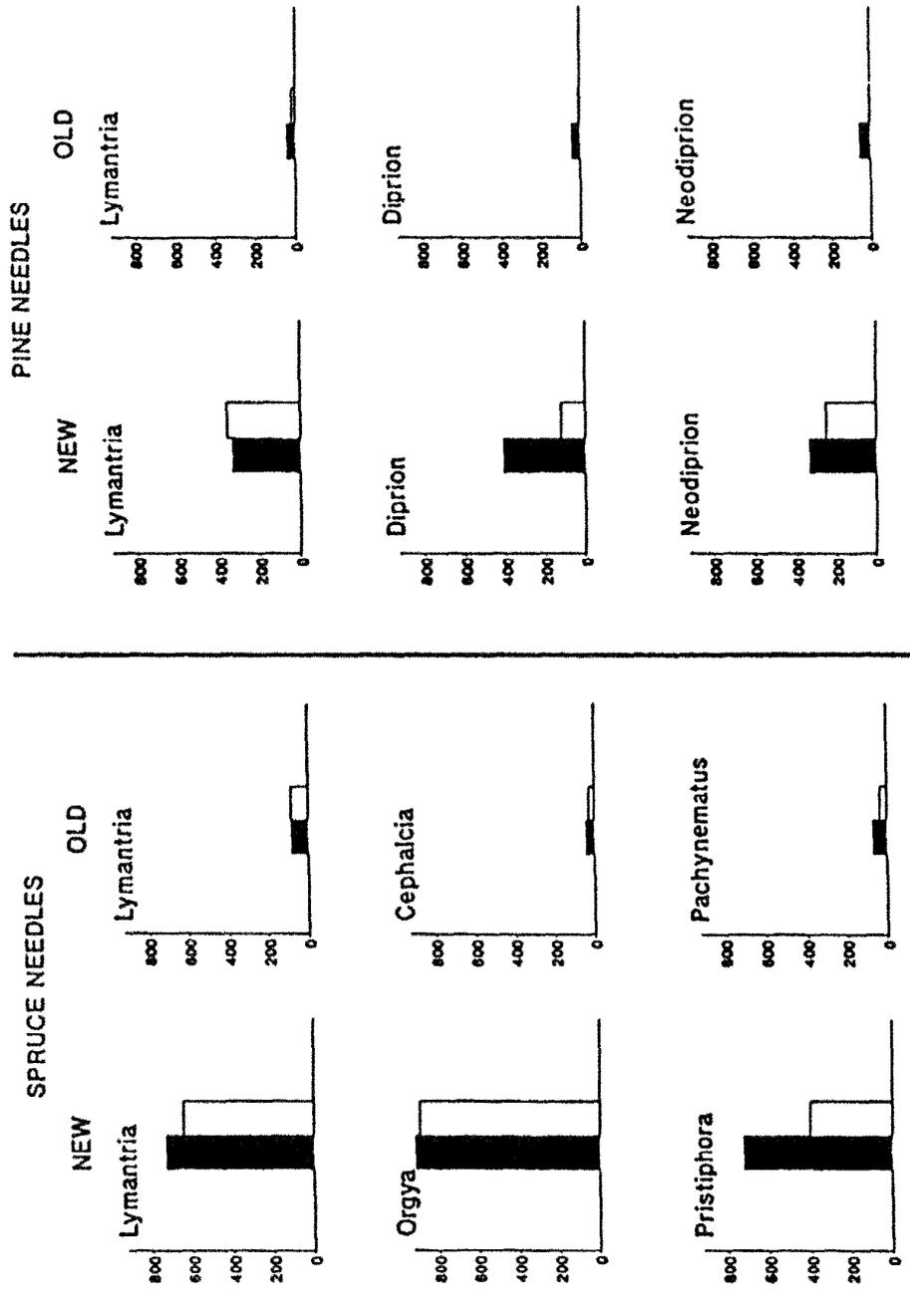


Figure 4. Concentrations of quinic acid in conifer needles and in herbivore frass.

# SHIKIMIC ACID (nmoles/g dwt)

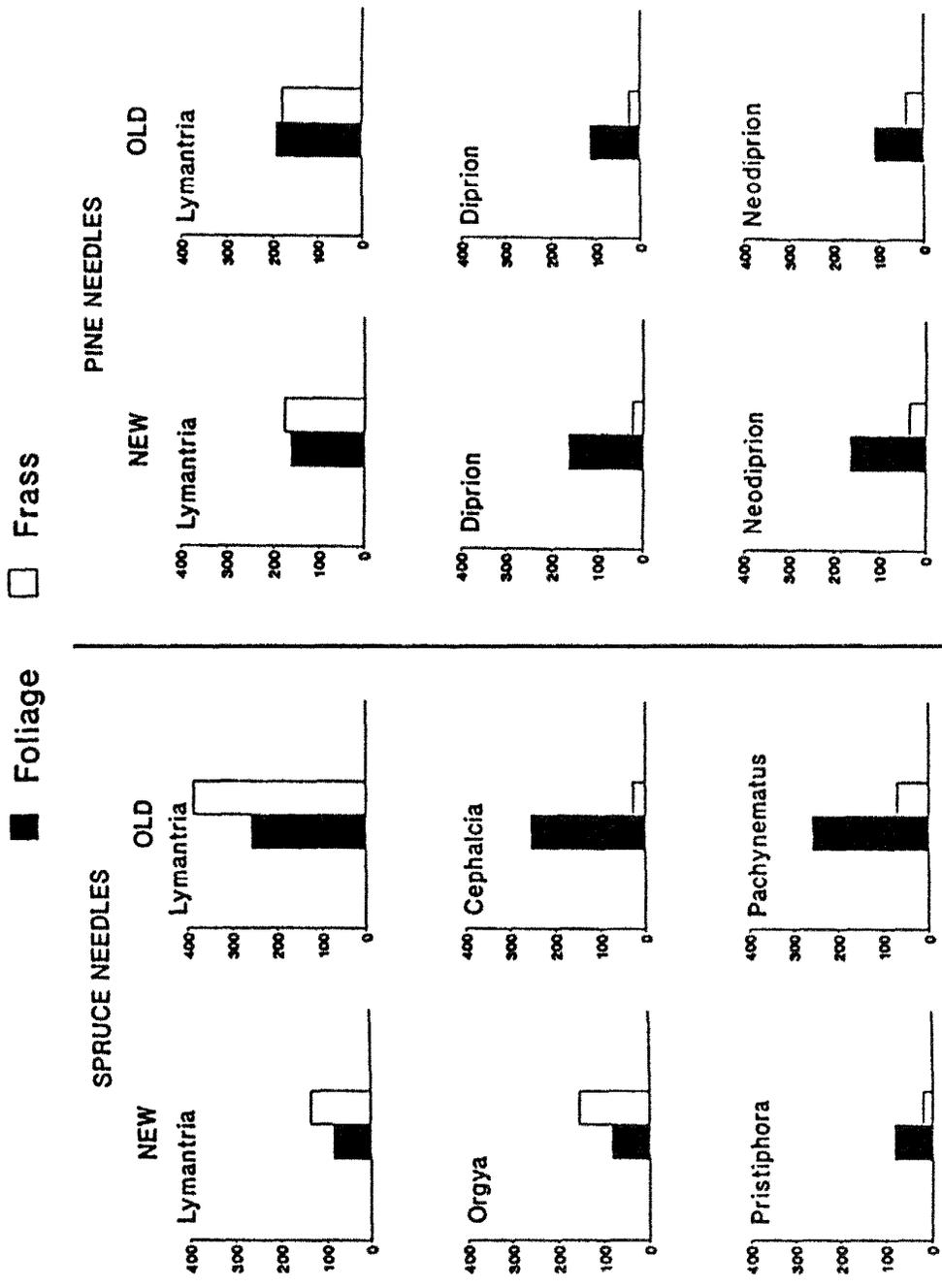


Figure 5. Concentrations of shikimic acid in conifer needles and in herbivore frass.

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, *Orgyia antiqua*, and the pine specialist lepidopterans, *Bupalus piniarius*, *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).

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## 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) Gelechiidae

*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.

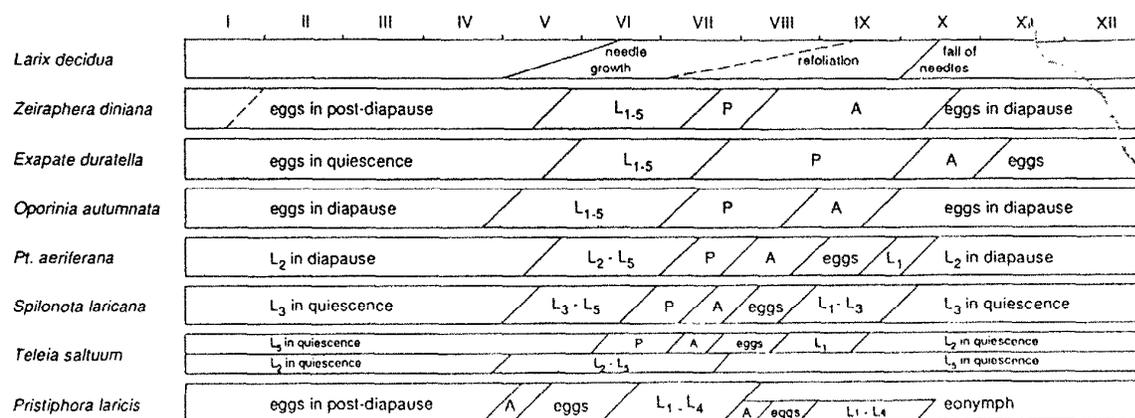


Figure 1. Phenology and biology of the folivore guild on larch (*Larix decidua* Mill.) in the European Alps.

#### 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 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  $Pl_t$  < 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 LBM $_t$  > 100 larvae/kg: Density  $x_{t+2}$  < Density  $x_{t+1}$ ;  
Density  $Pl_{t+1}$  < 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)

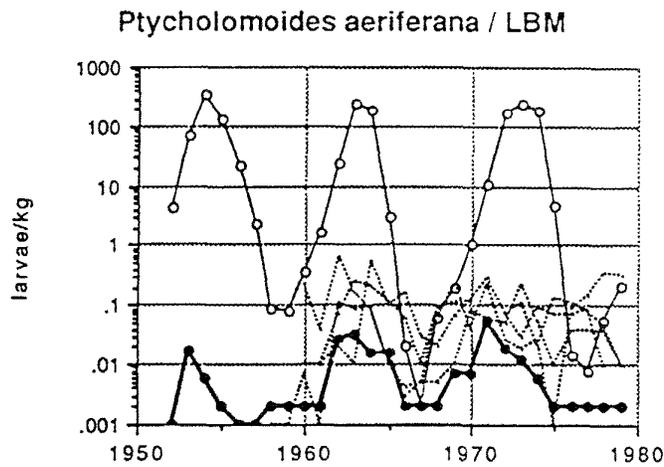
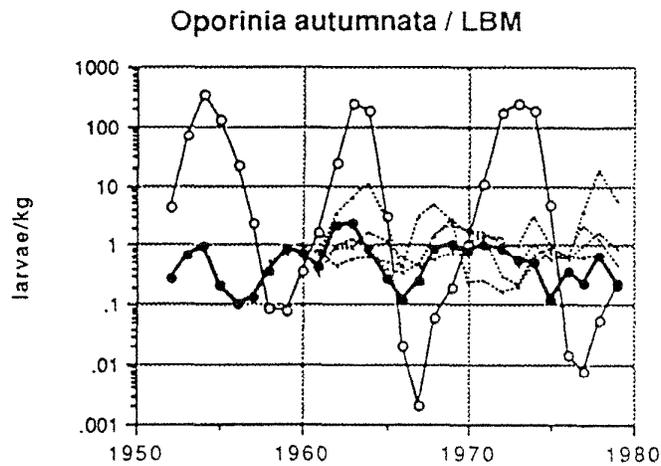
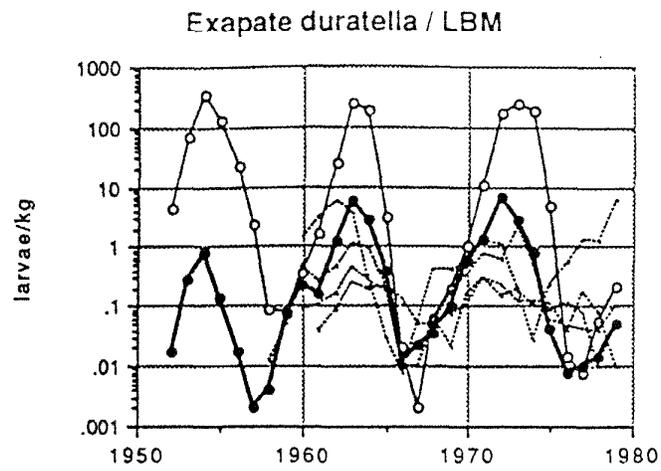
Year	Briançonnais	Goms	Oberengadin	Valle Aurina	Lungau
1952			0.181		
1953			0.198		
1954			0.352		
1955			0.084		
1956			0.225		
1957			0.887		
1958		1.901	2.587		
1959		1.345	2.657		
1960	0.525	2.500	1.986	4.500	
1961	0.514	0.394	0.949	1.920	2.340
1962	0.929	1.402	2.284	1.880	5.010
1963	0.360	0.400	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).

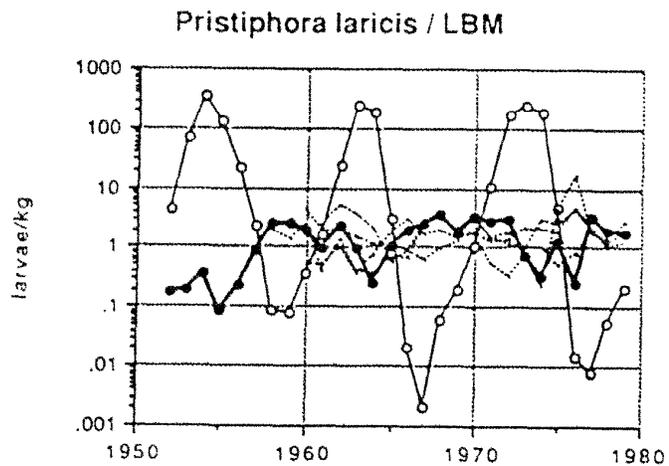
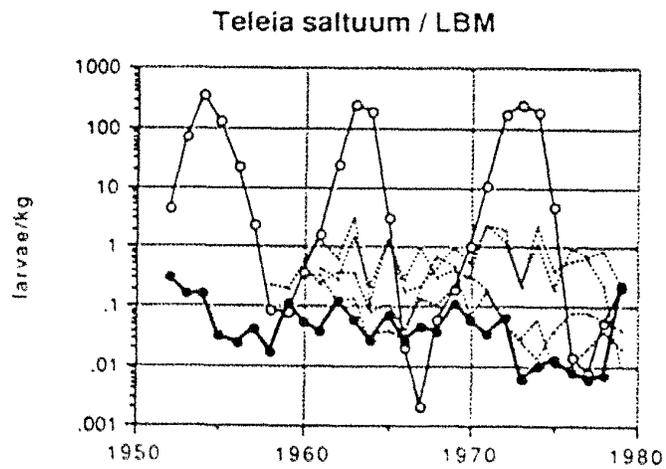
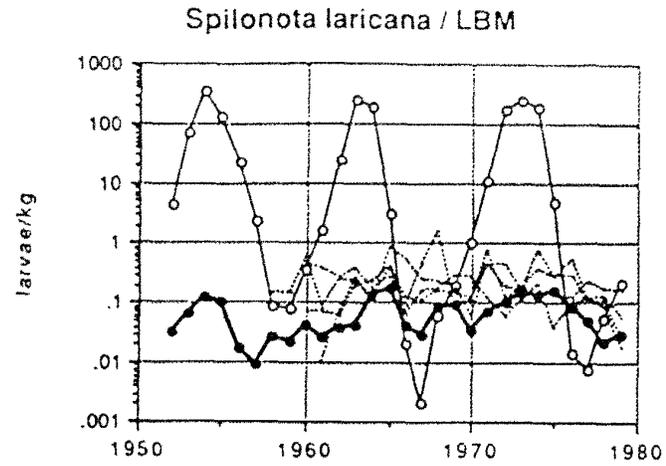
	Immediate response			Delayed response		
	Yes	No	%p	Yes	No	%p
<i>Exapate duratella</i>	13	2	0.45	14	1	0.08
<i>Oporinia autumnata</i>	11	4	7.07	9	6	43.86
<i>Pt. aeriferana</i>	10	5	19.67	10	5	19.67
<i>Spilonota laricana</i>	5	10	19.67	10	5	19.67
<i>Teleia saltuum</i>	8	7	79.63	8	7	79.63
<i>Pristiphora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



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 PI in the Engadine (Fig. 2b) suggests that an immediate impact is exerted by the LBM, i.e. the density of PI 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*, *Psycholomoides*, *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*, *Psycholomoides*, *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 *Psycholomoides*, *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*  $51.8 \pm 5.08$  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.

Exapate duratella / LBM - Valle Aurina

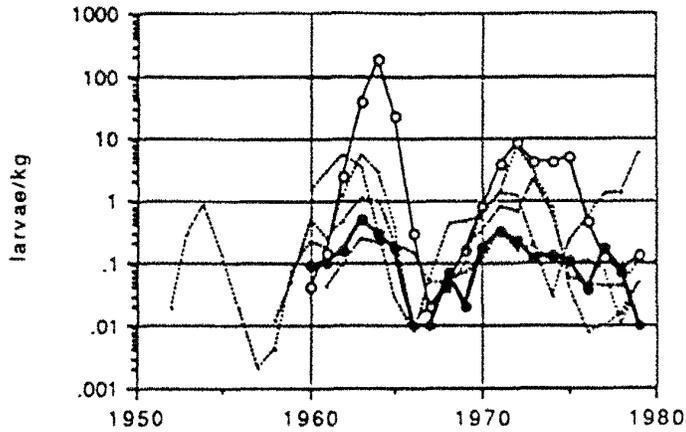


Figure 3. Comparisons of the fluctuation patterns of *Exapate duratella* and the larch bud moth (LBM) in the Valle Aurina (legend as in Figs. 2a and 2b).

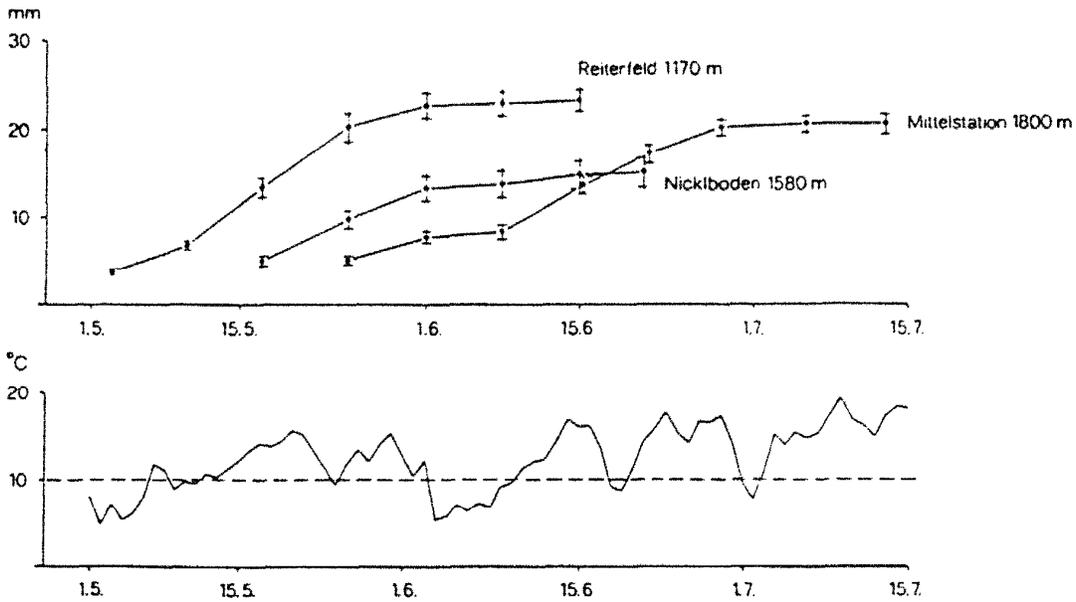


Figure 4. Growth curves of larch needles (mm:  $\bar{x} \pm s_x$ ) in the Lungau at three altitudes in 1975 compared with the daily mean temperature (station Tamsweg, 1021 m a.s.l., °C, min + max/2).

## 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.

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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<sup>2</sup>), 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  $5 \times 10 = 50$  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

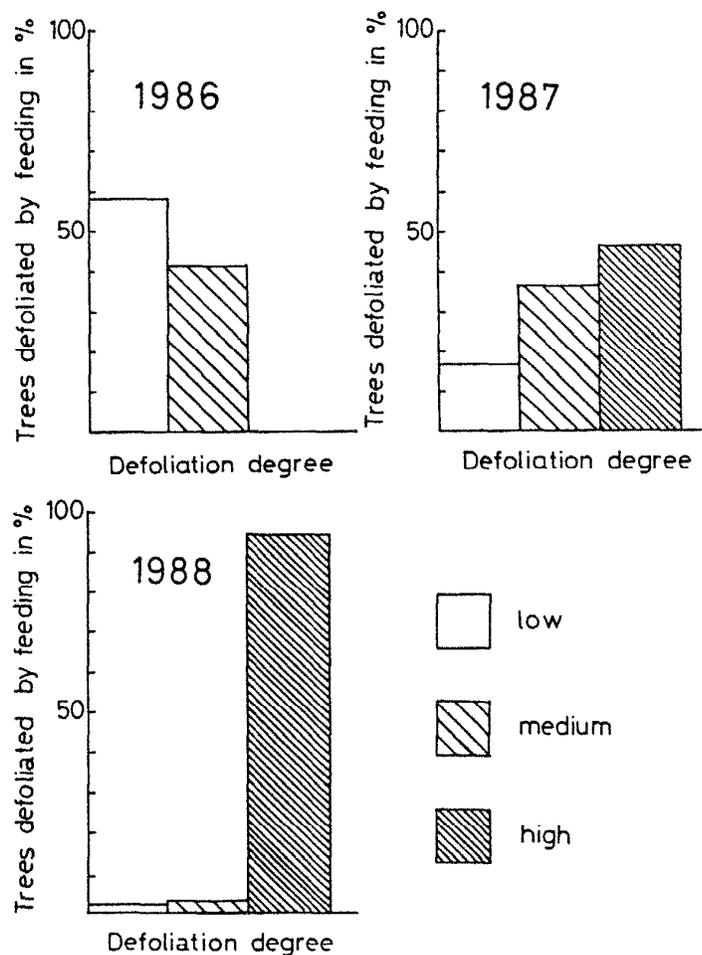


Figure 1. Increasing defoliation by *Zeiraphera rufimitrana* in the forest district of Staufen.

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

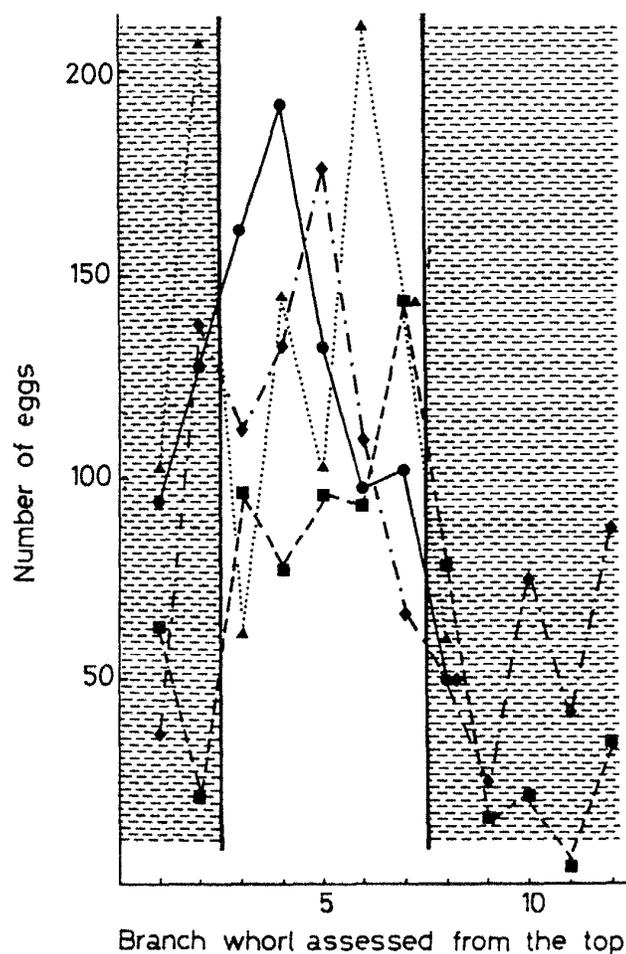


Figure 2. Distribution of the egg density (eggs/shoot) of *Zeiraphera rufimitrana* within the crown of four individual silver fir trees (whorl 1 was uppermost).

Table 3. Density of the descending larvae.

Forest district	Number of funnel traps	Larvae/m <sup>2</sup>
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<sup>2</sup> 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*.

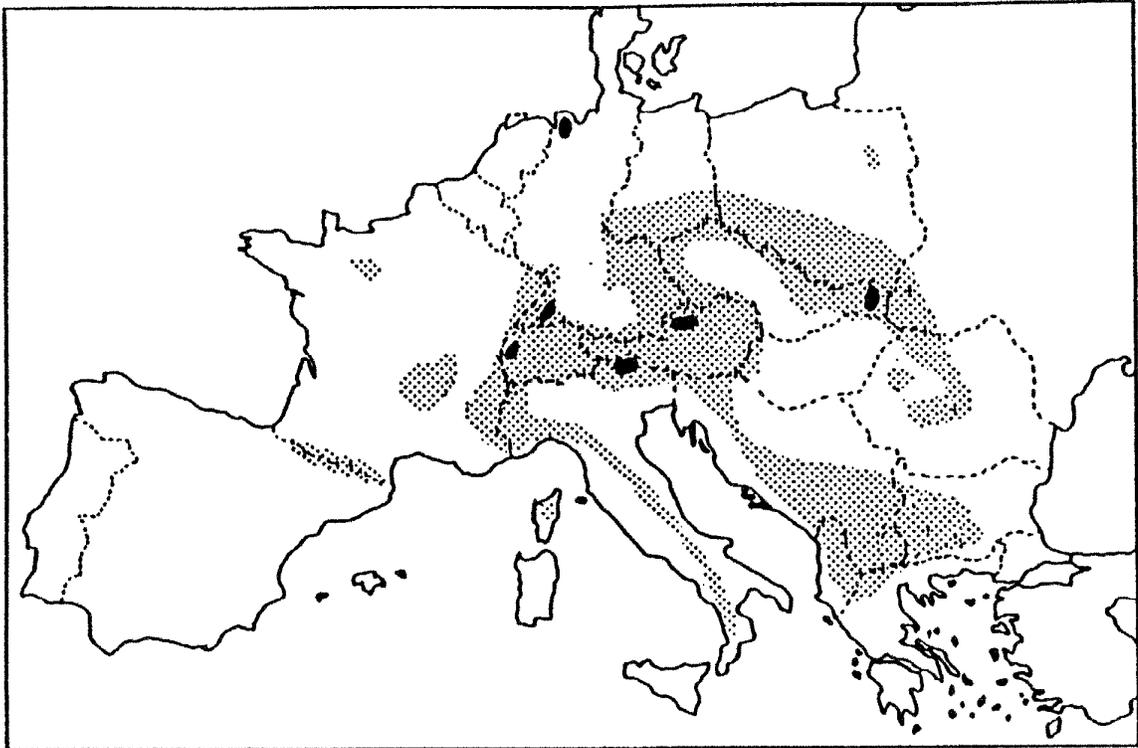


Figure 3. Natural habitat of *Abies alba* (dotted area) and zones of outbreaks of *Zeiraphera rufimitrana* since 1945 (shaded black).

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



# 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<sup>2</sup> 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

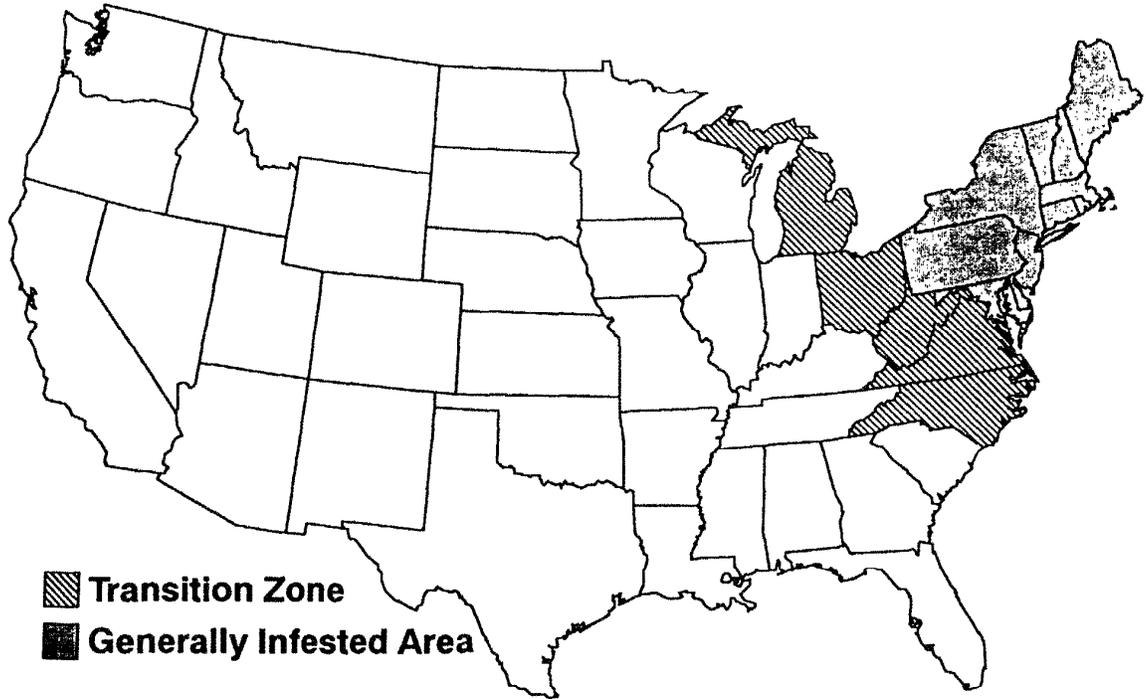


Figure 1. Current gypsy moth distribution

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<sup>2</sup> 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.

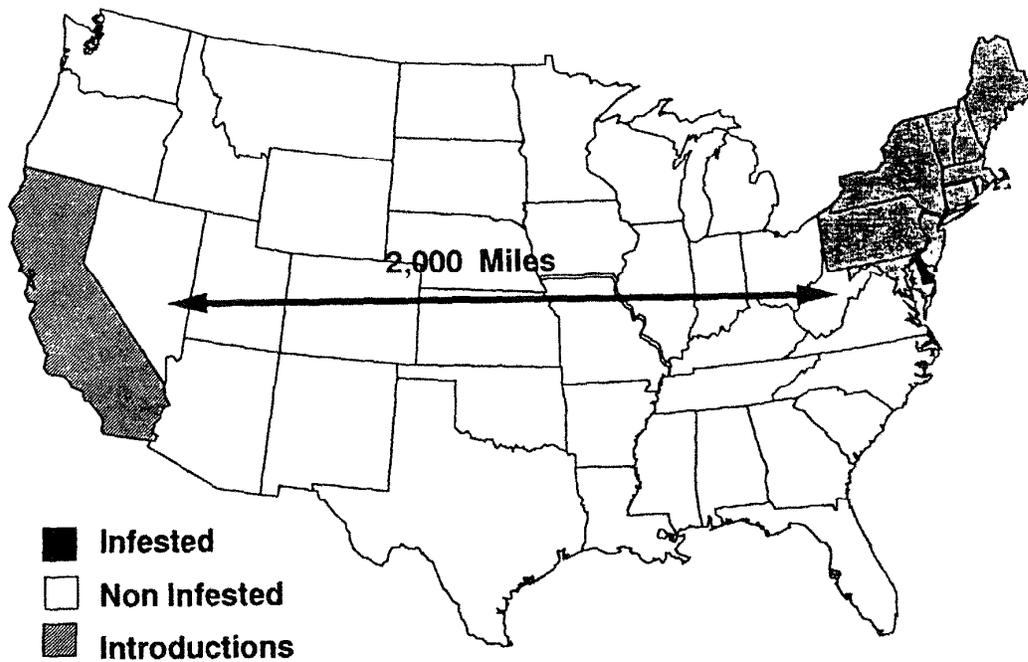


Figure 2. Introduction of gypsy moth into California

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

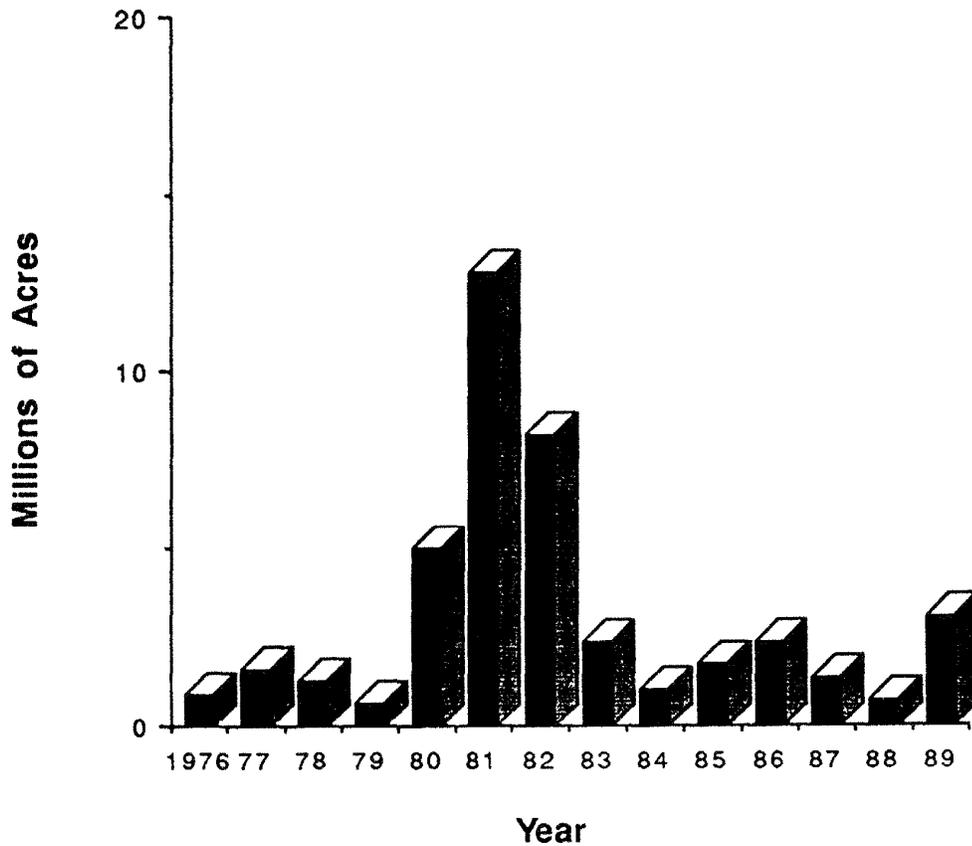


Figure 3. Acres defoliated by gypsy moth

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

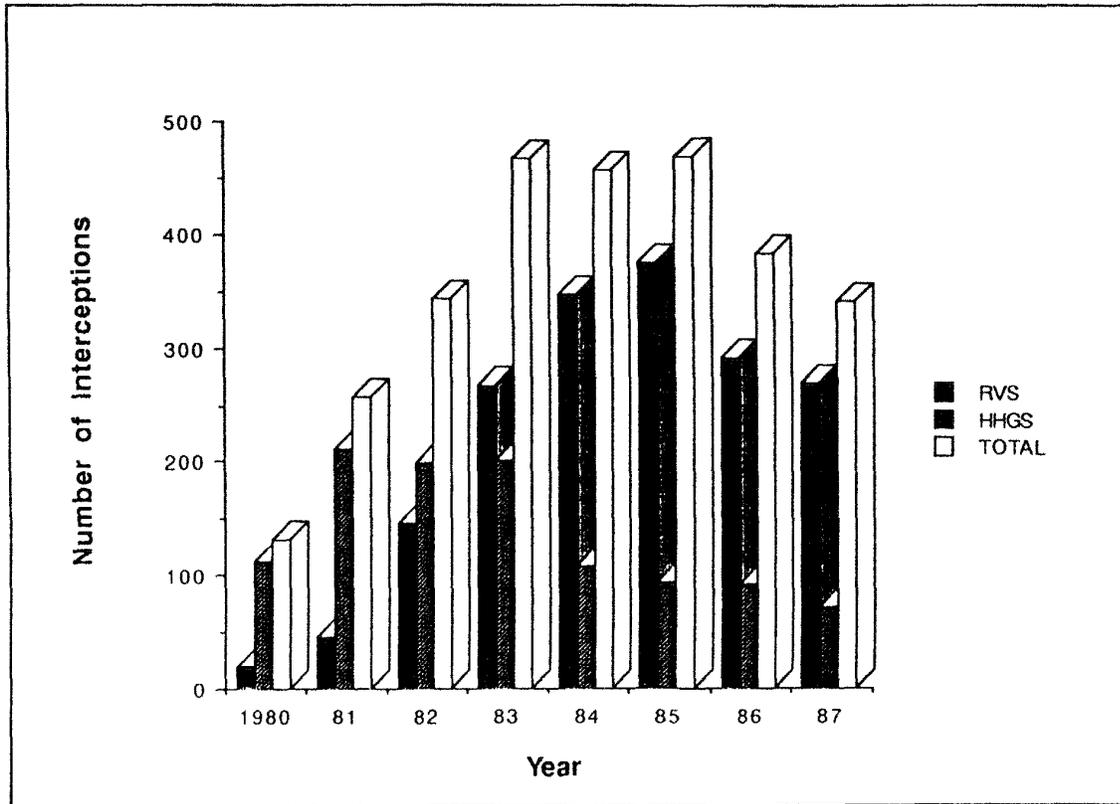


Figure 4. California interceptions from 1980-1987

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 Relling (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 re-leafing 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 Ketrion, 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 become 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 (Dusaussouy 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

$$MS = (\bar{dx}/\bar{dz})^{-1} \quad (1)$$

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:

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

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:

$$VS = s^2_z/s^2_x \quad (3)$$

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  $1 \text{ m}^2$  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  $18.6^\circ\text{C}$  and it did not change from year to year (the period of stability); then it increased up to  $21.1^\circ\text{C}$  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"

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

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  $18.6^\circ\text{C}$  to  $21.1^\circ\text{C}$ .

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  $y_1$  of population dynamics was evaluated using the equation:

$$y_1 = \beta_0 + \beta_1 v_1 + \beta_2 v_2 + \beta_{12} v_1 v_2 + \beta_3 v_3 + \dots, \quad (5)$$

where  $v_j$  is an integer variable indicating the dependence of the  $j$ -th ecological process on factors, and  $\beta_j$  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  $y_1$ . 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  $y_1$  was estimated using the model with different combinations of processes having the fixed rate. Then coefficients  $\beta_j$  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  $MS = 0.70 \pm 0.12$ ,  $VS = 0.30 \pm 0.19$ . 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 ( $\beta_1 = 0.51$ ,  $\beta_2 = 0.41$ ). Eonymph parasitoids give the greater contribution to the coefficient of v-stability of the host  $\beta_2 = 0.68$  than egg parasitoids ( $\beta_1 = 0.20$ ). Interaction of mortality processes associated with two groups of parasitoids destabilizes the sawfly population dynamics ( $\beta_{12} = -0.59$ ).

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  $101 \pm 36 \text{ m}^{-2}$  as compared with  $34 \pm 11 \text{ m}^{-2}$  in the period of stability. In the next year it increases to  $995 \pm 368 \text{ m}^{-2}$ . The reduction in larval mortality caused by diseases after drought when host plants are weakened is most important in population density increase ( $\beta_6 = 0.55$ ) (Table 1). Mass reactivation of sawflies in the first flight period is also important ( $\beta_4 = 0.35$ ).

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 ( $\beta_{16} = 0.46$ ,  $\beta_{15} = 0.37$ ,  $\beta_{14} = 0.32$ ).

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 ( $\beta_3 = 1.61$ ). 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 ( $\beta_{13} = 1.75$ ). If food is in plenty, parasitoids cannot suppress the sawfly population ( $\beta_1 = -0.83$ ,  $\beta_2 = 0.69$ ). Eonymph parasitoids cannot decrease the host density even in conditions of food shortage (coefficient  $\beta_{23}$  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.

B coefficients of equation (5)*	Quantitative characteristics of population dynamics **			
	$y_1 = MS$	$y_2 = VS$	$y_3 = \ln(N_0/N_s)$	$y_4 = \ln(N_0/N_c)$
0	0	0	0	$0.62 \pm 0.15$
1	$0.51 \pm 0.17$	$0.20 \pm 0.20$	0	$-0.83 \pm 0.38$
2	$0.41 \pm 0.11$	$0.68 \pm 0.09$	0	$0.68 \pm 0.26$
12	$-0.22 \pm 0.10$	$-0.59 \pm 0.10$	0	$0.54 \pm 0.35$
3	$-0.01 \pm 0.01$	$-0.02 \pm 0.01$	0	$1.61 \pm 0.50$
13	$0.01 \pm 0.01$	$0.02 \pm 0.01$	0	$1.75 \pm 0.52$
23	$0.01 \pm 0.01$	$0.02 \pm 0.01$	0	$-0.15 \pm 0.20$
123	$-0.01 \pm 0.01$	$-0.02 \pm 0.01$	0	$0.51 \pm 0.52$
4	0	0	$0.35 \pm 0.12$	$0.45 \pm 0.15$
14	0	$0.01 \pm 0.01$	$0.32 \pm 0.11$	$0.12 \pm 0.16$
24	0	0	$0.05 \pm 0.03$	$-0.34 \pm 0.15$
124	0	0	$0.05 \pm 0.03$	$-0.28 \pm 0.16$
34	$0.01 \pm 0.01$	$0.02 \pm 0.01$	0	$-0.36 \pm 0.11$
134	$-0.01 \pm 0.01$	$-0.02 \pm 0.01$	0	$-0.35 \pm 0.19$
234	$-0.01 \pm 0.01$	$-0.02 \pm 0.01$	0	$0.26 \pm 0.12$
1234	$0.01 \pm 0.01$	$0.02 \pm 0.01$	0	$0.33 \pm 0.26$
5	0	0	$0.15 \pm 0.09$	0
15	0	0	$0.37 \pm 0.27$	0
45	0	0	$0.13 \pm 0.04$	0
145	0	0	$0.17 \pm 0.12$	0
6	0	0	$0.55 \pm 0.15$	0
16	0	0	$0.46 \pm 0.15$	0
46	0	0	$0.24 \pm 0.07$	0
146	0	0	$0.13 \pm 0.12$	0
56	0	0	$0.20 \pm 0.05$	0
156	0	0	$0.29 \pm 0.16$	0
456	0	0	$-0.05 \pm 0.02$	0
1456	0	0	$-0.22 \pm 0.07$	0
Sum of the coefficients	0	0	$0.18 \pm 0.14$	0
Total	$0.70 \pm 0.12$	$0.30 \pm 0.19$	$3.37 \pm 0.45$	$4.56 \pm 1.08$

\* 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;  $N_s$ ,  $N_0$  and  $N_c$  are population densities of sawfly larvae per 1 m<sup>2</sup> in the second wave of development in the period of stability, outbreak and collapse, correspondingly.

appeared to be 1)  $8.0 \pm 3.4$ , 2)  $8.5 \pm 2.6$ , 3)  $6.8 \pm 4.2$ , 4)  $6.8 \pm 2.0$ , 5)  $1.2 \pm 1.6$ , correspondingly. In the control where no factor was deliberately changed, the coefficient of refractoriness was equal to  $7.5 \pm 3.5$ . 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	$3.85 \pm 0.20$	$1.53 \pm 0.24$
Yes	No	$4.62 \pm 0.27$	$1.36 \pm 0.34$
No	Yes	$5.66 \pm 0.39$	$0.46 \pm 0.12$
No	No	$5.94 \pm 0.36$	$0.40 \pm 0.05$

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, KORSCHTELLELLUS 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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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.

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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>, 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.

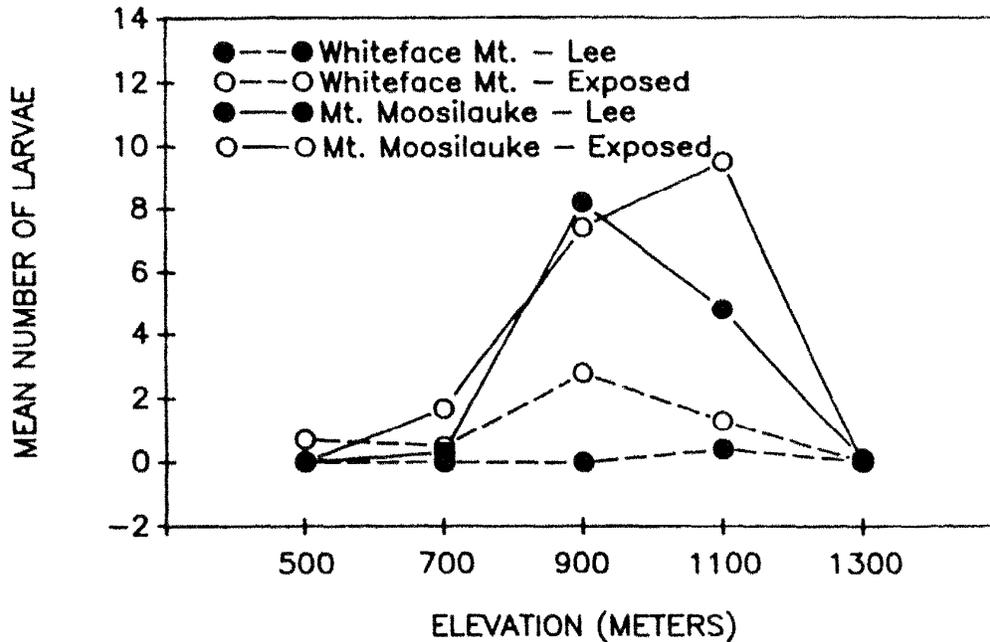


Figure 1. Fall distribution of the conifer swift moth, *Korscheltellus gracilis*, by elevation and location.

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).

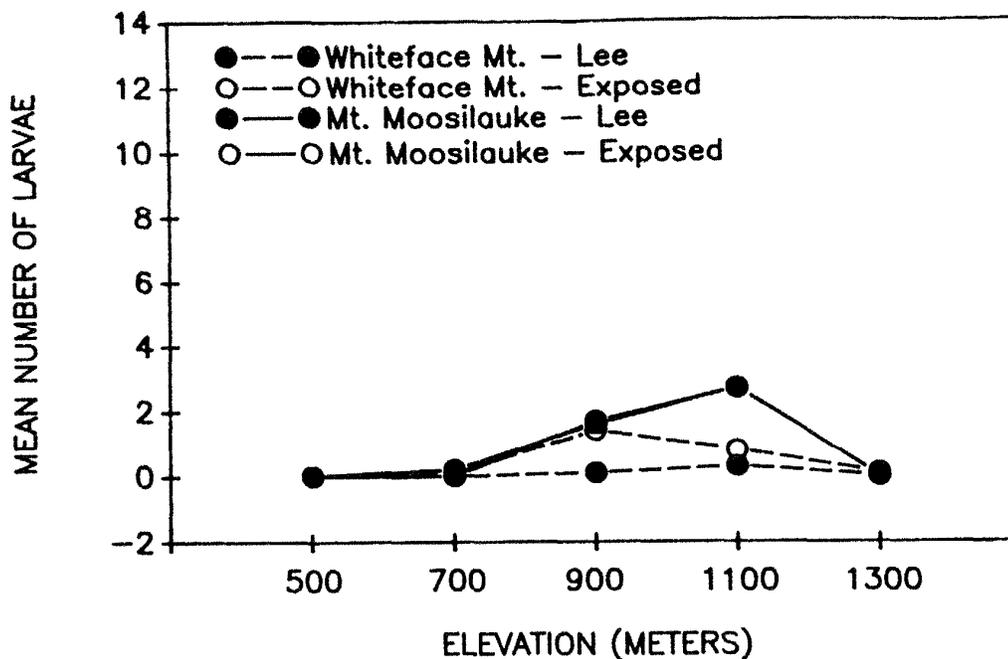


Figure 2. Spring distribution of the conifer swift moth, *Korscheltellus gracilis*, by elevation and location.

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	---

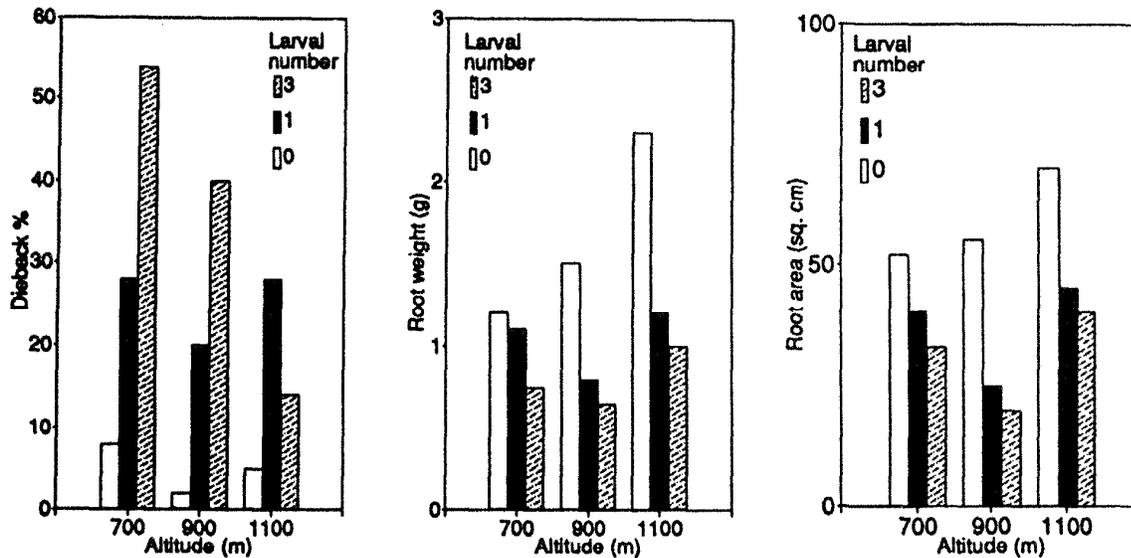


Figure 3. Response of red spruce seedlings to different densities of *Korscheltellus gracilis* larvae at different altitudes on Mt. Mansfield, VT.

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.

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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.

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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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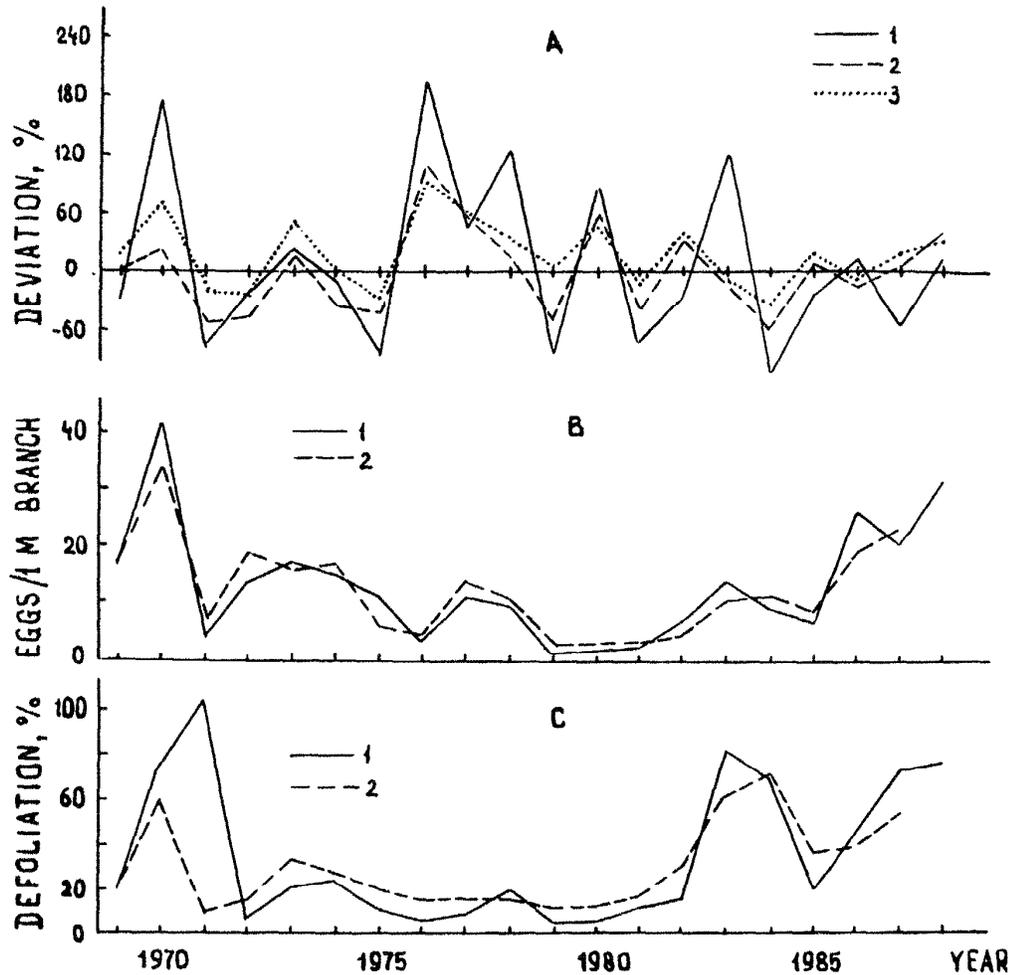


Figure 1. Weather conditions, oak leaf roller population density, and defoliation of oaks in the Tellerman oak forest from 1964 to 1988. A) hydro-thermal coefficient (HTC) deviations from the average values of many years: 1) HTC of May, 2) HTC of growing season (May to September), 3) annual HTC; B) oak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

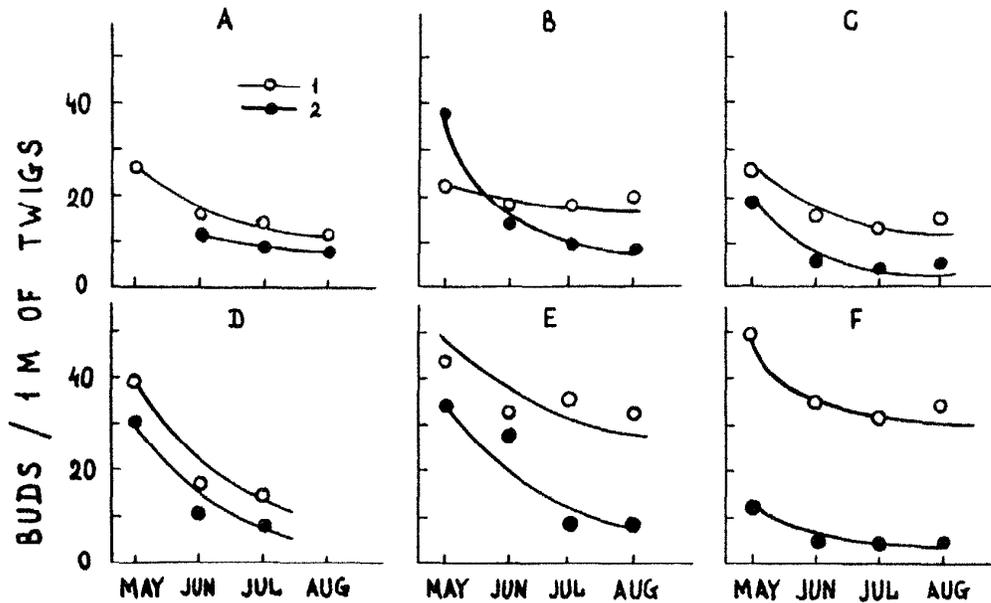


Figure 2. Numbers of nongrowing (reserved and dormant) buds in oak trees with 30 to 50 percent defoliation (1) and 75 to 100 percent defoliation (2). A), B), C), and D) 85-year-old stand from 1986 to 1989; E) and F) 105-year-old stand from 1987 to 1988.

(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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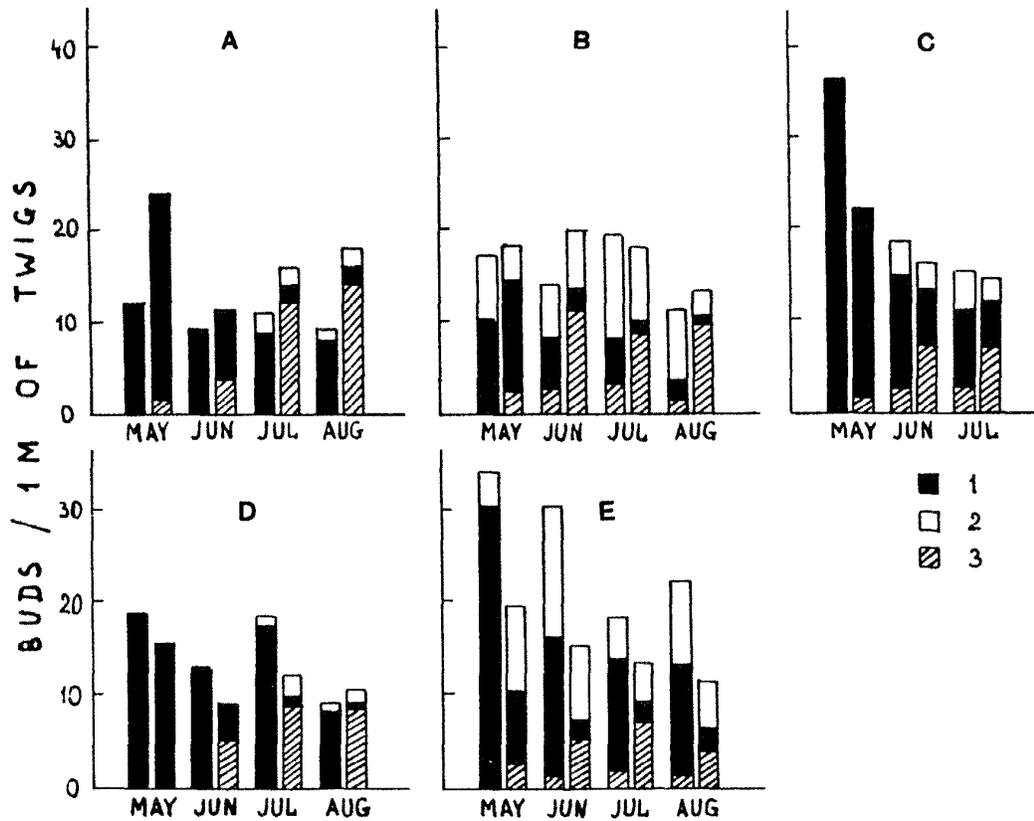


Figure 3. Numbers of reserved buds: in oak trees with 30 to 50 percent defoliation (left columns) and 75 to 100 percent (right columns). 1) alive, nongrowing; 2) dead; 3) buds grown after defoliation. A), B), and C) 85-year-old stand from 1987 to 1989; D) and E) 105-year-old stand in 1987-1988.

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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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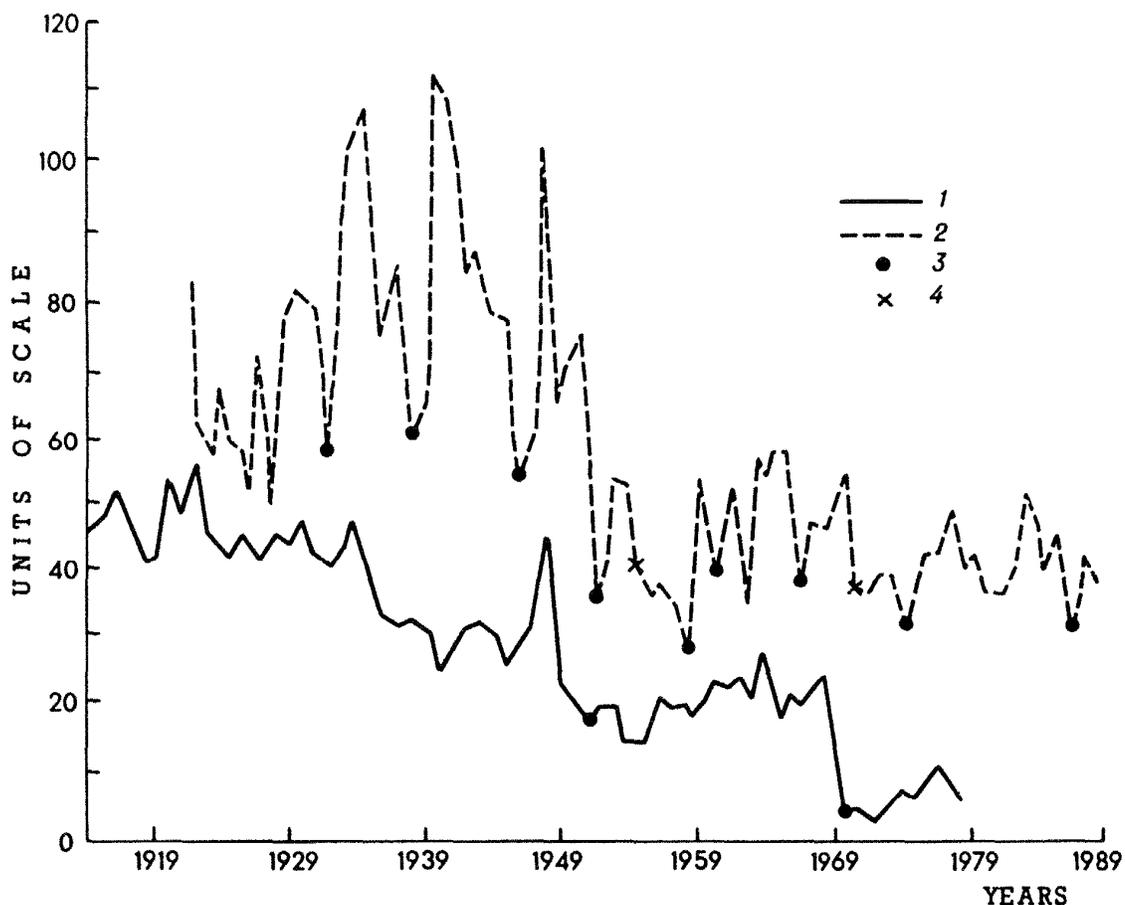


Figure 1. Fragment of dendrograms of *Larix sibirica* from different biotopes; 1. larch forests in the forest-steppe zone; 2. larch forests in the central taiga zone among herbs; 3. years of defoliation by larch bud moth; 4. years of defoliation by *Erannis jacobsoni* Djak.

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-cembra pine forests (Baltensweiler and Fischlin 1988). The heaviest defoliations occur at altitudes of 1600-2100 m, last  $2.93 \pm 0.21$  years, and recur at intervals of  $8.47 \pm 0.27$  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  $116 \pm 19.1$  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  $12.5 \pm 19.1$  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 ecologists 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 DNEIPER 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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